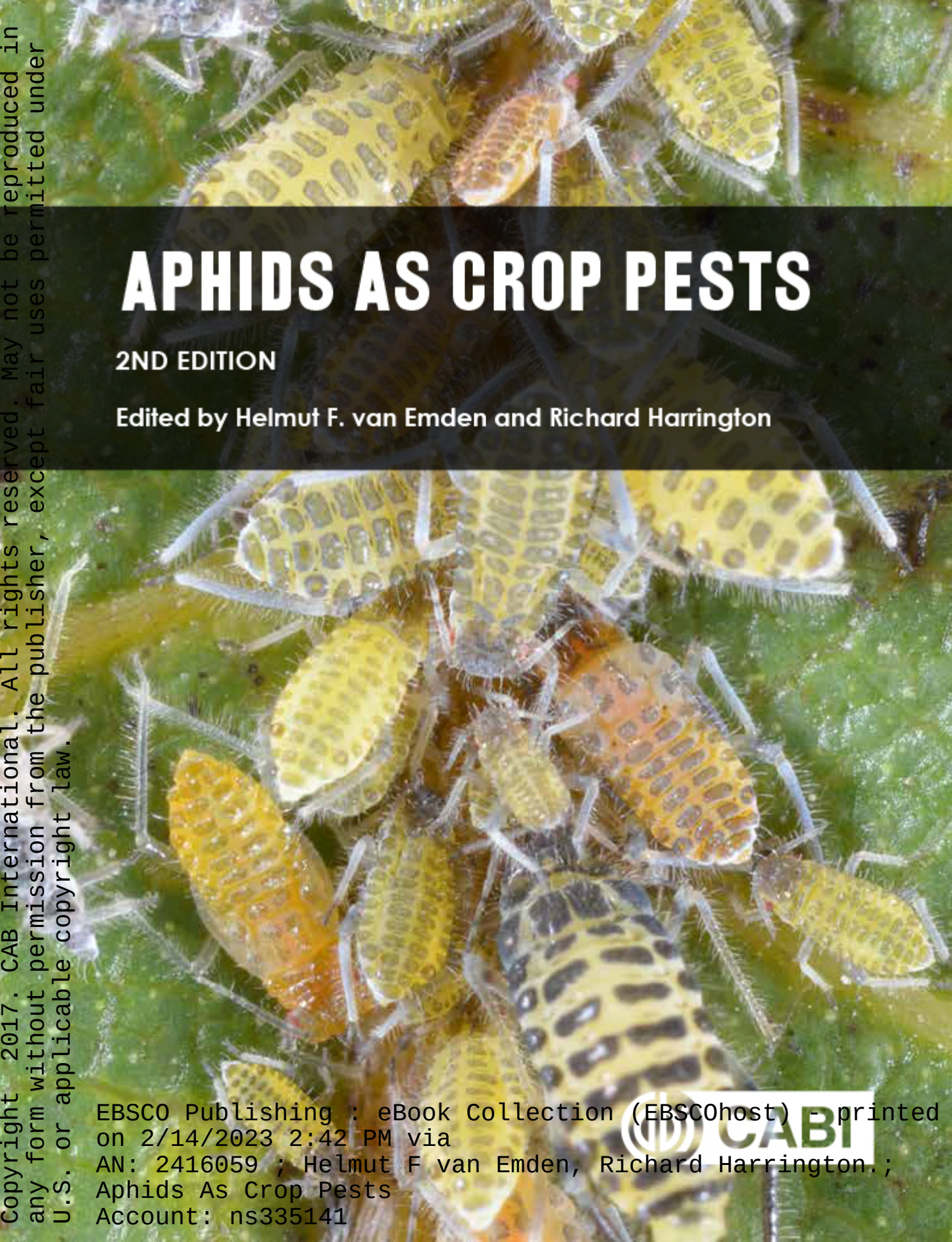

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Aphids as Crop Pests

Second Edition

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Aphids as Crop Pests

Second Edition

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Preface to the First Edition

Following the publication in 1998 of *Thrips as Crop Pests*, edited by Trevor Lewis, CABI commissioned *Aphids as Crop Pests* as a second in the series. However, in prefacing this book, we wish to pay tribute to another predecessor, *Aphids: Their Biology, Natural Enemies and Control*, edited by Albert Minks and Paul Harrewijn and published in three volumes by Elsevier between 1987 and 1989. This comprehensive and impressive work has been the standard reference text for aphidologists for nearly 20 years, and we would not presume to make it redundant with the publication of *Aphids as Crop Pests*. Therefore, in planning the content of our book, we have concentrated on the applied aspects of aphidology and have not sought to match the comprehensive coverage of morphology, physiology and ecology found in *Aphids: Their Biology, Natural Enemies and Control*. As far as aphid biology is concerned, we have emphasized instead areas such as current taxonomic issues (Chapter 1), host selection and feeding (Chapter 4), nutrition and symbionts (Chapter 5, which includes full instructions for successful long-term rearing of *Myzus persicae* on a synthetic diet), chemical ecology (Chapter 9) and reactions to stress (Chapter 11), where there have been major advances in the past 15 years. Especially, we would direct the reader to Chapter 2 on population genetics; molecular markers were hardly available when Minks and Harrewijn's book was being prepared. We have therefore given a large page allocation to this topic. In a similar vein, molecular methods have enabled many recent substantial advances in our understanding of the mechanisms of aphid resistance to insecticides (Chapter 10). We also felt that life cycles and polymorphism (Chapter 3), growth and development (Chapter 6) and aphid movement (Chapter 7) were areas particularly relevant to aphids as pests.

We have been greatly encouraged by the readiness with which the potential authors we first contacted agreed to participate. Having recruited scientists we felt were at the forefront of their subject, it made sense to leave the selection of any co-authors to them. The result is that Chapter 12 (on population dynamics) has been brought up to date with a strong modelling component, and that Chapter 8 on the natural enemies of aphids has involved four leading specialists – one for each of the major taxa. This led us to expand the page allocation for this chapter also.

The more identifiably applied part of the book starts with two chapters on the injury caused to crops by aphid feeding (Chapter 13) and by the transmission of plant viruses (Chapter 14). Both these chapters considerably update previous reviews on these topics. Separate chapters then cover the four main building blocks of pest management. Chapter 15 on chemical control has much new material with the advent of neonicotinoid compounds, which are especially effective against aphids, and Chapter 16 (on cultural control) highlights how far conservation biological control has come into practice. Chapter 17 covers host-plant resistance and Chapter 18 deals with biological control. This latter chapter describes practical interventions and avoids making a stronger case for the method than is realistic. The involvement of a specialist on aphid pathogens enables these important tools to receive adequate treatment.

Chapter 19 on monitoring and forecasting again is very different from what would have been written on this topic in the 1980s, since advances in information technology have enabled the feasibility of huge databases and have made possible rapid transmission of data and effective international networks.

Chapter 20 introduces the concepts and potential of IPM, pointing out that it originated in California with work on aphids. Specialists on aphid problems in selected cropping scenarios then review the status of IPM in a series of case studies (Chapters 21–30). We felt that the diversity of cropping systems, pests and natural enemies, the chemicals available, etc., in different continents made worldwide coverage of each crop too complex a proposition, so we encouraged authors to concentrate on the region in which they themselves worked. Imposing a template for these chapters would have clouded the very different issues that relate to

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aphids in these case studies, and we have taken the alternative approach towards consistency by ending each case study with an 'Executive Summary', written initially by the editors on the basis of the text supplied by the chapter author(s) but then mutually agreed with them. The final chapter on decision support systems is another topic that has only developed strongly since the 1980s.

Inevitably, various problems forced a few of our original authors to withdraw, and so we are especially grateful to those who started their chapters later and to the other authors for their patience when they saw these chapters delaying production of the book. We are indebted also to our authors for their invariably positive response to our comments and suggestions for changes; they all readily accepted that any large group of virtuoso performers needs a conductor!

The editors of a multi-author book face many problems, in particular that of repetition: take, for example, resistance to insecticides. Although our book has a specific chapter on this topic, it also is a phenomenon of population genetics, it governs what chemicals can be used and so is relevant to the chapter on chemical control and many of the IPM case studies. It would be tidy to eliminate duplication, but we are not so naïve as to think anyone is going to read our book from start to finish. Rather, each chapter needs to stand on its own as a comprehensive review. We have used cross references to other chapters as a partial solution, but frequently have left some discussion of a topic covered in another chapter where a cross reference alone would fail to make the point(s) the author had intended.

Another problem is the nomination of pesticides for aphid control, particularly in the IPM case studies. What products are permissible for use varies from country to country and changes almost weekly, even within countries! Individual experts therefore have referred to products in relation to their own experience and environment. Mention of a compound should not be taken to mean it could be used elsewhere, nor necessarily after 2006.

A 'Taxonomic Glossary' follows the chapters. Here, we have listed alphabetically under the appropriate taxon the Latin names of species mentioned in the book, together with the taxonomic authority and any generally accepted English common name(s). Such a glossary had to be compiled in order to maintain consistency between chapters in the citing of Latin names. By including it in the volume, we could avoid adding the taxonomic authority and Latin names of well-known crops in the individual chapters. In compiling the glossary, we have also encountered different practices in different taxa (e.g. insects, fungi, plants, etc.) in how authorities and subspecies are cited. Thus, entomologists tend to assume that a trinomial indicates a subspecies, whereas botanists still insert 'subsp.' before the last name. We decided to follow the accepted practice for each taxon rather than impose uniformity. We are extremely grateful to the specialists who advised on current taxonomic usage: Dr Anne Baker (mites); Dr Roger Blackman (aphids); Mr Barry Bolton (ants); Dr Roland Fox (other fungi and bacteria); Dr Francis Gilbert (syrphids); Dr Simon Gowen (nematodes); Mr Paul Hillyard (spiders); Dr Stephen Jury and Mr Ronnie Rutherford (plants); Dr Ivo Kovar and Dr Mike Majerus (coccinellids); Dr Martin Luff (carabids); Professor Tim New (lacewings); Dr Judith Pell (entomopathogens); and Mr Nigel Wyatt (Diptera). Another specialist was Professor Roger Plumb, who provided valuable advice in relation to the nomenclature of plant viruses.

Generous sponsorship from BASF and Syngenta has made it possible to include a section of colour plates of the aphids selected by the authors of Chapter 1 as the most serious aphid pests worldwide. The section also includes colour plates of representatives of important groups of natural enemies. We are extremely grateful for this encouragement and support from the agrochemical industry. The colour plates come from a variety of sources, and we greatly appreciate the permission of copyright holders to reproduce their images without a royalty payment. Many others (scientists and publishers) have also allowed us to use their material in various chapters; their colour images have been converted to greyscale. Our colleagues have, without exception, been most helpful in allowing us to use copyright material – in every case, we have acknowledged the source in the legends to colour plates and other figures.

Part of the value of this book is in the comprehensive bibliographies accompanying each chapter. In order not to restrict authors in reviewing their topic, the list of references was not included in their page allocation. The work of editing the references was thus considerable and we are grateful to Ms Berit Pederson and Mr Greg Bentley for assistance with this chore.

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We have both been researching on aphids for many years, and have become good friends in the process. We have enjoyed working together on this book and have both somehow found time to edit all chapters independently, though, in each case, one of us has taken the lead as 'first editor'. We will miss this collaboration now it has ended, but will feel rewarded if this book is appreciated by our aphidological colleagues and proves of value to them, and those beginning research on aphids, for a good number of years to come.

Helmut van Emden
Richard Harrington

19 June 2006

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Preface to the Second Edition

In the preface to the First Edition, published 10 years ago, we commented on how much we had enjoyed working together on the book and said, 'We will miss this collaboration now it has ended'. This was, perhaps, an instance of 'Be careful what you wish for'. The request from CABI that we edit a Second Edition came as a bolt from the blue. We were delighted to learn that the First Edition had nearly sold out but, remembering the hours involved by ourselves and the chapter authors, thought long and hard as to whether to accept the mission. We are glad we did. No other book has intervened to remove the need for an updated review of the more applied aspects of aphid research, and we believe that this volume is timely.

While we were delighted that the majority of authors of the First Edition embraced the idea of an update enthusiastically, inevitably not all were in a position to do so. The lead chapter authors of this Second Edition are those who volunteered to coordinate the revision, and the co-authors all made valuable contributions. Sometimes, the changes were major and the chapter given a whole new look and feel. Sometimes, they involved little more than removing some outdated references and replacing them with those demonstrating key advances in their field. In all cases, the contributions of the authors of the First Edition are hugely appreciated, and where the new chapter includes material from the earlier edition, these authors are acknowledged up front if they no longer feature in the authorship list.

Some aspects of aphidology are moving forward more rapidly than others. Unsurprisingly, those to which molecular techniques have contributed have advanced in leaps and bounds in the past 10 years, to the point that we considered it necessary to add a new chapter (Chapter 2) to introduce this area. Lin Field kindly agreed to lead this challenge. The speed of progress, though, is such that this chapter is in danger of becoming out of date rather sooner than we would wish. In particular, there has been a surge in work on molecular-level interactions between aphids and their symbionts, and how these symbionts influence interactions between aphids and their host plants and between aphids and their natural enemies. This became very clear at a joint meeting in Paris in November 2015 of primarily British and French aphidologists, where these topics dominated, perhaps worryingly at the expense of whole organism and population biology and ecology. Many of these advances, however, have not been published in time to make this Second Edition, but we are sure that they will add great excitement to the Third Edition!

In this Second Edition, the chapter on population dynamics (Chapter 13) is based on work on a cereal-feeding species. We are grateful to James Bell, Jean-Sébastien Pierre and Charles Dedryver for this chapter. However, we felt that the subject of population dynamics warranted a general introduction in the form of Chapter 12. This goes step by step through the stages of the aphid annual cycle, highlighting the processes leading to population changes at each stage. We could not find a previous attempt at a similar review and hope that it provides a useful complement to Chapter 13.

With hindsight, we felt that the order of chapters could be a little more logical than it was in the First Edition. There is no perfect order and we considered many options. Chapter 1 remains the introduction to taxonomy, which is fundamental to all aphidology. We cannot mention this chapter without lamenting the loss of the great Victor Eastop (1924–2012), whose work and utterly delightful personality have enlightened and enthused all involved in the study of aphids. He and Roger Blackman formed an inimitable and indefatigable team. The study of population genetics is clearly related closely to that of population dynamics, and involves making much use of the molecular technology described in Chapter 2. We decided that it should retain its place among the generalist chapters at the front (Chapter 3). Chapter 4 covers life cycles and polyphenism, again relevant to most other chapters. Growth and development (Chapter 5) depends to a large extent on nutrition and symbiosis (Chapter 6), which, if impaired, leads to stress (Chapter 7). Chapters 8–10 (chemical ecology, host-plant selection and feeding, movement) cover the location of suitable habitat and

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escape from unsuitable conditions. Chapter 11 on natural enemies is a prerequisite to understanding population dynamics (Chapters 12 and 13, as outlined above). We then move on to the damage caused by aphids through feeding injury (Chapter 14) and virus transmission (Chapter 15). In order to help prevent such damage while optimizing control options, monitoring and forecasting (Chapter 16) and associated decision support (Chapter 17) are essential. These should always guide the use of chemical control (Chapter 18) in order to minimize problems from insecticide resistance (Chapter 19). Creating favourable conditions for biological control (Chapter 20), and the use of cultural control (Chapter 21), including host-plant resistance (Chapter 22), should also be front-line strategies aimed at sustainable pest management. We have retained the case studies (Chapters 23–33), which show how the various control options are used in particular settings.

As in the First Edition, the chapters are followed by a taxonomic glossary and we are grateful to the following experts who have ensured its accuracy: Roger Blackman (aphids); Manfred Mackauer (Braconidae); Oldrich Nedved (Coccinellidae); Tim New (Neuroptera); Chris Lyal (other animals); Françoise Munaut (bacteria and fungi); and Peter Rooney (plants).

Another innovation of the Second Edition is the use of colour throughout. Where possible and sensible, the black and white illustrations of the First Edition, and the new illustrations, have been produced in colour, and the colour plates have been distributed to Chapters 1 and 11, rather than being lumped together in the middle. Many thanks to those who provided the colour photographs, especially Bernard Chaubet of INRA, whose collection of aphid photographs is probably unsurpassed and who won the competition to find the best cover photograph. Although this is not of an aphid that most of us will encounter, it is certainly one of our more photogenic species!

Aphids are not all bad. They provide important food for birds and other organisms, their honeydew sustains the larvae of some of our iconic butterflies, and they even provide medicinal compounds. Some are of conservation concern. Most of us employed in their study, however, are attempting to reduce the self-inflicted harm caused to our monoculture-based system by the relatively few of the 6000 or so species that get the group as a whole a bad name. We suspect that most of the authors, like us, have a grudging admiration for them and are grateful that they have kept us in satisfying employment. We hope that our enthusiasm for our adversaries shines through herein, but that we win a few more battles, if not the war, as a result.

Our grateful thanks to all our hard-pressed chapter authors for their expertise, enthusiasm, friendship and time. If only institutions would give more credit to the producers of state-of-the-art reviews! Thanks also to the many people at CABI with whom we have worked on the Second Edition, particularly Joris Roulleau and Ward Cooper, who were both involved in arranging for colour to be used throughout the book and for the indexing of the taxonomic glossary (the lack of such an index in the First Edition was raised by several reviewers). We hope that the Second Edition of *Aphids as Crop Pests* will prove valuable for many years.

We will miss this collaboration now that it has ended – but we will rely on others to edit the Third Edition!

Helmut van Emden
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1 Taxonomic Issues

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Introduction

There are more than 5000 species of Aphididae in the world (Remaudière and Remaudière, 1997; Favret, 2014). Of these, about 450 species have been recorded from crop plants (Blackman and Eastop, 2000), but only about 100 have exploited the agricultural environment successfully to the extent that they are of significant economic importance (Table 1.1). The agriculturally important species are mostly in the subfamily Aphidinae, not only because this is the largest subfamily but also because it contains a very high proportion of the aphids that feed on herbaceous plants (Blackman and Eastop, 2006). Some quite large aphid subfamilies – the Calaphidinae and Lachninae, for example – are associated almost exclusively with woody plants, as are most of the smaller ones.

The Aphididae is one of three families of Aphidoidea, the other two being the Adelgidae, or conifer woolly aphids, and the Phylloxeridae, which are also nearly all associated with trees but include the notorious *Daktulosphaira* (= *Viteus*) *vitifoliae* (grape phylloxera) (Table 1.1). In the context of the order Hemiptera as a whole, the superfamily Aphidoidea is placed in the suborder Sternorrhyncha, along with Coccoidea (scale insects and mealybugs), Aleyrodoidea (whiteflies) and Psylloidea (psyllids or jumping plant lice).

All these insects are phytophagous, and most of them are sap sucking. Historically, the Sternorrhyncha have been grouped with the Auchenorrhyncha (leafhoppers, cicadas, etc.) as Homoptera, but molecular work has provided strong support for the long-standing view, based on morphological and embryological evidence, that Sternorrhyncha and Auchenorrhyncha do not share a common ancestor, so this grouping is not phylogenetically sound. The general consensus now is that the primary division of the Hemiptera is into Sternorrhyncha and a sister group comprising Auchenorrhyncha plus Heteroptera (von Dohlen and Moran, 1995).

One major feature, their well-known cyclical parthenogenesis, sets aphids apart from other Hemiptera, and has influenced every aspect of their biology. The system of alternating one bisexual generation with a succession of parthenogenetic, all-female generations evolved in the ancestral line of all Aphidoidea, probably as far back as the Triassic. At first, the parthenogenetic females must have laid eggs like their sexual counterparts, as do the parthenogenetic females of present-day adelgids and phylloxerids. Then, in the line leading to all modern Aphididae, the parthenogenetic generations developed the further refinement of viviparity, which effectively 'telescoped' generations into one another, thereby greatly reducing the generation time and enabling far more efficient exploitation of periods of rapid plant growth.

Aphids (Aphididae) can be recognized by a number of shared morphological characteristics that developed before the divergence into present-day subfamilies: e.g. siphunculi (secretory organs, but with their precise function still strangely enigmatic); five- or six-segmented antennae composed of two basal segments and a segmented flagellum with a terminal process; two-segmented tarsi, with the first segment much shorter than the second; and a cauda, or tail, that is often used for flicking away droplets of honeydew from the anus. These features have been modified, reduced, or secondarily lost in some species, but are evident in most aphids that are pests of crop plants.

Of the present-day subfamilies of Aphididae, one in particular was successful at exploiting the rapid expansion of numbers and diversity of herbaceous flowering plants in the Tertiary period. This subfamily, the Aphidinae, with 2900+ extant

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Table 1.1. Biological features and distribution of agriculturally important species among the major groups of aphids.

Taxon	Characteristic host plants	Geographical distribution	Host alternation?	Number of agriculturally important spp./total spp.	Representative genera
Adelgidae	Coniferae	Holarctic	Most	0/60	*Adelges*, *Pineus*
Phylloxeridae	Fagaceae, Juglandaceae	Holarctic (mostly Nearctic)	Some	1/70	*Phylloxera*, *Daktulosphaira*
Aphididae:					
Eriosomatinae	Ulmaceae, Salicaceae, Anacardiaceae, roots of gymno- and angiosperms	Holarctic, Oriental	Many or most	9/365	*Eriosoma*, *Pemphigus*, *Prociphilus*
Hormaphidinae	Hamamelidaceae, Styraceae, palms, bamboos	Mostly Oriental	Many or most	5/222	*Astegopteryx*, *Cerataphis*, *Ceratovacuna*
Anoeciinae	*Cornus*, grass roots	Holarctic	Most	2/30	*Anoecia*
Calaphidinae	Deciduous trees	Holarctic	None	6/351	*Chromaphis*, *Myzocallis*, *Therioaphis*
Saltusaphidinae	Sedges	Holarctic	None	0/59	*Iziphya*, *Subsaltusaphis*, *Thripsaphis*
Chaitophorinae	Salicaceae	Holarctic	None	2/173	*Atheroides*, *Sipha*
Greenideinae	Dicotyledonus trees	Eastern Palaearctic, Oriental	None	2/180	*Anomalosiphon*, *Greenidea*
Aphidinae:					
Aphidini	Many families, including Rosaceae, Poaceae,	Holarctic, a few southern hemisphere	Some	20/808	*Aphis*, *Rhopalosiphum*, *Schizaphis* *Acyrthosiphon*, *Brevicoryne*,
Macrosiphini	Asteraceae		Some	60/2116	*Macrosiphum*, *Myzus*
Lachninae	Trees (dicotyledonous and coniferous)	Holarctic	None	4/400	*Cinara*, *Lachnus*, *Trama*
15 other subfamilies	Mostly dicotyledonous trees	Some are Oriental and southern hemisphere	None	0/185	

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species, is predominantly a northern temperate group, with life cycles closely tied to temperate seasonality and the phenologies of temperate plants. Originally on woody plants, they evolved a system of host alternation, migrating to completely unrelated herbaceous plants for the summer months, where their parthenogenetic generations could continue to utilize stages of rapid plant growth. However, today, only about 15% of Aphidinae host alternate. Some of the other 85% live only on woody plants, but most of them, including some of the largest and most successful genera, have lost or given up the ancestral woody (primary) host and now live all year round on herbaceous plants. Host alternation has, in fact, evolved independently in several other aphid subfamilies (von Dohlen and Moran, 2000), but the Aphidinae are the only subfamily to exploit numerous families and genera of flowering plants.

In the rest of this chapter, we will look at aphids from a taxonomist's viewpoint. We will highlight some of the problems of interpreting the observed variation within and between species, and discuss what the names we give to aphids really mean. Then, as examples, we will discuss 15 taxa that probably head the list of economically important aphid species.

Interpreting Variation in Aphids

In 2000, soybean crops in the USA and Australia were attacked for the first time by large numbers of an aphid closely resembling the well-known polyphagous species, *Aphis gossypii* (cotton or melon aphid), but obviously with a far greater affinity for soybean. Taxonomists identified the species as *Aphis glycines* (soybean aphid), previously known only from the Far East. It had been introduced probably a year or two earlier, building numbers and spreading until field entomologists and growers realized that they had something new on their hands (see review by Tilmon *et al*., 2011). *Aphis glycines* is biologically quite different from *A. gossypii*; it is specific to soybean in summer and has host alternation, overwintering on *Frangula* spp. Identification immediately unlocked much crucial information about this species and its biology, as well as where to look for its natural enemies. In this case, the question 'What is it?' seems to have a fairly clear-cut answer; the soybean aphid is a relatively well-known and well-studied species in eastern Asia. Although morphologically resembling *A. gossypii* and requiring specialist identification, it is clearly a distinct species. There are plenty of other cases, however, including other close relatives of *A. gossypii*, where the question of identity is not so easily answered. Several of these are discussed in the next section of this chapter. Sometimes, taxonomic difficulties arise as a result of founder effects and, even in the case of the soybean aphid, it may be necessary to bear in mind that the introduced population has been through a recent 'bottleneck' and can be expected to have less allelic diversity than East Asian populations.

Taxonomy and identification are a matter of interpreting observed variation. The first problem to be overcome is the effect of the environment on the phenotype, especially if the only available data are morphological. Most species are distinguished and described originally, often from one small sample only, using morphological criteria, and most identifications are based on keys that use morphological discriminants. As a group, aphids are renowned for the considerable extent to which the phenotype is influenced by environmental factors. Within any aphid species, there are a number of different forms (morphs) with discrete morphological differences, which may be triggered by specific environmental stimuli such as day length or crowding. It is well known, for example, that in most aphids, the parthenogenetic females can be winged or wingless, the differences being not just in the presence or absence of wings but involving every part of the body. Separate identification keys are therefore needed for each morph, but the structural distinction between the winged and wingless morphs is not always as clear as might be expected, as wingless individuals may occur with some tendency towards the characters of the winged morph. Likewise, intermediates between other morphs can occur; for example, between viviparous parthenogenetic females and oviparous sexual females.

The range of continuous morphological variation is also wider than in many other insect groups. Increases or decreases of size due to nutritional effects, for example, can accumulate over several generations, because the size of the mother can affect the size of her offspring. There may be large seasonal differences, with some species producing dwarf individuals when food quality is poor in midsummer. The parthenogenetic female that hatches from the overwintering egg – the fundatrix or stem mother – is morphologically different from the later

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generations of parthenogenetic females, and sometimes the particular features of the fundatrix are only gradually lost in subsequent generations. In some aphid groups – although not in most Aphidinae – the generations on the secondary host differ greatly in morphology from those on the primary host, and were described originally as different species and often placed in different genera. The temperature experienced during development can also have profound effects on morphology, involving not only general body size and pigmentation but also having more subtle influences on the length relationships between body parts (allometry), which can play havoc with the morphometric ratios and functions often used to discriminate between closely related species (Blackman and Spence, 1994).

Thus, it is important to take into account the possible effects of season, host plant and climate when examining samples of field-collected aphids. It is also necessary to bear in mind that a sample might consist of a single clone, especially if it comes from a warm temperate or subtropical region where the population has not gone through a sexual phase and is therefore more likely to be clonally structured. All the aphids in a clone are, discounting mutations, genetically identical, so a sample consisting of a single clone will give a misleading idea of the range of variation in the species. Sometimes, 'abnormal' morphological features may occur, which may be due to mutation but are often no more than character states near the extremes of a range of continuous variation, and part of the natural variation of all living organisms. In sexually reproducing organisms, any particular abnormal character state is likely to occur in only the occasional rare individual within a population, and thus will be instantly recognizable as an extreme or rare condition. In aphids, it is possible to find a whole colony of individuals all with the same anomalous characters. Such a colony has sometimes been described erroneously as a new species.

The Taxonomy of Pest Aphids – What's in a Name?

The species that become pests are those that are best able to adapt to and exploit human-modified environments. Many of them belonged to groups that were probably already speciating rapidly before human intervention, and the colonization of new geographical regions and/or new habitats were potent factors leading to further divergence and change. Several examples of this are discussed in the concluding part of this chapter. Although it is clear that pest aphids are highly dynamic, rapidly evolving systems, there still seems to be a tendency, among agricultural entomologists in particular, to regard pest species identifications provided by taxonomists as names set in stone, and to react with alarm to the suggestion that certain common and well-known pest species may, in fact, be described more accurately as species complexes. The name has great importance, as it is the key to what we know about a species and its way of life, and to how we might expect it to behave. The name *Myzus persicae*, for example, identifies a set of populations that are closely related and share numerous attributes. But this must not be allowed to mask the heterogeneity that is also present, and which may include populations that have diverged genetically to such an extent that they have evolved past the stage of being host races and achieved a degree of permanency, so that they can be regarded as incipient or sibling species (or subspecies) with particular attributes of their own.

The recognition of such divergent populations or taxa can add to our understanding of the ecology and evolution of a pest species complex and increase the possibility of devising effective control measures. It is also important that they are named in some way, because without any consistent method of referring to them, new information is inaccessible, lost in the mass of literature about the species as a whole. Yet both the recognition and the naming of such categories are fraught with difficulty. Discrimination of recently derived taxa may require sophisticated techniques, which are likely to be time-consuming and/or expensive. It is also hard to decide what to call them. Insect taxonomists are usually reluctant to provide formal names and descriptions and to give full species status to members of species complexes that cannot be distinguished readily by their morphology alone, even where consistent differences can be demonstrated in biology and/or host relationships. This is understandable, given that they will probably be asked to recognize and identify dead specimens of their 'new' species!

The subspecies category is the only intraspecific category recognized by the Zoological Code of Nomenclature, and therefore the only one that can be used formally to designate new taxa in animal taxonomy. It was developed mainly by vertebrate taxonomists who defined subspecies as geographically

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localized populations that were distinguishable morphologically. In aphid taxonomy, considerable use has been made of the subspecies category. Remaudière and Remaudière (1997) list 141 accepted subspecies names in the subfamily Aphidinae alone. Unfortunately, the subspecies designation has been used with an almost total lack of consistency. In some cases, a single sample has been described as a subspecies, for no other reason than that it shows some deviation from the known range of variation of a species. This could be due simply to it comprising a single clone with certain anomalous features, or a colony that developed under unusual microclimatic conditions, or it might be part of a continuous geographical cline of variation from which intermediate populations have not been sampled.

Aphid taxonomists studying groups of very closely related taxa ('species complexes') have also used subspecies in a completely different way to define populations that are morphologically very similar but that have been shown by field observation and/or experimental studies to differ in their life cycle or host-plant relationships (Müller, 1986). Such an approach recognizes that speciation processes in aphids may be very different from those of vertebrates, with changes in life cycle and/or host relations acting as the primary isolating mechanism and trigger for speciation, rather than spatial isolation (Guldemond and Mackenzie, 1994). Crucial evidence that such speciation processes operate in aphids was provided by Hawthorne and Via (2001). Thus, in rapidly speciating groups of aphids, one may expect to find incipient species that are at an early stage of divergence, where they can be distinguished more easily by biological rather than by morphological properties.

Every speciation process is a unique event, or series of events, that may include transitional phases involving a wide variety of reproductive relationships between the incipient species. It is impractical to try to define such transitional phases except in the most flexible terms. Rakauskas (2004) revived Müller's (1986) proposal for a broader use of the subspecies category to validate its application to aphid species complexes and – of particular relevance to the present chapter – to meet the practical need of providing names that identified intraspecific categories in groups that included pest species. We support this idea and accommodate it in our discussion of the taxonomy of some of the major pest aphids, which occupies the last part of this chapter.

We propose that an aphid subspecies should be defined as a group of populations that is recognizably part of an existing species, yet maintains a consistent suite of properties that distinguishes it from other populations within that species. The species should be sufficiently well known for it to be reasonably certain that the observed variation is discontinuous, and the constancy of this discontinuity should be demonstrated by samples from more than one time and place. The likely cause of the discontinuity should be identifiable; for example, a difference in host-plant relationships, life cycle properties, or geographic location, and should not be of such a kind as to make it irreversible (e.g. permanent parthenogenesis).

The description of a new subspecies should give a clear and accurate account of its morphological and biological properties in comparison with other populations within the species, and include the best possible morphological discriminants. One clone should be designated as the type, with slide-mounted specimens deposited in a national collection, and other specimens of the same clone deep-frozen and/or preserved in ethanol for future DNA studies.

The Use of Molecular Methods in Aphid Taxonomy

Major developments have occurred in recent years, both in the techniques used to acquire data on genetic variation within and between taxa and in the range of computer software available for the analysis and interpretation of results. Perhaps of most interest to the applied entomologist is the technique of DNA bar-coding, which uses a 658 bp region of the mitochondrial (mt) cytochrome *c* oxidase 1 (COI) gene as an agreed standard for all animals. Barcoding may be particularly useful for the identification of aphids on crops, e.g. cereals (Shufran and Puterka, 2011), with the clear advantage of being independent of morph or stage of development. At the time of writing, the bar-code sequences of more than 1200 aphid species have been determined (BOLD; www.barcodinglife.org). Foottit *et al.* (2008) tested the effectiveness of the method with more than 300 aphid species in more than 130 genera and found that 96% of species were well differentiated. Coeur d'acier *et al.* (2014) analysed bar-coding data for 1020 specimens of 274 species in Europe and discussed its use in aphid identification, as well as its limitations. Lee *et al.* (2014) and Lee and Akimoto (2015) identified other mitochondrial genes

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(ATP6 and ATP8) as potentially more useful and more reliable than COI as tools for aphid species identification. Nevertheless, preliminary research will always be advisable to establish the amount of intraspecific DNA sequence variation as it is possible for mtDNA to vary unpredictably, both within and between populations (e.g. Hurst and Jiggins, 2005). Another reason for caution is that at least some of the sequences deposited in GenBank will be based on misidentified or mislabelled specimens.

Recently diverged species, or those in the process of speciation in rapidly evolving species groups, present particular challenges to the taxonomist, and there is no longer any doubt that several aphid pest species are at this stage of evolution, including several of those discussed later in this chapter. In such cases, reliance on one particular fragment of mtDNA is unwise. One way of increasing reliability is to combine an analysis of DNA sequence data with a multivariate morphometric study, as was done by Rakauskas *et al*. (2014) to confirm that *Myzus cerasi* populations on two species of cherry in Europe (*Prunus avium* and *Prunus cerasus*) were distinct at least to the level of subspecies. Most DNA studies employ a multilocus approach. There are two ways of doing this. Several mitochondrial and nuclear sequences – and sometimes also DNA from the endosymbiont *Buchnera* – may be amplified separately and the data then compared and concatenated. This method is widely used for phylogenetic studies at and above the genus level, which do not directly concern us here, but it has also enabled the recognition of 'cryptic species' in several aphid species groups. The genus *Hyalopterus* was confirmed to contain three species, each utilizing a different *Prunus* species as primary host (Lozier *et al*., 2008), and the cosmopolitan pest aphid, *Brachycaudus helichrysi*, has now been revealed to comprise two sibling species, again with different *Prunus* as primary hosts (Piffaretti *et al*., 2013a,b). Foottit *et al*. (2010) confirmed that the banana aphid, *Pentalonia nigronervosa*, was a separate taxon from its close relative *Pentalonia caladii* by combining analysis of mitochondrial and nuclear DNA with a morphometric study.

The other multilocus approach is fundamentally different, using primers to select and amplify parts of the genome, the lengths of which are then used as genetic markers. One such technique is a version of genetic fingerprinting, called amplified fragment length polymorphism (AFLP), which can generate a very large number of markers, the presence or absence of which can be used not only to identify clonal genotypes but also to assess patterns of genetic divergence (Liu *et al*., 2010). Another method, now widely used for aphids, employs specific primers to isolate sections of non-coding DNA containing long series of simple sequence repeats (SSRs), also called microsatellites (or microsats). These have many features, such as selective neutrality, co-dominance and a high degree of polymorphism, that make them ideal for within-species population genetic studies (Chapter 3, this volume), but they also provide a powerful tool for identifying recently diverged (and diverging) taxa.The problem of designing specific primers has been largely obviated by the demonstration that existing microsatellite markers can be amplified in a wide range of aphid species (Wilson *et al*., 2004; Weng *et al*., 2007). In the next section of this chapter, there are several examples of the use of microsatellite markers to study the taxonomy of pest aphids.

It can be anticipated that the rapid advances that are now taking place in functional genomics – using techniques such as high-throughput DNA sequencing and transcriptome analysis to relate the genetic make-up of an aphid species to the way in which it 'works' – will soon be opening up many more ways to study the similarities and differences between and within aphid taxa.

The 15 Aphid Species of Most Agricultural Importance

There is a very large literature about all the major pest aphid species. Much of the recent work is readily accessible on the Internet, and summary accounts are provided by Blackman and Eastop (2000, 2006 – the content of the latter publication is now revised and frequently updated online at http://www.aphidsonworldsplants.info). The treatments that follow are therefore largely concerned with the taxonomic issues raised by these 15 species, and the two factors that have the greatest influence on intraspecific variation in aphids, the life cycle and the host plant. These factors are considered further in Chapter 3, this volume, from a population geneticist's viewpoint.

Acyrthosiphon pisum (pea aphid) (Fig. 1.1)

Acyrthosiphon pisum is a rather large, green or pink aphid with long, slender appendages, forming colonies on young growth and developing pods of

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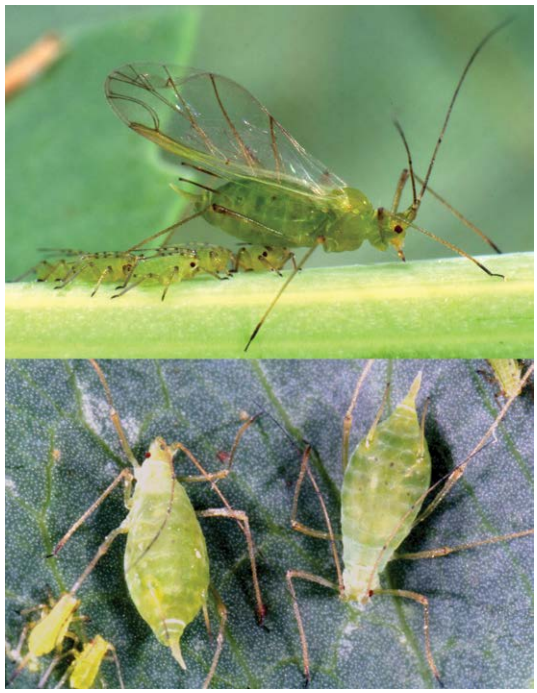

Fig. 1.1. *Acyrthosiphon pisum* – pea aphid. (Photograph courtesy of B. Chaubet and INRA.)

many leguminous plants. Its host plants are mostly Fabaceae of the tribes Genisteae (*Cytisus*, *Genista*, *Spartium*), Trifolieae (*Medicago*, *Metilotus*, *Ononis*, *Trifolium*, *Trigonella*), Fabeae (*Lathyrus*, *Lens*, *Pisum*, *Vicia*) and Hedysareae (*Hippocrepis*, *Onobrychis*), and it also colonizes a few members of other tribes; for example, *Lotus* spp. (Loteae) and *Glycine max* (Phaseoleae). Many legumes, including some of economic importance (e.g. *Phaseolus*), and almost all other plants are not usually colonized, although under dry conditions it is sometimes found on *Capsella bursa-pastoris*. It is a vector of more than 30 virus diseases, including non-persistent viruses of beans, peas, beet, clover, cucurbits, *Narcissus* and Brassicaceae, and the persistent viruses, *Pea enation mosaic virus* (PEMV) and *Bean leaf roll virus* (BLRV).

Originally a Palaearctic species, *A. pisum* now has an almost worldwide distribution (see CABI Distribution Map 23, last revised 1982). In cold temperate regions, it is holocyclic, producing oviparae and males on various leguminous hosts. As in other members of the genus *Acyrthosiphon*, there is no true host alternation. The ancestral primary host was presumably a member of the Rosaceae, as in some related genera, but this was probably lost long ago. Clones may produce either apterous or alate males, or both. At warmer latitudes, it overwinters without a sexual phase.

In Europe and central Asia, *A. pisum* has been recognized for many years as a complex of races and subspecies with different host ranges and preferences (Müller, 1980, 1985). Populations attacking peas (*Pisum sativum*) in Europe consist entirely of green genotypes and have some morphological differences from those colonizing other leguminous crops such as lucerne (alfalfa, *Medicago sativa*), which may be green or pink. They produce alate sexuparae and males in autumn, and go through a sexual phase on *Vicia*. Molecular work using microsatellite markers showed that populations colonizing peas, lucerne and red clover in France were genetically divergent and also differed in their symbionts (Simon *et al*., 2003). Subsequent studies have distinguished no less than 11 different sympatric populations of *A. pisum* in Western Europe associated with different host plants (Peccoud *et al*., 2009a). Eight of these populations showed evidence of hybridization and were considered to be host races, but no hybrids were detected in the other three, which also showed greater genetic differentiation and might possibly have achieved the status of separate species. Of these three, one living on *Ononis* is morphologically recognizable and is currently regarded as a subspecies, *A. pisum ononis* (Koch) (Favret, 2014). The second lives on *Cytisus* and other members of the tribe Genisteae and has been given subspecies status, as *A. pisum spartii* (Koch), by Eastop (1971). The third, although previously unrecognized, is perhaps the most genetically divergent, and feeds specifically on *Lathyrus pratensis*. An available name for this taxon is *Acyrthosiphon lathyri*.

Populations introduced to other parts of the world must at least originally have been genetically depauperate, and hence their biology and host-plant relations may have diverged significantly from the species in Europe. The genotype(s) introduced to North America initially lacked the dominant red (pink) allele that was frequent in European populations, and were particularly well adapted to lucerne. They were named as a new species (Johnson, 1900), and this name (*destructor*) has been proposed as a subspecific name not only for the North American populations (Hille Ris Lambers, 1947) but also for the green, pea-adapted form in Europe, from which it was originally assumed to have been derived (Müller, 1985; but see below).

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In ground-breaking work that illuminated the evolutionary processes that might be going on in crop-colonizing aphids, Via (1991, 1999) demonstrated that populations of *A. pisum* on lucerne and red clover (*Trifolium pratense*) in north-eastern USA performed significantly better on their respective host plants and were reproductively isolated from one another as a result of inherited differences in host selection by alatae, which led to assortative mating. Hawthorne and Via (2001) showed that there was close genetic linkage at several loci between the two key traits involved in host specialization; that is, host selection by alatae and the subsequent performance (measured by fecundity) of populations on each host. This could lead to extremely rapid divergent selection of pea aphids on lucerne and clover. Schwartzkopf *et al*. (2013) have now demonstrated a similar link between host selection and performance in European populations from pea, lucerne and clover.

The implications of this work are far-reaching, although much is still unclear. The origins of the populations studied by Via's group in the USA are unknown, but the subsequent work in Europe suggests that the observed differences may be long-standing and the result of separate introductions from the Palaearctic of two genotypes with different host associations, as seems to have happened with some other pest aphids in North America (see under *Therioaphis trifolii*, *Schizaphis graminum* and *M. persicae*). More detailed genetic comparisons of European and North American populations are needed to confirm this. However, regardless of their origins, Via's *A. pisum* populations seem to have a genetic system that can lead to rapid divergence and incipient speciation in crop environments. Add in the probability that the same processes of selection and reinforcement of correlations between key traits are occurring in large populations throughout the regions where these crops are grown and there seems to be a very potent mechanism for evolutionary change.

The pea aphid has thus become not only the primary target for genomic studies (see Chapter 2, this volume) but also an important example of rapid evolution and host plant-mediated speciation (Peccoud and Simon, 2010). Some estimates of the timescale in which these changes have taken place in Europe have been achieved by analysing rapidly mutating DNA sequences in the aphid's endosymbiont *Buchnera* (Peccoud *et al*., 2009b). If these estimates are accurate, then it seems that much of the diversification leading to the present situation of *A. pisum* in Western Europe has occurred in the past 10,000 years, and may have been brought about by changes in the abundance of plant species at the end of the last glacial period, coupled with the spread of agriculture and the cultivation of leguminous crops.

If the host-adapted forms of *A. pisum* demonstrated by the American and French groups are indeed 'incipient species', should any of them be classed as subspecies or full species? It would obviously be undesirable to give names to locally divergent populations, even though the first stage in the speciation process can occur only at the level of the local population. To conform with the working definition of the aphid subspecies above, it would be necessary to demonstrate that the observed differences were consistent in both time and space, and to verify the existence of monophyletic host-adapted lineages. It is already apparent that the name used originally for the North American lucerne-feeding form (*destructor*) was applied wrongly to the pea-feeding populations in Europe, although it still might be valid for a lucerne-adapted clade if this is common to both continents. Recent studies indicate that the populations in Europe on *Ononis*, and also those on Genisteae and *Lathyrus*, may be functioning as three fully independent species, and there are names available that could be applied to them. The *Ononis* feeder has had long-term recognition as a separate taxon morphologically distinguishable from *A. pisum* and qualifies for separate species status, and perhaps the other two forms should be formally designated as subspecies of *A. pisum* pending further information on their biology, distribution and constancy of host association.

Aphis craccivora (cowpea aphid) (Fig.1.2)

This is a small, dark brown aphid with a shiny black dorsal shield. It occurs most commonly on legumes, but is much more polyphagous than *A. pisum*, with a wide range of hosts not only in the Fabaceae (e.g. *Arachis*, *Colutea*, *Glycine*, *Medicago*, *Melilotus*, *Trifolium*, *Vicia*) but also in many other plant families. Altogether, it attacks about 50 crops in 19 different plant families. It is a vector of about 30 plant virus diseases, including non-persistent viruses of beans, cardamom (*Elettaria cardamomum*), groundnuts, peas, beets, cucurbits and crucifers, and the persistent *Subterranean clover stunt virus*, *Peanut mottle virus* and the complex of viruses

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Fig. 1.2. *Aphis craccivora* – cowpea aphid. (Photograph courtesy of B. Chaubet and INRA.)

causing groundnut rosette disease. Jones (1967) compared two clones from East and West Africa differing in ability to transmit strains of groundnut rosette and found that there were also differences in the ability to colonize various host plants. There has been little work since then on variation in crop populations (but see http://www.aphidsonworldsplants.info).

Aphis craccivora now occurs in most parts of the world (for detailed distribution, see http://www.cabi.org/iscbeta/datasheet/6192), but its origins are clearly in Europe as the most polyphagous member of a group of closely related species (subgenus *Pergandeida*), most of which are specific to particular species of Fabaceae. None of this group of *Aphis* has host alternation. *Aphis craccivora* has a sexual phase on various Fabaceae in central Europe (Germany), and sexual morphs have also been reported from India and Argentina, but through most of the world reproduction seems to be exclusively parthenogenetic. It is particularly common as a pest in warmer climates, and it seems likely that the pest populations may have originated from the warmer part of its original distribution area in southern Europe or the Middle East.

Aphis fabae (black bean aphid) (Fig. 1.3)

Aphis fabae is perhaps the most familiar aphid in Europe, due to its predilection for *Phaseolus* and *Vicia*, although it is probably just as important as a pest and virus vector of sugar beet. Adult apterae in new colonies on young plant growth are matt black in life, most of the pigmentation of the body being internal, so that it is no longer present in cleared specimens prepared for the microscope. Individuals in older colonies and feeding on leaves tend to develop white wax markings.

Fig. 1.3. *Aphis fabae* – black bean aphid. (Photograph courtesy of Syngenta.)

Aphis fabae is a very polyphagous species, but the actual host range of the aphid that colonizes beans and sugar beet is unclear, because it is a member of a bewildering complex of species, some of

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which at least also have wide host ranges. Many people have tried to sort out this complex. Stroyan (1984: 119–122) reviewed the taxonomy and host relations of the group as then understood. There has been significant work since then (e.g. Müller and Steiner, 1986; Thieme, 1987, 1988; Thieme and Dixon, 1996; Raymond *et al*., 2001), but a lot of questions still remain. To summarize the situation in northern Europe as succinctly as possible, there are five closely related taxa, four of which go through their sexual phase on the spindle tree, *Euonymus europaeus*:

1. *Aphis fabae sensu stricto* (*A. fabae* ssp. *fabae*), which has *Euonymus* as its only primary host and migrates for the summer to a wide range of plants, including *Vicia faba*, sugar beet, *Chenopodium album* and poppies, but not *Solanum nigrum*.
2. *Aphis solanella*, which also has *Euonymus* as its only primary host and migrates to a wide range of plants including *S. nigrum*, the leaves of which it crumples and curls characteristically, but will not colonize beans, sugar beet, *C. album*, or poppies. *Aphis solanella*, which has shorter hairs than *A. fabae* and a greater tolerance of high temperatures, has usually been classed as a subspecies of *A. fabae*, but Thieme and Dixon (2004) suggested that it should have full species status. It is a pest in its own right, especially on Solanaceae.
3. *Aphis fabae cirsiiacanthoidis*, which normally uses *Euonymus* as a primary host, can also go through its sexual phase on *Viburnum opulus*. This form is hardly distinguishable morphologically from *A. fabae sensu stricto*, but has *Cirsium arvense* as its most characteristic summer host. It can colonize certain other plants, but is not found on *Vicia* or *Solanum*.
4. *Aphis euonymi*, which is a brown aphid that stays on *Euonymus* all year round.
5. *Aphis fabae mordvilkoi*, which again is almost indistinguishable from *A. fabae sensu stricto*, but with sexual generations on *V. opulus* or *Philadelphus coronarius* and migrating for the summer mainly to various secondary hosts, but not colonizing *Vicia*, *Solanum*, or *Cirsium* and often occurring on *Arctium* spp. and *Tropaeolum majus*.

However, the host ranges of all members of the group except *A. euonymi* seem to overlap, and some plants, such as *Rumex obtusifolius*, seem to be accepted by all of them (Thieme, 1987, 1988).

To complicate the story still further, the primary host relationships of the members of the group are also not at all clear-cut. *Aphis fabae sensu stricto* and *A. solanella* are able to live on *Viburnum* and *Philadelphus*, the primary hosts of *A. f. cirsiiacanthoidis* and *A. f. mordvilkoi*, and may in autumn produce males on these plants, but not oviparae (Iglisch, 1968). Hybridization between any members of the group is therefore possible theoretically, and can be accomplished rather easily in the laboratory, even between slightly less closely related forms such as *A. fabae* and the brown species, *A. euonymi* (Müller, 1982). However, it is now clear that such results are misleading, and that strong prezygotic isolating mechanisms are likely to be operating to prevent hybridization and promote assortative mating in the field. *Aphis fabae sensu stricto* and *A. solanella* occurring together on *Euonymus* show differences in the diurnal patterns of pheromone release by oviparae and male responsiveness, and in choice experiments males preferred the sex pheromones of conspecific females (Thieme and Dixon, 1996). Prezygotic isolating mechanisms have also been demonstrated in the laboratory between *A. fabae sensu stricto* and *A. f. mordvilkoi*, although these subspecies do not share the same primary host in nature (Raymond *et al*., 2001).

In spite of this evidence of substantial reproductive isolation between the members of the *A. fabae* complex, analysis of mtDNA and of a plasmid from their symbionts showed differences within, but not between, species (Raymond *et al*., 2001). This is similar to the situation in *A. pisum* already discussed (where host/habitat selection rather than mate selection is the isolating factor), and suggests that such isolating mechanisms may evolve very rapidly, possibly by the process known as reinforcement (Coyne and Orr, 1989; Mackenzie and Guldemond, 1994).

On the evidence of its primary host and closest relatives, *A. fabae* must be of European origin. *Aphis fabae sensu stricto* occurs in Europe, western Asia, Africa and South America. It is a vector of more than 30 plant viruses, including non-persistent viruses of beans and peas, beets, crucifers, cucurbits, *Dahlia*, potato, tobacco, tomato and tulip, and the persistent *Beet yellow net virus* (BYNV) and *Potato leaf roll virus* (PLRV). In warmer regions – the Mediterranean and the Middle East, the Indian subcontinent and hotter parts of Africa and South America – it is replaced by *A. solanella*, reproducing parthenogenetically throughout the year on its secondary host plants, particularly Solanaceae, Asteraceae and Polygonaceae. The *Tropaeolum*-feeding subspecies

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A. f. mordvilkoi has a more northerly, Holarctic distribution, and uses *Viburnum trilobum* as its main primary host in Canada (Barber and Robinson, 1980, as *A. barbarae*).

Aphis gossypii (cotton or melon aphid) (Fig. 1.4)

If the multiplicity of populations that are lumped under the name *A. gossypii* are really all one species, then it is indeed a remarkable one, with greater diversity in terms of host relationships, life cycle and geographical range than any other aphid. Small aphids that vary greatly in colour from pale yellow dwarfs at high temperatures, through dirty yellow-green to dark bluish-green or almost black at lower temperatures, occur on plants in numerous families, including nearly 100 species of crop plants, throughout the world. Crops attacked include cotton, cucurbits, citrus, coffee, cocoa, aubergine, peppers, potato and okra, and many ornamental plants including chrysanthemums and *Hibiscus*. Populations on cotton and cucurbits can be particularly large and damaging. More than 50 plant viruses are transmitted, including non-persistent viruses of beans and peas, crucifers, celery, cowpea, cucurbits, *Dahlia*, lettuce, onion, pawpaw, peppers, soybean, strawberry, sweet potato, tobacco and tulips, and the persistent *Cotton anthocyanosis virus*, *Lily symptomless virus*, PEMV and lily rosette disease.

In all the warmer parts of the world, *A. gossypii* reproduces continuously by parthenogenesis. It is particularly abundant and widely distributed in the tropics, including many Pacific islands. During prolonged dry seasons in hot countries, small colonies may survive on a great variety of plants on which they are seldom seen during the growing season, including Poaceae. Deguine and Leclant (1997) provide a comprehensive account with an extensive bibliography.

Certain morphological features – short hairs on legs and antennae, and a cauda that is usually paler than the siphunculi and bears rather few hairs – make it easy to apply the name *A. gossypii* to aphids collected on crops or other non-indigenous plants anywhere in the world. This is, however, a considerable oversimplification of the taxonomic problem, as becomes evident, for example, when one compares accounts of *A. gossypii* in Europe and East Asia.

In Europe (Stroyan, 1984; Heie, 1986), *A. gossypii* has been classed as a subspecies in the *Aphis frangulae* complex, a group of closely related and morphologically almost indistinguishable indigenous European species that use buckthorn (*Rhamnus frangula*) as their primary host. *Aphis gossypii* was widely regarded (that is, more or less defined) as the only member of the group without a sexual phase on buckthorn, overwintering parthenogenetically in northern Europe in protected situations such as glasshouses. One might conclude from this scenario that this worldwide pest originated in Europe as a permanently parthenogenetic, highly polyphagous and adaptable offshoot of the *A. frangulae* complex,

Fig. 1.4. *Aphis gossypii* – cotton or melon aphid. (Photograph courtesy of B. Chaubet and INRA.)

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and spread from there to all parts of the world as the classic 'general purpose genotype'.

However, such a conclusion was difficult or impossible to reconcile with accounts of what was purportedly the same species in Japan and China, where the parthenogenetic generations seemed equally polyphagous, but there was an annual sexual phase, with overwintering as eggs on a variety of unrelated woody plants including *Rhamnus* ssp. and *Hibiscus syriacus* (see below). Populations in Connecticut, USA, also have a sexual phase, using *H. syriacus* and also *Catalpa bignonioides* as primary hosts (Kring, 1959). Several DNA markers have now been found that discriminate between *A. frangulae* collected on *Rhamnus* in Europe and *A. gossypii* collected from diverse host plants and different parts of the world (Carletto *et al*., 2009a; Cocuzza *et al*., 2009). One can conclude from this work that *A. gossypii* is not a member of the European *frangulae* group.

Since the first edition of this book, there has been some very significant work on the host-plant relationships of *A. gossypii* in different parts of the world, and a remarkably complex and puzzling picture has started to emerge. Studies of *A. gossypii* from four continents using microsatellite DNA have established that there is no common 'general purpose genotype' of *A. gossypii*. On the contrary, it has developed host-specialized populations with worldwide distributions, not only on Cucurbitaceae, as demonstrated previously using random amplified polymorphic DNA (Vanlerberghe-Masutti and Chavigny, 1998) but also on Malvaceae and Solanaceae (Carletto *et al*., 2009b). Aphid genotypes specializing within the Solanaceae on potato, aubergine and peppers have also been identified. This work concentrated on particular crop plants and did not include other plant families. However, Margaritopoulos *et al*. (2006) have demonstrated, using multivariate morphometrics, that there is also a host-specialized form of *A. gossypii* – also distributed throughout the world – on Asteraceae.

Particular host associations had been noted previously in *A. gossypii*, in European glasshouses for example, where aphids from chrysanthemums would not colonize cucumber and vice versa (Guldemond *et al*., 1994). It now seems, however, that *A. gossypii* populations are host-specialized on a global scale, and that at least some of these associations are at the level of the host-plant family. The ability to recognize and select between plant families involves the development of a level of behavioural and physiological sophistication – see, for example, Najar-Rodríguez *et al*. (2009) – that must surely have involved genetic recombination. Yet populations of *A. gossypii* on cultivated plants throughout much of the world consist mostly of a small number of host-specialized clone groups, reproducing asexually, with the minor DNA differences within each clone group accountable as due solely to mutation (Carletto *et al*., 2009b). This suggests that multiple dispersions of host-specialized forms have occurred from a region (or regions) where a regular annual sexual phase occurs, probably in East Asia.

The host associations of the bisexual generation of *A. gossypii* seem to be just as enigmatic. Host alternation occurs in China and Japan, with several unrelated woody plants acting as primary hosts, including *Rhamnus* spp., *H. syriacus*, *Celastrus orbiculatus*, *Rubia cordifolia* (Inaizumi, 1980; Zhang and Zhong, 1990) and *Citrus* (Komazaki and Toda, 2008). However, monoecious holocyclic populations, producing sexual morphs without migration, also occur on both cotton and *Hibiscus* in China; Liu *et al*. (2006) have carried out hybridization tests between these monoecious strains and those migrating between cotton and *Hibiscus*. Komazaki and Toda (2008) obtained wingless gynoparae from some holocyclic clones originating from various host plants in Japan, indicating that monoecy occurs there also. Differences in the numbers of sexual morphs produced by populations on cotton and cucumber are reported from China (Gao and Liu, 2008). It is possible that some of the host-alternating populations have diverged as a result of differential selection among primary hosts. Populations overwintering on *R. cordifolia* in Japan, for example, seem to be isolated from those on other primary hosts, and are possibly a separate taxon (Inaizumi, 1981).

The glasshouse populations on both chrysanthemums and cucurbits in Europe are normally parthenogenetic, but can produce sexual morphs under certain conditions (Guldemond *et al*., 1994, and Fuller *et al*., 1999, respectively). Microsatellite DNA analysis of the genetic structure of spring populations on melon plants has now established that *A. gossypii* is reproducing sexually in the field in western France, and has revealed great genetic diversity in the alatae arriving on the newly planted crop and their immediate progeny (Thomas *et al*., 2012). The melon crop is thus acting as a selective filter, so that only cucurbit-specialized genotypes are present in samples taken later in the season. The sources of the spring migrants – both those that

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had overwintered parthenogenetically and those originating from sexually produced eggs – remain unknown.

Many questions remain to be answered before an assessment is possible of the taxonomic status of any of the host-specialized forms of *A. gossypii*. This species is recorded from more than 100 plant families, and presumably it has not developed specific host associations with all of them. The forms specialized on Malvaceae and Cucurbitaceae differ very little in both mitochondrial and nuclear DNA sequences (Coeur d'acier *et al*., 2007; Najar-Rodriguez *et al*., 2009), indicating recent divergence, probably since the large-scale cultivation of crops. The development and maintenance of the co-adapted genetic systems involved in host specialization are presumably favoured in agroecosystems, where newly recombinant genotypes can build up large clonal populations on crop plants. Little is known as yet about the genetic diversity and structure of populations of *A. gossypii* on non-crop hosts.

How has this remarkable insect evolved systems in which host selection and specificity can operate and be maintained at the family level? We also need to know the extent to which host-specialized genotypes are involved in sexual reproduction, wherever this occurs and the plants on which it occurs. *Hibiscus* seems to play a special role in the biology of *A. gossypii*, as it can act not only as a primary host (in Europe and America, as well as Asia) but also as a reserve or 'refuge' host for permanently parthenogenetic genotypes that are specialized on plant families other than Malvaceae (Margaritopoulos *et al*., 2006; Carletto *et al*., 2009b).

Aphis spiraecola (spiraea aphid or green citrus aphid) (Fig. 1.5)

This is a small, yellow or greenish-yellow aphid with black siphunculi and cauda, found in dense, ant-attended colonies, curling and distorting leaves near the stem apices of a wide range of plants, particularly those of shrubby habit. Its numerous hosts are in more than 20 plant families, especially Caprifoliaceae, Asteraceae, Rosaceae, Rubiaceae, Rutaceae and Apiaceae. Probably its most important crop host is *Citrus*. Although not particularly efficient at transmitting viruses, very large populations occur in spring in some regions – the Middle East, for example – and can make it an important vector of *Citrus tristeza*. It also transmits *Cucumber mosaic virus* (CMV), *Plum pox virus*, an isolate of *Alfalfa mosaic virus* from *Viburnum*, *Watermelon mosaic virus* 2 and *Zucchini yellow mosaic virus* (ZYMV).

Fig. 1.5. *Aphis spiraecola* – green citrus aphid. (Photograph courtesy of B. Chaubet and INRA.)

Now almost worldwide, there seems little doubt that *A. spiraecola* is indigenous to East Asia. It has been in North America since at least 1907 and had reached Australia by 1926, New Zealand by 1931, Argentina by 1939, the Mediterranean region by about 1939 and Africa by 1961 (see also CABI Distribution Maps of Plant Pests No 256, revised 2001). Populations in most parts of the world are permanently parthenogenetic on secondary hosts, but in East Asia and North America *A. spiraecola* has a sexual phase on *Spiraea*.

There is an extensive literature on *A. spiraecola*, particularly in relation to its economic importance on *Citrus* (it was referred to as *A. citricola* in the literature from 1975 to 1988 because of a misidentification). The most comprehensive accounts of *A. spiraecola* as a *Citrus* pest are by Barbagallo (1966) in Italy and Miller (1929) in Florida. On other plants, especially Rosaceae, *A. spiraecola* is often confused with *Aphis pomi* (green apple aphid). For example, Cottier (1953) wrote an account of *A. spiraecola* in New Zealand under the name *A. pomi*, and Singh and Rhomberg (1984) studied allozyme variation in populations nominally of *A. pomi* on apples in North America and found two forms, one of which was almost certainly *A. spiraecola*. *Aphis pomi* has a longer last rostral segment than *A. spiraecola*, more hairs on the cauda and usually has lateral tubercles on abdominal segments 2–4 (see also Halbert and Voegtlin, 1992; Foottit *et al*., 2009; Rakauskas *et al*., 2015). There also is possible confusion of identity with *Aphis eugeniae* in East and South-east Asia and Australia that can

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occur on the same hosts; *A. eugeniae* can be recognized by the peg-like hairs on the hind tibia and by the presence of a median sense peg between the pair of hairs on the first segment of the hind tarsus.

Compared with the problems raised by *A. fabae* and *A. gossypii*, the taxonomic status, origins and identity of *A. spiraecola* seemed to be fairly clear. However, Komazaki *et al.* (1979) found that *A. spiraecola* in Japan was using *Citrus reticulata* as well as *Spiraea thunbergii* as a primary host, and experimental work demonstrated that there were genetically inherited differences in hatching time (Komazaki, 1983, 1986) and egg diapause (Komazaki, 1998), correlated with esterase differences (Komazaki, 1991), that seemed to indicate a degree of genetic isolation and divergence between the populations on the two primary hosts. Presumably, the ancestral primary host was the rosaceous plant (*Spiraea*) and *Citrus* was acquired more recently as a primary host. This seems to be an example of incipient speciation, as in Via's (1999) populations of *A. pisum*, but again it is not yet clear whether it is more than a local phenomenon. There are no records of sexual generations on *Citrus* outside Japan, and it could be that they are unable to survive on *Citrus* species other than *C. reticulata*. In Japan, alatae migrating from spring populations that had developed from overwintering eggs on *C. reticulata* seemed to be the most important source of infestations of *Citrus* groves at a time when the main migration from *Spiraea* had already taken place (Komazaki, 1983).

Diuraphis noxia (Russian wheat aphid) (Fig.1.6)

This small, narrow-bodied, yellow-green aphid was little known outside southern Russia until the late 1970s, but it then took only a little over 10 years to colonize the main wheat- and barley-growing areas of East Asia, South Africa and both North and South America. It is still expanding its range northward in Europe (Thieme *et al.*, 2001). Hughes and Maywald (1990) have assessed the suitability of the Australian environment for *D. noxia*, and in 2016 it arrived in South Australia (see http://www.cabi.org/iscbeta/datasheet/9887).

Diuraphis noxia feeds only on Poaceae, concentrating particularly on wheat and barley. It does best on late-sown crops on poor soils. It transmits *Barley yellow dwarf virus*, but its feeding also has a rapidly toxic effect on the plant, the leaves of which become rolled into tubes and desiccated, and infested ears become bent. In cold temperate regions of Europe and Asia, *D. noxia* has a sexual phase without host alternation on wheat and barley. The introduced population in Chile and Argentina is also predominantly holocyclic (Clua *et al.*, 2004; Ricci *et al.*, 2011). In North America, *D. noxia* was for

Fig. 1.6. *Diuraphis noxia* – Russian wheat aphid. (Photograph courtesy of B. Chaubet and INRA.)

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many years thought to have no sexual phase. Kiriac *et al.* (1990) found some oviparae in Idaho and Oregon, but no males were found, and genetic variation was limited (Puterka *et al.*, 1992, 1993). It was not until 2007 that a holocyclic population was found in Colorado that produced sexuales and overwintered as eggs (Puterka *et al.*, 2012). In 2003, new wheat resistance-breaking genotypes started to appear, although little variation was detected between these using several genetic markers (e.g. Shufran and Payton, 2009). Then a wide-ranging survey using a genome-wide technique (AFLP) provided evidence that there might have been at least two separate introductions into North America, the first possibly of Middle Eastern origin via South Africa and Mexico, and the second from Europe (Liu *et al.*, 2010). It is likely that this second introduction was of aphids able to produce males and complete the sexual phase, releasing the potential to develop new resistance-breaking genotypes (Puterka *et al.*, 2012). An interesting adjunct to this story is that Mimeur (1942) collected *D. noxia* in North Africa in 1938, described it as a new species (*Cavahyalopterus graminearum*) and obtained oviparae in culture, but no males. Thus, the absence of males may be a long-standing feature of the population introduced to South Africa, and of the original introduction into the USA.

There are no problems with the identity of *D. noxia* as a species. Puterka *et al.* (2010) provided a key and illustrations comparing *D. noxia* with native *Diuraphis* spp. in the US Rocky Mountain region. In Europe, there is a very similar aphid, *Diuraphis muehlei*, which feeds specifically on *Phleum pratense*, turning the leaves yellow. This species was synonymized with *D. noxia* by Miller *et al.* (2005), but is morphologically and biologically distinct. A useful discriminant is that almost all specimens of *D. muehlei* have a shorter antennal terminal process than *D. noxia*; the ratio of the terminal process to the base of the last segment in apterae is 1.05–1.65 (*muehlei*), as opposed to 1.55–2.0 (*noxia*), and in alatae 1.2–1.9 (*muehlei*), as opposed to 1.8–2.7 (*noxia*).

There is an extensive older Russian literature on *D. noxia*, one of the most comprehensive studies being that of Grossheim (1914). The rapid spread and great economic importance of this aphid have resulted in more recent extensive studies; see Poprawski *et al.* (1992) for a bibliography and general accounts by Pike and Allison (1991) and Hughes (1996). Berest (1980) studied the parasite and predator complex of *D. noxia* in Ukraine, and Tanigoshi *et al.* (1995) described biological control measures. Chen and Hopper (1997) studied its population dynamics and the impact of natural enemies in southern France. Zhang *et al.* (2012) studied microsatellite and mitochondrial DNA variation in holocyclic populations in north-west China. Botha (2013) reviewed and discussed its co-evolutionary interactions with its host plants.

Lipaphis pseudobrassicae (mustard aphid, also known as the false cabbage aphid) (Fig. 1.7)

Lipaphis pseudobrassicae is a cosmopolitan pest of cruciferous crops. Apterae are small to medium-sized, yellowish, grey, or olive green, with a waxy bloom that in humid conditions becomes a dense coat of white wax. It can occur in large colonies on the undersides of leaves or in inflorescences of many species and genera of Brassicaceae, including *Barbarea*, *Brassica*, *Capsella*, *Erysimum*, *Iberis*, *Lepidium*, *Matthiola*, *Nasturtium*, *Raphanus*, *Rorippa*, *Sinapis*, *Sisymbrium* and *Thiaspi*. Often, the leaves are curled and turn yellow. It is a vector of about 10 non-persistent viruses, including *Turnip mosaic virus* and *Cauliflower mosaic virus*. It occurs throughout the world (C1E Distribution Map 203, 1965), but particularly is a pest in warmer climates, reproducing throughout the year by continuous parthenogenesis. Agarwala *et al.* (2009) compared its morphology and performance on three different species of Brassicaceae in India.

The origin and identity of *L. pseudobrassicae* were long in doubt. In North America, it was at first confused with *Brevicoryne brassicae*, until Davis (1914) recognized it as distinct and named it *Aphis pseudobrassicae*. Because of its weakly clavate siphunculi, it was subsequently transferred by Takahashi (1923) to the genus *Rhopalosiphum*, and it was referred to in the economic literature as *Rhopalosiphum pseudobrassicae* (Davis) until 1964. Börner and Schilder (1932) recognized that *pseudobrassicae* should be placed in *Lipaphis*, a genus erected by Mordvilko (1928) for a Palaearctic crucifer-feeding aphid, *erysimi*. *Lipaphis erysimi* is a holocyclic species with a 2n = 10 karyotype (Gut, 1976; Blackman and Eastop, 2000) that occurs commonly on wild crucifers in northern and central Europe, but is not usually found on brassica crops (Müller, 1986; Heie, 1992). Hille Ris Lambers (1948) could not find characters to discriminate

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Fig. 1.7. *Lipaphis pseudobrassicae* – mustard aphid. (Photograph courtesy of B. Chaubet and INRA.)

pseudobrassicae from *erysimi*, but nevertheless stopped short of making it a synonym. Others regarded it as a subspecies of *erysimi* (e.g. Eastop, 1958a; Müller, 1986). Despite these uncertainties, the name *erysimi* was used for the widely distributed crucifer pest from 1975 to 2000.

Although most mustard aphid populations throughout the world are continuously parthenogenetic, a holocycle does occur on cruciferous crops (*Brassica rapa* subsp. *rapa*, *Raphanus sativus*) in western Honshu, Japan (Kawada and Murai, 1979). These aphids have 2n = 8, and thus differ in karyotype from the holocyclic populations of *Lipaphis* in northern Europe. Chen and Zhang (1985) also reported 2n = 8 for *Lipaphis* in China. In West Bengal, mustard aphid populations are economically important on field crops of mustard, *Brassica nigra*, and here the common karyotype is also 2n = 8 (Kar and Khuda-Bukhsh, 1991). Sexual morphs have been reported from northern India, but populations there are probably mostly anholocyclic. Most permanently parthenogenetic mustard aphid populations throughout the world have a 9-chromosome karyotype, probably derived from the 8-chromosome form by dissociation of one autosome to produce a small, unpaired element. In multivariate morphometric analysis, samples with 8 and 9 chromosomes grouped together and were separated from samples of European *L. erysimi* with 10 chromosomes (V.F. Eastop and R.L. Blackman, unpublished), so it was concluded that *L. pseudobrassicae* should be reintroduced for the worldwide crucifer pest and that it probably originated in eastern Asia (Blackman and Eastop, 2000). Finding simple morphological discriminants for the two species is not easy. *Lipaphis pseudobrassicae* has relatively longer antennae and relatively shorter siphunculi, and the function '(length of antennal segment III + length of processus terminalis) divided by length of siphunculus' discriminates most specimens. The value of this function is more than 2.4 in 90% of apterae of *L. pseudobrassicae* and less than 2.4 in 90% of apterae of *L. erysimi*. The equivalent discriminating value for alatae is 3.4.

Macrosiphum euphorbiae (potato aphid) (Fig. 1.8)

Macrosiphum euphorbiae is one of the few cosmopolitan aphid pests of field crops that are undoubtedly of North American origin. The earliest European record is from potato at Wye, Kent, England, in 1917, after which it soon became common in Britain and spread to continental Europe (Eastop, 1958b). It is a medium-sized to large spindle-shaped aphid, usually green but sometimes pink or magenta; the adult apterae are often rather shiny in contrast to the immature stages, which have a light dusting of greyish-white wax. In north-eastern USA, it has a sexual phase on *Rosa*, using both wild and cultivated species as primary hosts (Shands *et al*., 1972). In Europe, and probably elsewhere, *M. euphorbiae* is mainly anholocyclic, although sexual morphs are produced occasionally and the holocycle may sometimes occur

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Fig. 1.8. *Macrosiphum euphorbiae* – potato aphid. (Photograph courtesy of B. Chaubet and INRA.)

(Möller, 1970). The pink form has become much more common in Europe in recent years. On secondary hosts, *M. euphorbiae* is highly polyphagous, feeding on more than 200 plant species in more than 20 different plant families. It is a vector of more than 40 non-persistent and 5 persistent viruses, including BYNV, PEMV, BLRV, *Sweet potato leaf-speckling virus*, ZYMV and PLRV. It is an important pest of potato, but as a vector of PLRV under field conditions it seems to be relatively unimportant in comparison with *M. persicae* (Robert, 1971; Woodford *et al.*, 1995), although direct feeding by large numbers early in the season can cause 'false top roll'.

There is a very large literature, but surprisingly little is known about intraspecific variation and specific aphid–host interactions of *M. euphorbiae*. In western North America there are several little-known, and even some undescribed, species closely related to and almost indistinguishable from *M. euphorbiae* (MacDougall, 1926, and V.F. Eastop, unpublished). In Europe, there is a group of closely related species with more specific host associations (Watson, 1982; Heie, 1994); of these, *M. euphorbiae* is most easily confused with *Macrosiphum tinctum*, which feeds only on *Epilobium* spp. It can be hybridized in the laboratory with *Macrosiphum stellariae*, which is usually found on *Stellaria holostea*, and can colonize other plants, but not potato (Möller, 1971).

Meier (1961) provided a general account of *M. euphorbiae* in Europe, Barlow (1962) studied its development on potato and MacGillivray and Anderson (1964) studied the factors controlling sexual morph production in eastern Canada. Parasitoids and hyperparasitoids were studied in North America by Shands *et al.* (1965) and Sullivan and van den Bosch (1971). Raboudi *et al.* (2011, 2012) studied the genetic diversity of populations on different host plants in Tunisia. See also http://www.cabi.org/iscbeta/datasheet/32154.

Metopolophium dirhodum (rose–grain aphid) (Fig. 1.9)

Metopolophium are pale, spindle-shaped aphids with pale siphunculi that lack any polygonal reticulation, so that they superficially resemble *Acyrthosiphon*. However, their typical life cycle involves host alternation between roses and grasses, as in *Sitobion*, which are possibly their closest relatives. *Metopolophium dirhodum* is a species of western Palaearctic origin that is now an important cereal pest and vector of BYDV throughout the temperate regions of the world, in both the northern and southern hemispheres. In Europe, as its common English name implies, *M. dirhodum* has a bisexual generation on *Rosa*, but anholocyclic overwintering on grasses occurs in England (Prior, 1976), and populations introduced to other parts of the world – or at least those in New Zealand (Nicol *et al.*, 1997) and Brazil (Lopes-da-Silva and Vieira, 2007) – seem to be permanently parthenogenetic on grasses and cereals.

Apterae of *M. dirhodum* are pale green or greenish yellow and typically have a distinctive bright green longitudinal mid-dorsal stripe. Colonies are usually easy to detect as they develop on the upper parts of cereal plants, and large populations cause

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Fig. 1.9. *Metopolophium dirhodum* – rose–grain aphid. (Photograph courtesy of Rothamsted Research.)

yellowing of leaves and direct feeding damage. The population dynamics of *M. dirhodum* have been studied intensively, but less is known about genetic variation within species and the extent of occurrence of host races. Several other European species of *Metopolophium* are morphologically almost indistinguishable from *M. dirhodum* but have specific secondary host associations with particular grasses, or are restricted to certain habitats (Stroyan, 1982). The existence of these species warrants the assumption that *M. dirhodum* is part of yet another actively speciating aphid group, and that one might therefore expect to find evidence of host race formation and incipient speciation.

Weber (1985) investigated the performance of 150 clones of *M. dirhodum* on barley, wheat and oats in Germany, and found significant intraspecific differences in the degrees of adaptation to these three host plants. All the clones that he tested for life-cycle category produced sexual morphs under short-day conditions, i.e. were holocyclic. Using genetic fingerprinting, de Barro *et al.* (1995) sampled *M. dirhodum* populations from wheat and from roadside grasses in southern England. They found plenty of genetic variation within and between locations, indicative of regular genetic recombination, but no clear differences between the two host types (in contrast to similar studies of *Sitobion avenae* – see below). The only other work looking for host-related variation in *M. dirhodum* was in Brazil, where the introduced populations of *M. dirhodum* were thought to be anholocyclic. Using RAPD markers, Lopes-da-Silva and Vieira (2007) found an unexpectedly high level of genetic diversity among populations sampled from wheat and oats, and some evidence of the existence of genotypes better adapted to, or preferring, oats.

Further work is clearly needed to confirm whether or not host races associated with oats or any other cereals occur in *M. dirhodum*. In future work, it will be important to avoid confusion with another European *Metopolophium* that feeds on cereal crops, *Metopolophium festucae* ssp. *cerealium*, which is now recognized to be present in both North and South America and may also have been introduced to other parts of the world but so far undetected. Alatae of *M. festucae cerealium* are distinguished easily from those of *M. dirhodum* by their distinctive pattern of dark dorsal abdominal markings, but apterae of the two species are more difficult to separate (Stroyan, 1982; Blackman, 2010; Halbert *et al.*, 2013). As *M. festucae cerealium* is recorded from Bolivia and Chile (Remaudière *et al.*, 1993), it is likely also to be in southern Brazil. The karyotype variation recorded for *M. dirhodum* in Brazil (Rubín de Celis *et al.*, 1997) could perhaps be due to the presence of this species (European populations of *M. dirhodum* have 2n = 18, whereas those of *M. festucae cerealium* have 2n = 16).

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Myzus persicae (peach–potato aphid) (Fig. 1.10)

Myzus persicae is an exceptional species in many respects; cosmopolitan, extremely polyphagous, highly efficient as a virus vector and with a great range of genetically based variability in properties such as colour, life cycle, host-plant relationships and methods of resisting insecticides. Adult apterous parthenogenetic females of *M. persicae* are small to medium-sized, pale greenish-yellow or various shades of green, pink, red or almost black (apart from the genetically determined colour variation, any one genotype will be more deeply pigmented in cold conditions). Alatae have a shiny black dorsal abdominal patch, as in other members of the genus *Myzus*, and immature alatae are often red or pink, even of genotypes where the apterae are green. Immature males are always some shade of yellow or yellow-green.

The sexual phase of *M. persicae* occurs predominantly on *Prunus persica* (including var. *nucipersica*), except in parts of north-eastern USA and eastern Canada, where *Prunus nigra* is the main primary host (Shands *et al*., 1969). Host alternation occurs in the temperate regions of all continents, wherever peaches are available and the autumn temperatures are low enough to allow production of the sexual morphs (Blackman, 1974). Spring populations on peach become very dense, severely curling the leaves. In contrast to its extreme primary host specificity, the secondary hosts are in more than 40 different plant families. They include very many economically important plants, on most of which the populations are highly dispersed and individuals are found feeding singly on the older leaves. The great economic importance of *M. persicae* is due to its efficiency as a virus vector. It has been shown to be able to transmit considerably more than 100 plant viruses, including the persistent viruses BLRV, *Turnip yellows virus* (formerly *Beet western yellows virus*), *Beet mild yellowing virus*, BYNV, PEMV, PLRV, *Tobacco vein distorting virus*, *Tobacco yellow net virus* and *Tobacco yellow vein virus*. The relationship with PLRV has received particular attention (e.g. Ponsen, 1972; Eskanderi *et al*., 1979). *Myzus persicae* is also a very efficient vector of numerous non-persistent viruses; for example, CMV and *Bean yellow mosaic virus* to lupins in Western Australia (Bwye *et al*., 1997).

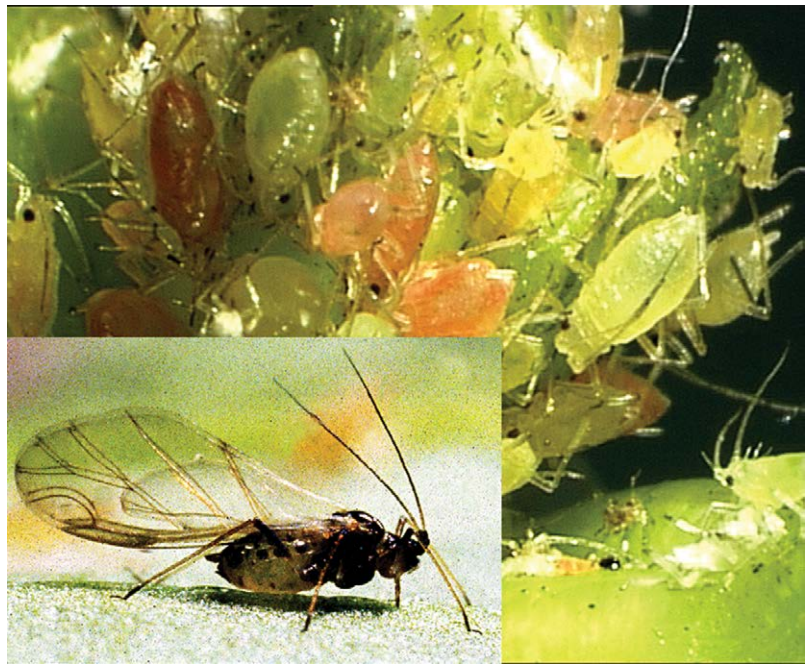

Fig. 1.10. *Myzus persicae* – peach–potato aphid. (Photograph courtesy of U. Wyss; inset courtesy of A.M. Dewar.)

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As its principal primary host is thought to originate from China, one would presume this to be the original homeland of *M. persicae*. This presumption is, however, not without its problems. First, one might expect to find its closest relatives in China. Yet the species that seem most closely related to *M. persicae*, including what many would regard as its sibling species, *Myzus certus*, and others with which it readily hybridizes in the laboratory such as *Myzus myosotidis*, are all European. It is difficult to see how this situation arose. There are no clues from biology, as all other species in the *Myzus* subgenus *Nectarosiphon* except *M. persicae* have lost their ancestral primary host and live all year round on their herbaceous host plants. A second problem concerns the relationship of *M. persicae* with PLRV, which seems to be intimate and therefore long-standing, but this is in conflict with their respective origins. It is possible, however, that potato leaf roll occurs in some unrecognizable or symptomless form in an Asian member of the Solanaceae.

As might be expected of such an adaptable and fast-evolving genome, biology and host relationships are likely to be changing faster than morphology, causing problems of identification and identity. Specimens of *M. certus* on slides are difficult enough to distinguish from those of *M. persicae*, although this species is clearly very different in its biology and host relations (living all year on Caryophyllaceae and Violaceae, and having its sexual phase on those plants, with apterous males). Two other taxa, *Myzus dianthicola* and *Myzus antirrhinii* (snapdragon aphid), are even more like *M. persicae*, and individual slide-mounted specimens cannot be distinguished reliably from that species. These two are both permanently parthenogenetic, as far as is known, and their karyotypes are structurally heterozygous (Blackman, 1980). *Myzus dianthicola* is found only on *Dianthus*, usually in glasshouses, where its consistently deep yellow-green colour and the leaf chlorosis that it causes distinguish it respectively from *M. certus* and *M. persicae*. *Myzus antirrhinii* may be almost as polyphagous as *M. persicae*, but has certain characteristic hosts such as *Antirrhinum* and *Buddleja* and a more consistent mid-green to dark green colour, and there are also differences in allozymes and at rDNA and microsatellite loci (Fenton *et al*., 1998; Terradot *et al*., 1999). Both *M. dianthicola* and *M. antirrhinii* are found in Europe and North America, the former also being found in New Zealand and the latter in Australia. Although probably of recent origin, they seem to be isolated from other members of the group by their obligate parthenogenesis, and are therefore best treated as discrete taxa (Blackman and Brown, 1991). The karyotype of *M. antirrhinii* is remarkably variable, and is of cytogenetic interest because fusions and dissociations of chromosomes have apparently occurred in the absence of genetic recombination (Hales *et al*., 2000).

Although complicating the practical identification of *M. persicae*, none of the forms discussed above have questionable taxonomic status. However, for many years it has been recognized that populations of *M. persicae* on tobacco (the 'tobacco aphid') are distinct from populations on other plants (de Jong, 1929; Brain, 1942; Müller, 1958; Takada, 1986). The aphid attacking commercial varieties of *Nicotiana tabacum* forms large, dense colonies at the growing points and on the youngest leaves, and seems able to avoid or tolerate the exudates of the glandular trichomes, which are not only sticky but contain repellent or toxic chemicals (Georgieva, 1998; Wang *et al*., 2001). Apterae on tobacco are predominantly pink/red in colour and have acquired resistance to insecticides far more slowly than those on other crops (Takada, 1979; Semtner *et al*., 1990). Blackman (1987) demonstrated, using multiple discriminant analysis, that samples from tobacco in many parts of the world could be differentiated from *M. persicae* on other crops, indicating that populations on tobacco worldwide constituted a monophyletic lineage for which he proposed the name *Myzus nicotianae*. Most of the samples analysed by Blackman (1987) were from regions where populations were permanently parthenogenetic. However, Margaritopoulos *et al*. (2000, 2007) found that the tobacco aphid was reproducing sexually on peach in northern Greece, and that the populations on peach and tobacco could also be discriminated morphometrically and by their microsatellite DNA from those on peach and other crops away from tobacco-growing regions. Differences in mating behaviour were also found (Margaritopoulos *et al*., 2007) that would function as a prezygotic isolating mechanism.

Genetic isolation between tobacco-adapted and non-tobacco-adapted forms cannot be complete, as the E4 and FE4 genes amplified in insecticide-resistant aphids are identical in the two forms (Field *et al*., 1994). However, these genes apparently have taken many years to cross into tobacco aphids. For example, holocyclic populations of *M. persicae* on peach in southern Europe have been resistant to

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organophosphates since about 1962, yet such resistance in tobacco aphids was first reported in holocyclic populations in northern Greece in the mid-1980s. This may be where introgression of these genes into tobacco-adapted genotypes occurred, selection then strongly favouring their spread to other populations. The absence of complete reproductive isolation between the two forms, perhaps in conjunction with a very recent origin of the tobacco-adapted form, may explain the failure to find consistent diagnostic genetic markers (Fenton *et al*., 1998; Margaritopoulos *et al*., 1998; Clements *et al*., 2000a,b), or the divergence of gene sequence that one might normally expect to find between separate taxa (Clements *et al*., 2000a). However, the degree of isolation must have been sufficient to preserve the integrity of the tobacco-adapted genome for at least 85 years, and it would be unwise to regard this form simply as synonymous with *M. persicae*, as suggested by Clements *et al*. (2000a,b), as this would lose important information.

Eastop and Blackman (2005) proposed that the tobacco aphid should have subspecies status, as *Myzus persicae nicotianae*, and the importance of recognizing and naming it as a distinct taxonomic identity has been confirmed by subsequent studies. Margaritopoulos *et al*. (2009) used microsatellite markers to study the global distribution patterns of *M. persicae*, providing further evidence that *M. p. nicotianae* was monophyletic, and Zepeda-Paulo *et al*. (2010) mapped the invasion route of *M. p. nicotianae* from North to South America. The tobacco aphid is clearly an important example of rapid evolution and a possible new 'species in the making'. Significant new research has revealed the genetic changes involved in the host shift to tobacco (Bass *et al*., 2014), and suggests that *M. p. nicotianae* could be a key to a better understanding of the evolutionary processes that are involved in the acquisition of new hosts and subsequent speciation of phytophagous insects.

The literature on *M. persicae* (*sensu lato*) is immense. There have been extensive reviews of its ecology (van Emden *et al*., 1969; Mackauer and Way, 1976), as well as discussions of migration and spatial dynamics (Taylor, 1977) and biological approaches to control (Blackman, 1976). This aphid has also been the subject of much laboratory research including, for example, studies of anatomy and function of the gut (Forbes, 1964), nutritional studies using host plants (e.g. van Emden, 1977) and artificial diets (e.g. Mittler, 1976), and photoperiodic responses (Takada, 1982). Genetic variation and the evolution of insecticide resistance in *M. persicae* are covered elsewhere in this book (Chapters 3 and 19, this volume).

Rhopalosiphum maidis (corn leaf aphid) (Fig. 1.11)

Apterae of *Rhopalosiphum maidis* are small to medium-sized, elongate oval, olive to bluish-green aphids with short antennae and dark legs, siphunculi and cauda. They feed on the young leaves of their host plants and are a particular problem on *Zea mays*, *Sorghum bicolor* and *Hordeum vulgare*, also colonizing many other grasses and cereals in more than 30 genera including *Avena*, *Secale*, *Triticum*, *Oryza* and *Saccharum*, and also found occasionally on Cyperaceae and Typhaceae. *Rhopalosiphum maidis* is an important vector of the persistent *Barley yellow dwarf virus* (BYDV), *Millet red leaf virus* (MRLV), *Abaca mosaic virus* (AbaMV), *Sugarcane mosaic virus* (SCMV) and *Maize dwarf mosaic virus* (MDMV).

This is probably the most important aphid pest of cereals in tropical and warm temperate climates throughout the world, but the pest populations are all permanently parthenogenetic and cannot survive outdoors in regions with severe winter climates. Males occur sporadically, but for some years the sexual phase was only known to occur in Pakistan (Remaudière and Naumann-Etienne, 1991) on a

Fig. 1.11. *Rhopalosiphum maidis* – corn leaf aphid. (Photograph courtesy of S. Barbagallo.)

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species of *Prunus* native to that region, *Prunus cornuta*. The pest populations may therefore have originated from there, as one or more dispersals of permanently parthenogenetic genotypes. However, Lee *et al*. (2002) have since reported that *Prunus mume* and *P. persica* are primary hosts of *R. maidis* in Korea, so the holocycle may occur more widely than was originally thought.

Despite the apparent lack of sexual reproduction, pest populations of *R. maidis* show differences in host preference (e.g. Painter and Pathak, 1962), karyotype (Brown and Blackman, 1988) and rDNA (Lupoli *et al*., 1990), although no mtDNA variation was detected by Simon *et al*. (1995), and there is conflicting data on whether there is any allozyme variation (Steiner *et al*., 1985; Simon *et al*., 1995). Host preference differences seem quite complex in *R. maidis*, and in some cases must involve many loci, especially when they result in a high degree of host species specificity, such as that shown by the 10-chromosome form that colonizes barley and eupanicoid grasses in the northern hemisphere (Blackman and Brown, 1991; Jauset *et al*., 2000) but does not feed on maize or sorghum, which are colonized by aphids with 2n = 8. In eastern Australia, populations of *R. maidis* on eupanicoid grasses are characterized by a 9-chromosome karyotype and do not occur on maize and sorghum (de Barro, 1992). Karyotype variation is a common feature of permanently parthenogenetic aphids, but it is difficult to conceive how the complex genetic traits involved in the selection of host species could have arisen in the absence of genetic recombination. This leads one to conclude that the host-related variation now observed in pest populations of *R. maidis* may be due to multiple origins from the sexually reproducing population in Asia, rather than to mutations within parthenogenetic lineages. Further analysis of variable regions of the nuclear DNA might help to resolve this problem. The absence of the primary host and sexual reproduction means, however, that in its genetic structure, and therefore in the way it is treated taxonomically, *R. maidis* must differ fundamentally from some of the other invasive pest aphids, such as *A. pisum*, *S. graminum* and *Therioaphis trifolii maculata* (Brown and Blackman, 1988).

Rhopalosiphum padi (bird cherry–oat aphid) (Fig. 1.12)

Rhopalosiphum padi attacks all the major cereals and pasture grasses, and is probably the major pest

Fig. 1.12. *Rhopalosiphum padi* – bird cherry–oat aphid. (Photograph courtesy of Rothamsted Research; inset courtesy of U. Wyss.)

of temperate cereal crops on a world scale. Apterae of *R. padi* on grasses and cereals are broadly oval, varying in colour from green mottled with yellowish-green to olive-green, dark olive or greenish-black, and often with rust-coloured patches around the bases of the siphunculi. For a grass-feeding species, it is relatively catholic in its tastes, for as well as feeding on numerous species of Poaceae, it can colonize many other monocotyledonous plants, and some dicotyledonous ones. It is a vector of BYDV (particularly strain BYDV-PAV) and of *Cereal yellow dwarf virus*-RPV, *Filaree red leaf virus*, *Maize leaf fleck virus* and *Rice giallume virus*, as well as oat yellow leaf disease, AbaMV, *Onion yellow dwarf virus*, MDMV and several other non-persistent viruses.

Now distributed worldwide, it is difficult to pin down its origins, as it has a sexual phase on *Prunus padus* (bird cherry) in Europe and on *Prunus virginiana* (common choke-cherry) in North America, and seems equally at home on both. Halbert and Voegtlin (1998) argue for a North American origin of the genus *Rhopalosiphum* (and of BYDV), but *R. maidis* is clearly a Palaearctic species (see above), as also is *Rhopalosiphum rufiabdominale* (rice root

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aphid), which has East Asian *Prunus* species as its primary hosts. The genus as a whole, therefore, has a Holarctic distribution. *Rhopalosiphum padi* could be of Nearctic origin, as there are several closely related North American species, but it has been in Europe at least since the time of Linnaeus in the mid-18th century.

French populations of *R. padi* have been the subject of some interesting work (Delmotte *et al*., 2001, 2003; Halkett *et al*., 2005, 2006, 2008), which is discussed in more detail in Chapter 3, this volume, but should be mentioned here as it has important relevance to the taxonomic treatment of parthenogenetic lineages. Using a combination of life cycle, mtDNA sequence and microsatellite data, Delmotte *et al*. (2001) demonstrated the existence of an ancient monophyletic group of parthenogenetic lineages, with an mtDNA haplotype (I) that was quite distinct from that of all other lineages, which were of a second haplotype (II), the two haplotypes having possibly diverged for about 400,000 years. If they have been genetically isolated for that length of time, one might expect to be able to treat them as separate taxa. The microsatellite data, however, show that the nuclear genomes are not completely isolated. There is some gene flow from parthenogenetically to sexually reproducing lineages, and this is presumably mediated by the males that are still produced by the otherwise permanently parthenogenetic haplotype I lineages. The gene flow may be restricted by temporal differences in the production of sexual morphs (Halkett *et al*., 2006).

Sequence analysis of two nuclear DNA markers (Delmotte *et al*., 2003) showed rather conclusively that the haplotype I lineages originated from one or more relatively recent hybridization events between European *R. padi* and another closely related species, possibly of Asian (or North American?) origin, which remains to be identified. This is the first clear evidence for the hybrid origin of permanent parthenogenesis in an aphid, and it raises interesting questions about the taxonomic status of *R. padi*. These can only be resolved by further studies, which also need to take into account other apparently undescribed taxa in the *R. padi* group that have been introduced to Australia (Hales and Cowen, 1990) and New Zealand (Bulman *et al*., 2005a,b).

Schizaphis graminum (greenbug) (Fig. 1.13)

Schizaphis graminum was the first introduced aphid to have a significant economic impact in the

Fig. 1.13. Ovipara of *Schizaphis graminum* – greenbug. (Photograph courtesy of B. Chaubet and INRA.)

main winter wheat areas of North America. The small, yellowish- to bluish-green apterae with pale, dark-tipped siphunculi feed on the leaves of grasses and cereals, often causing yellowing and other phytotoxic effects. They restrict their feeding almost exclusively to Poaceae, but species in many genera are attacked, including *Agropyron*, *Avena*, *Bromus*, *Dactylis*, *Eleusine*, *Festuca*, *Hordeum*, *Lolium*, *Oryza*, *Panicum*, *Poa*, *Sorghum*, *Triticum* and *Zea*. Several important viruses are vectored, including BYDV (especially strain BYDV-SGV), MRLV, SCMV and MDMV.

Schizaphis graminum is a Palaearctic aphid, possibly of Middle Eastern or central Asian origin, now distributed widely through southern Europe, Asia, Africa and North and South America. A problem with interpreting early records is that when *M. dirhodum* was first introduced to a region, it was sometimes misidentified as 'greenbug'. Records of *S. graminum* from Australia and the Philippines all seem to be referable to the Asian species, *Schizaphis hypersiphonata*. This feeds particularly on *Digitaria*, but can occur on other species of Poaceae, and is recorded on wheat in the Philippines, but it does not have the same phytotoxic effects as the greenbug. Records of *S. graminum* on grasses in Western Europe are now thought to apply to other species (Tambs-Lyche, 1959; Stroyan, 1960, 1984; Pettersson, 1971).

The history of the greenbug in North America is quite well documented, and is an interesting example of multiple introductions and their consequences. For many years, this story was confused, partly because of the description of a series of biotypes, but it has been made much clearer by DNA studies. The 'biotype concept' was useful to plant

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breeders, but the term 'biotype' referred only to host resistance-breaking traits and was perhaps given greater significance than it deserved. These traits could be identified and studied when they first appeared, because aphids carrying them could be isolated and maintained in clonal cultures. A greenbug biotype was thus any genotype that had a particular resistance-breaking trait. In the absence of a sexual phase, this might be a single clone, but it is now clear that sexual morph production and genetic recombination occurs regularly in North American greenbug populations (Shufran *et al*., 1991, 1997), so that there is great genetic diversity, and it follows that field populations may therefore have these traits portrayed in numerous genetic backgrounds (Anstead *et al*., 2002).

The original introduction in about 1882 was of a highly virulent genetic stock, very damaging and phytotoxic to wheat and barley. In 1961, a very successful wheat variety (DS-28 A) carrying a gene for greenbug resistance was found to be susceptible to a 'new form' of the aphid, designated as biotype B to distinguish it from the original biotype A (Wood, 1961). Then, in about 1968, another 'new form' appeared, designated as biotype C, this one for the first time inflicting severe damage to cultivated sorghum. Since then, a series of new 'biotypes' (or more accurately, resistance-breaking traits) have been described, and many more are present in populations on uncultivated grasses (Burd and Porter, 2006).

Shufran *et al*. (2000) compared mtDNA sequences of clones of *S. graminum* representing all the available North American 'biotypes', and found that they fitted into three distinct clades, the divergence of which pre-dated modern agriculture. These must therefore represent at least three separate introductions into North America. The form originally introduced ('biotype A') reproduced sexually in the northern states (Webster and Phillips 1912), and was presumably represented by a clone started in 1958 (the 'NY isolate') and by clones with the resistance-breaking traits F and G, which clustered with it to form clade 2 (Shufran *et al*., 2000). The second introduction (clade 3), with resistance-breaking trait B, has different probing behaviour and is more damaging to susceptible wheat and barley (Saxena and Chada, 1971). It reproduces possibly only parthenogenetically in North America, so this clade may represent a single parthenogenetic lineage. Shufran *et al*. (2000) found that it had a very similar mtDNA sequence to a sample from Germany, but it has subsequently emerged that the German sample originated from North America (T. Thieme, unpublished). The third introduction, originally recognized as the sorghum-adapted biotype C, seems to have been the source population for all the remaining resistance-breaking mutations (represented by biotypes G, E, K, I and J), all of which have very similar mtDNA sequences (clade 1). This sorghum-adapted form, which has for many years now been the predominant form on wheat and sorghum in North America, differs morphologically from the others in several respects (V.F. Eastop, unpublished) and may have come from further south in Europe or Asia, as suggested by its predilection for sorghum and by its ability to produce sexual morphs and overwinter as eggs at more southerly latitudes in the USA. It is still unclear whether any interbreeding occurs between members of clades 1 and 2, or whether isolating mechanisms exist between them.

One other North American isolate, 'biotype H', is distinct from the rest (Anstead *et al*., 2002), and both its morphology and mtDNA sequence indicate that it is probably another introduced European species, *Schizaphis agrostis* (Kati *et al*., 2013).

The three clades have probably diverged sufficiently to provide a range of discriminant characters, using both multivariate morphometric and DNA diagnostics, and clades 1 and 2 have all the necessary attributes to warrant their description as subspecies according to the guidelines proposed earlier in this chapter. This would provide a sounder basis for further work on the genetics and evolution of *S. graminum* in North America.

Sitobion avenae (grain aphid) (Fig.1.14)

The concept of the genus *Sitobion* has recently changed somewhat so that it now includes fewer species, all of which are Eurasian or African, and a greater proportion of which are grass feeders. The ancestral life cycle of the genus probably involves host alternation from Rosaceae to grasses, as in the related genus *Metopolophium*. *Sitobion* are superficially very like *Macrosiphum*, particularly in having similar siphunculi with polygonal reticulation, but this feature may have developed independently in these two genera. A closer relationship to *Metopolophium* is also supported by the karyotype, which is 2n = 16 or 18 in both *Sitobion* and *Metopolophium*, whereas *Macrosiphum* usually have 2n = 10.

The majority of *Sitobion* species no longer have host alternation, and *S. avenae* is one of these.

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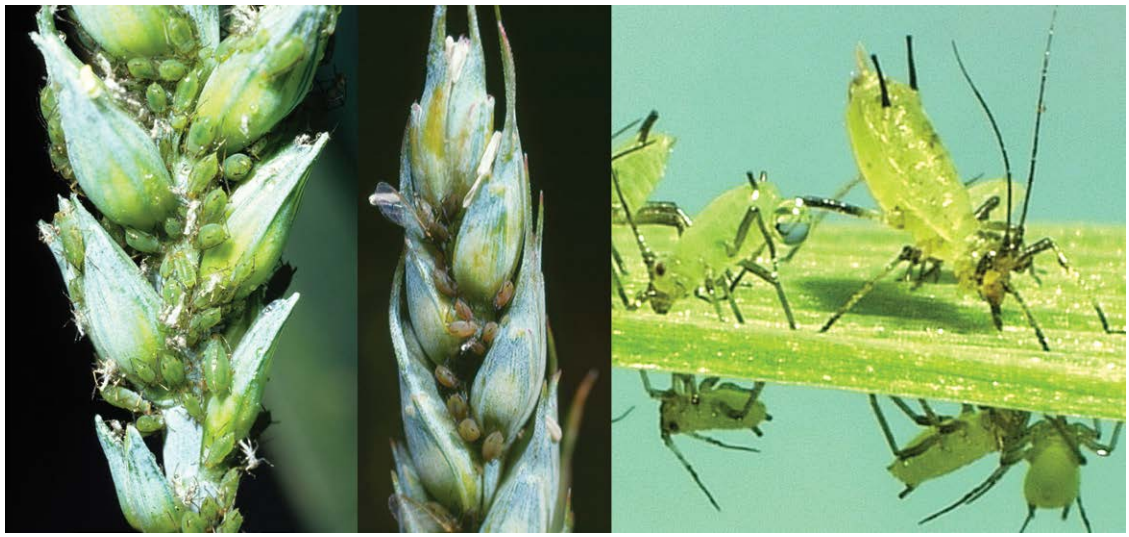

Fig. 1.14. *Sitobion avenae* – grain aphid. (Photograph left courtesy of A.M. Dewar; photograph right courtesy of U. Wyss).

Its apterae on grasses and cereals are medium-sized, broadly spindle-shaped, yellowish-green to dirty reddish-brown, sometimes rather shiny, with black antennae and siphunculi and a pale cauda. It colonizes numerous species of Poaceae, including all the cereals and pasture grasses of temperate climates, and can also feed on many other monocotyledonous plants. As well as the direct damage caused to cereals by feeding on the developing ears, *S. avenae* is an efficient vector of BYDV (especially strains BYDV-PAV and BYDV-MAV), both within and between crops. Probably European in origin, *S. avenae* now occurs throughout the Mediterranean area, eastwards to India and Nepal, in northern and southern Africa and in North and South America. Records from eastern Asia are probably all referable to *Sitobion miscanthi*, a closely related species indigenous to the Far East that has spread to Australia, New Zealand and several Pacific islands, including Hawaii. Choe *et al*. (2006) compared variation in morphology and in an mtDNA sequence of *S. avenae* from England and North America with *S. miscanthi* and another close relative, *Sitobion akebiae*, and concluded that the latter two should be treated as synonyms of *S. avenae*. This has created some confusion, with populations on wheat in China being identified as *S. avenae* by some authors (e.g. Xu *et al*., 2011; Xin *et al*., 2014; Zhang *et al*., 2016) and as *S. miscanthi* by others (e.g. Wang *et al*., 2009; Li *et al*., 2011). Hales *et al*. (2010) concluded that there was insufficient evidence for this synonymy, and that a more thorough study of oriental *Sitobion* was needed. It is possible that there is a complex situation in China involving both introduced *S. avenae* and indigenous *S. miscanthi*, which could explain the high levels of genetic diversity revealed in a recent study using microsatellite markers (Xin *et al*., 2014). The complete mitochondrial genome has now been published by Chinese workers (Zhang *et al*., 2016), and it seems important to confirm the identity of the sample(s) used for this analysis.

Sitobion avenae produces sexual morphs and lays overwintering eggs on many species of Poaceae in Europe, but also continues reproducing parthenogenetically through the year wherever winters are mild enough. Studies of the genetic structure of populations in southern England (de Barro *et al*., 1995; Sunnucks *et al*., 1997a) and France (Haack *et al*., 2000) have produced some unexpected results (described in more detail in Chapter 3, this volume), which have certain taxonomic implications. This work has shown: (i) that based on analysis of microsatellite DNA, *S. avenae* sampled in southern England fell into three genotypic groups, apparently almost non-interbreeding, although there was evidence of high levels of genetic recombination within each group; (ii) two of these groups showed complete host specificity, even when collected at the same time and place, one of them occurring only on wheat and the other only on cocksfoot grass (*Dactylis glomerata*); (iii) the genotypic group

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found only on *Dactylis* had introgressed microsatellite alleles and mtDNA from the related species *Sitobion fragariae* (blackberry–cereal aphid), which colonized *Dactylis* but rarely occurred on wheat; and (iv) microsatellite analysis of French (Brittany) populations of *S. avenae* showed that there were host-adapted genotypes on maize differing from those on adjacent wheat and barley, but also revealed the existence of some very common host-generalist clones that persisted parthenogenetically between years.

Host-related genetic divergence and potential incipient speciation thus seem to be going on in Western European *S. avenae*, in a way comparable to that found in *A. pisum*, but in the case of *S. avenae* there is an additional element, the introgression of alleles from a related species, which may also include genes influencing aphid–host interactions. Again, the question remains, are the observed divergences transient local population phenomena or are they representative of longer-term evolutionary trends, and manifest over a wider geographical area?

Therioaphis trifolii (alfalfa aphid or yellow clover aphid) (Fig. 1.15)

Therioaphis trifolii is unusual among crop pest aphids in being a member of the subfamily Calaphidinae, most genera of which live on deciduous trees (Table 1.1). It has the characteristic features of this subfamily that set it apart from the other species discussed in this chapter, such as a knobbed cauda and a bi-lobed anal plate. The members of the genus *Therioaphis* are all Palaearctic, and all live on various species of Fabaceae. Apterae of *T. trifolii* are distinctive, pale yellow or greenish-white, rather shiny, with rows of dorsal tubercles, pigmented light or dark brown and bearing capitate hairs. It seems to be by far the most polyphagous species in the genus, as European populations can be found on numerous species of Fabaceae in the genera *Astragalus*, *Lotus*, *Medicago*, *Melilotus*, *Onobrychis*, *Ononis* and *Trifolium*. However, to judge from the host preferences shown by genotypes introduced to other parts of the world, there is also in this species a considerable amount of intraspecific genetic heterogeneity in the utilization of these host plants.

Therioaphis trifolii is a native of Europe, the Mediterranean area and South-west Asia, but in one form or another it now occurs as a pest of legumes in North and South America, South Africa,

Fig. 1.15. *Therioaphis trifolii maculata* – spotted alfalfa aphid. (Photograph courtesy of B. Chaubet and INRA.)

Japan and Australia. The history of introductions of *T. trifolii* into North America has some remarkable parallels with that of *S. graminum* discussed above, and is an excellent example of the consequences of founder effects, worthy of inclusion in any textbook. The story has been told before (Blackman, 1981), so will only be summarized here. Two morphologically distinct forms of *T. trifolii* occur in North America, evidently due to separate introductions, about 70 years apart, of genotypes with different specific host associations: (i) the yellow clover aphid (YCA), which feeds almost exclusively on *T. pratense*; and (ii) the spotted alfalfa aphid (SAA, also known as *T. trifolii maculata* – or in North America, simply as *T. maculata* – which feeds mainly on, and can be very injurious to, lucerne (alfalfa). Although originally introduced, respectively, to eastern and south-western USA, these two forms now occur sympatrically and have annual sexual reproduction in the northern states, yet are effectively isolated by their association with different host plants and thus function as separate species.

SAA has subsequently spread to South America, South Africa, Australia, New Zealand and Japan (Blackman and Eastop, 2000). In Australia, it now

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coexists with a third form, the spotted clover aphid (SCA), which preferentially colonizes subclover, *Trifolium subterraneum*. SCA can be distinguished from SAA morphologically and by RAPD-PCR, and the differences in mtDNA sequence between these two forms indicate that SCA is a separate, more recent immigrant to Australia (Sunnucks *et al*., 1997b). It is possible that SCA is present also in South Africa, as populations there are reported to colonize *Trifolium* as well as *Medicago*.

If these three forms are at all representative of the populations from which they originated, then there must be considerable partitioning of resources and subspecific structuring of *T. trifolii* on its different host plants in Europe and the Middle East. Hopefully, this will be the subject of future work. However, even on present evidence, there seems ample justification for giving SAA and SCA the status of subspecies. SAA can therefore become *T. trifolii maculata*, but SCA has yet to be formally named.

Conclusions

Studies of intraspecific variation and evolution of pest aphids have now reached a very interesting point, where enough light has been shed on some of the important pest species to show the way forward. Also, molecular tools and analytical methods are now available to cope with the complex population genetics of insects with variable life cycles. It has long been suspected that most major pest aphids show intraspecific partitioning of resources (Blackman, 1990), and there is now plenty of evidence of this among some of the best-studied species. It seems that speciation processes, where these involve assortative mating due to differential selection among potential host plants, can: (i) progress very rapidly; and (ii) take place in the face of gene flow, leading to situations where subspecies can be recognized by biological differences, yet show minimal genetic divergence of markers that are unlinked to host-related traits. If this is so, then some reassessment may be needed of the taxonomic significance of genetic distance parameters calculated from molecular data.

This makes it all the more important not to lose sight of the continuing need for morphotaxonomy. The new knowledge always needs to be related to the old – with the 'old' mainly represented by museum specimens and a taxonomic literature based largely on morphology. We find it alarming that some population geneticists and others studying aphid variation are still not depositing voucher specimens in the major insect collections, especially when clonal reproduction makes it possible to have representative individuals of the actual genotypes preserved for morphological study. Multiple discriminant analysis and the use of canonical variates, in which clones or samples from clearly defined populations are used as the groups in the analysis (it is important to note that there should be no a priori grouping by taxon or host plant), has proved to be a very powerful technique for partitioning the variance into its environmental and genetic components, and thus demonstrating genetic differences between closely related aphid taxa (Blackman, 1992), and even between different genotypes (Blackman and Spence, 1994). It is especially useful in conjunction with other methods (e.g. Blackman *et al*., 1995; Blackman and de Boise, 2002; Rakauskas *et al*., 2014). Developments in image analysis now make the acquisition of morphometric data far quicker and easier, and it is hoped that future work on aphid species complexes using molecular methods will always aim to include parallel morphological studies.

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2 Aphid Genomics and its Contribution to Understanding Aphids as Crop Pests

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Introduction

The International Aphid Genomics Consortium (IAGC) was 'born' at an inaugural meeting in Paris in June 2003, called to coordinate advances in developing aphids as a model system for evolutionary genetics and genomics, to cut down on unnecessary redundancy and to enhance the likelihood of securing funds for a large-scale project. The ultimate goal of this network was to develop the aphid model system to the same level of molecular, cell and developmental biological understanding as other model insects. To this end, it was decided to start by securing funds to sequence the *Acyrthosiphon pisum* (pea aphid) genome and the Steering Committee submitted a proposal that was funded by the National Human Genome Research Institute, which was part of the National Institutes of Health in the USA. After two annotation workshops and a coordinated international effort of manual annotation of specific gene families by experts (list in AphidBase (http://bipaa.genouest.org/is/aphidbase/); Legeai *et al*., 2010b), the genome was finally published in 2010 (International Aphid Genomics Consortium, 2010). That this would be a rich source of new studies on aphids was already evidenced by the publication of a Special Issue of *Insect Molecular Biology* (Volume 19, Supplement 2), also in 2010, which featured 23 'companion' papers reporting the use of the genome data in diverse areas, by a range of 'aphidologists'.

The subsequent use of the *A. pisum* genome was greatly facilitated by its availability online at AphidBase in a user-friendly format, allowing many aspects of aphid biology and comparisons of *A. pisum* with other aphid species (e.g. Ollivier *et al*., 2010). The paper reporting the genome sequence has been referenced around 300 times (as of February 2016). Since the publication of the *A. pisum* genome, genome sequences for *Myzus persicae* (peach–potato aphid) have also been made available on AphidBase and many other genome resources for other aphid species reported (e.g. Bai *et al*., 2010). The IAGC has continued to meet (the 8th and last meeting being in the UK, at Rothamsted Research, in January 2013) and promote aphid research.

Having aphid genomes has inevitably led to other genomic resources, such as the generation of more than 550,000 cloned full-length cDNAs (Shigenobu *et al*., 2010b), arrays, high through-put sequencing, RNAi and other techniques to make sequence changes *in vivo* and spin-off benefits for protein studies (e.g. Cilia *et al*., 2011b). In addition, the aphid genome has been used in wider studies, such as understanding the evolutionary position of the insects among arthropods and the relationship between insect Orders (Yeates *et al*., 2012). The combination of insect genomes now available makes many comparative studies possible. For a review of how 'omics' technologies have been integrated and applied in insect biology,

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see Boerjan *et al*. (2012), and for a review of best practice in insect genome sequencing, see Richards and Murali (2015).

In this chapter, we will consider some examples of how aphid genomes have contributed to understanding aphids as crop pests. It will not be an exhaustive review, and where possible we have cross-referenced other chapters in this book, which themselves demonstrate the all-pervading use of aphid genomes/genomics/'omics.

Aphid Genome Properties

The sequence of the *A. pisum* genome reveals that it is made up of 464 Mb, with the lowest GC (guanine-cytosine) content of any insect genome sequenced previously and with more than 34,000 predicted genes (International Aphid Genomics Consortium, 2010). A comparison of the genome with that of other insects is shown in Table 2.1. Subsequent early analyses of the genome sequence allowed its functional properties to be determined and compared to other aphid species. Thus, using *A. pisum* as a reference genome and comparing it with expressed sequence tag (EST) data from three other aphid species Ollivier *et al*. (2010) showed that a fraction of the genes had evolved very fast, often associated with duplication events. Furthermore a phylogenetic analysis of all of the predicted proteins in *A. pisum*, and their homologues in 13 other sequenced arthropods, gave a phylome that also suggested multiple gene expansions specific to aphids (Huerta-Cepas *et al*., 2010). It is interesting that a similar expansion is seen for genes that aphids have acquired from fungi. Thus, following the finding that the *A. pisum* genome has genes for carotenoid biosynthesis, reflecting an ancestral transfer from a fungus, Novakova and Moran (2012) explored the evolution of the carotene desaturase gene family within aphids, using sequences retrieved from 34 species (representing numerous deeply diverging lineages of aphids). This showed that all aphids had at least one copy of the gene and some had up to seven, with species of Macrosiphini, which often show colour polymorphisms, typically having the largest number. This ability for aphid genes to evolve relatively quickly and to duplicate may have been important for their colonization of different host plants and their subsequent pest status. It is interesting that Ollivier *et al*. (2012) used the *A. pisum* genome and ESTs from five other aphid species to show that the evolutionary rate of genes in aphids is affected by their reproductive mode.

Bickel *et al*. (2013) used low-coverage genome resequencing of 21 clonal *A. pisum* lines from lucerne in North America to show that there had been widespread selection across coding and non-coding DNA in the genome, a first step to understanding the genetic diversity and evolutionary pressures on the genome. It has been concluded that gene expansion in aphids has largely not involved transposable elements (TEs), although approximately 38% of the genome is composed of TEs. The *A. pisum* genome has subsequently

Table 2.1. Comparison of *Acyrthosiphon pisum* genome with other insect species.

Species	Estimated size (Mb)	Estimated number of genes	Accession Number
Acyrthosiphon pisum	447	10,249	ABLF000000000
Aedes aegypti	1,318	15,419	AAGE00000000
Anopheles gambiae	239	13,111	AAAB00000000
Apis mellifera	233	10,157	AADG00000000
Bombus terrestris	248		AELG00000000
Bombyx mori	530	18,510	BABH00000000
Camponotus floridanus	240	17,064	AEAB00000000
Danaus plexippus	273	16,866	AGBW00000000
Drosophila melanogaster	137	13,718	AABU00000000
Harpegnathos saltator	330	18,564	AEAC00000000
Heliconius melpomene	269	12,669	CAEZ00000000
Locusta migratoria	6.3 Gb	17,307	AVCP000000000
Nasonia vitripennis	240	17,279	AAZX00000000
Pediculus humanus	108	10,773	AAZO00000000
Tetranychus urticae	90	18,414	CAEY00000000
Tribolium castaneum	152	16,404	AAJJ00000000

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contributed to methods for identifying TEs in genome sequences (Flutre *et al*., 2011) and subsequent analyses of TEs in other aphids, such as piggyback-like elements in *Aphis gossypii,* the cotton aphid or melon aphid (Luo *et al*., 2011), and mariner-like elements in *Aphis glycines,* the soybean aphid (Mittapalli *et al*., 2011).

The paper announcing the *A. pisum* genome (International Aphid Genomics Consortium, 2010) pointed out that this aphid had a full complement of DNA methylation genes and that there were two broad classes of genes with different methylation status. Subsequent studies have shown that in insect genomes, methylation is targeted primarily to genes with possible roles in mRNA splicing and regulation of transcription (Glastad *et al*., 2011). The latter was thought for a long time to be true only for vertebrates, although interestingly, as early as 1989 it had been shown that changes in DNA methylation were associated with loss of insecticide resistance in *M. persicae* (Field *et al*., 1989). This was subsequently demonstrated to be because the change in methylation affected the expression of amplified esterase genes, a good example of how understanding genome events could be linked to an important phenotype for crop protection.

Polyphenism and Reproduction

Polyphenisms are a major reason for the success of the insects (Simpson *et al*., 2011), allowing them to partition their life-history stages (larvae dedicated to feeding and growth and adults dedicated to reproduction and dispersal), to adopt different phenotypes in response to environmental change (seasonal morphs), to cope with temporally heterogeneous environments (dispersal morphs) and to partition labour within social groups (the castes of eusocial insects). This is especially true in aphids (Chapter 4, this volume) that exhibit many types of polyphenism and which are likely to have played a major role in their adaptation to different niches and their resulting pest status.

Polyphenism is the production of different phenotypes from the same genotype, and genomics has contributed much to our understanding of this phenomenon in aphids. For example, gene expression analysis has identified genes involved in the production of alate/apterous morphs in *A. pisum* (Brisson *et al*., 2010), and similar studies have identified genes underlying wing-morph determination in *Megoura crassicauda*, even in the absence of a genome (Ishikawa *et al*., 2012a). A role for the aphid 'foraging' gene in polyphenism has been identified by studies showing that expression of this gene changes at key stages of development, and may promote the shift from a sedentary to an exploratory behaviour (Tares *et al*., 2013). Genomics have also played a very important role in understanding reproductive polyphenism. For example, in *A. pisum* high-throughput sequencing and bioinformatics have identified microRNAs that likely play a crucial role (Legeai *et al*., 2010a), and gene-expression profiling has suggested that expanded aphid *piwi* and *ago3* genes have distinct roles in asexual and sexual reproduction (Lu *et al*., 2011). The *A. pisum* genome has also allowed the identification of genes involved in the juvenile hormone (JH) pathway, and expression levels of genes upstream and downstream of JH action have shown that JH esterase is significantly higher in aphids reared under short-day conditions, suggesting that the JH degradation pathway may be responsible for the lower JHIII titre in aphids exposed to short days, leading to the production of sexual morphs (Ishikawa *et al*., 2012b). A cDNA microarray experiment has also shown that the regulation of transcripts involved in JH synthesis and signalling plays a key role in the reproductive mode switch (Le Trionnaire *et al*., 2012).

A transcriptomics/gene ontology study of genes involved in the onset of the divergent mechanisms that determine sexual versus asexual modes in *A. pisum* suggested that both involved common genetic programmes but diverged by adapting the specificity of expression in germ cells and oocytes (Gallot *et al*., 2012). However, another study on the key maternal and axis patterning genes has concluded that the novel asexual developmental pathway in aphids is not a modification of an ancestral system but has resulted from two very different mechanisms occurring in a single species (Duncan *et al*., 2013). That changes in the expression of individual genes in different phenotypes can be identified is likely to play a major role in understanding how the 'switch' from one phenotype to another occurs. However, understanding what is responsible for the changes in gene expression is still a challenge, and the molecular basis for this epigenetic inheritance in aphids, and how this type of inheritance system could have evolved, are still unanswered questions. For a review of epigenetic phenomena in aphids and recent progress toward elucidating the molecular basis of epigenetics in aphids, see Srinivasan and

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Brisson (2012). These authors have suggested that the discovery of a functional DNA methylation system, a small RNA system and an expanded set of chromatin-modifying genes in aphids provide a platform for analysing these pathways in the context of aphid plasticity, noting that aphids are an emerging model system for studying the molecular epigenetics of polyphenisms.

Host Location

Aphids have evolved to colonize a wide range of hosts, including many crops, which is why they are considered as 'pests'. The location of suitable hosts and the avoidance of non-hosts relies on both visual and olfactory cues, the latter being the subject of a widely studied area of 'chemical ecology', which has established many of the plant volatiles, or semiochemicals, that aphids use as signals (Chapter 8, this volume).

The functioning of the aphid visual system is still not well understood but, in one study, intracellular recordings showed that responses of *A. pisum* to monochromatic light involved green receptors and there was an additional sensitivity to short-wave light. The presence of green receptors was supported by using comparative genomics to identify genes encoding the necessary *A. pisum* opsins (Döring *et al.*, 2011).

Understanding the molecular basis of insect olfaction has been greatly facilitated by having insect genomes. For example, the identification of genes encoding odorant-binding proteins (OBPs) and chemosensory proteins (CSPs) that are involved in the first interception of semiochemicals has been possible because these proteins have regular patterns of cysteine residues, and sequences encoding these patterns can be found in insect genomes using an appropriate algorithm, MotifSearch (Fig. 2.1). For aphids, this was done first for the *A. pisum* genome (Zhou *et al.*, 2010) and has now been extended to many other aphid species. For *A. pisum*, the annotation identified 12 OBP and 10 CSP genes that have more, and longer, introns in each gene than those of any other insect species (Zhou *et al.*, 2010). We have used the *A. pisum* OBP and CSP gene sequences in BLAST (basic local alignment search tool) searches against transcriptome data of other aphid species to identify OBP and CSP homologues, demonstrating highly conserved OBPs between the aphid species (unpublished; Fig. 2.2). For *A. gossypii*, transcriptome analysis has been used to identify OBP transcripts overexpressed in the antennae (in comparison to the bodies) and highly expressed in winged aphids compared to wingless morphs, suggesting a role in host location (Gu *et al.*, 2013). The genome annotation of *A. pisum* olfactory proteins has also facilitated

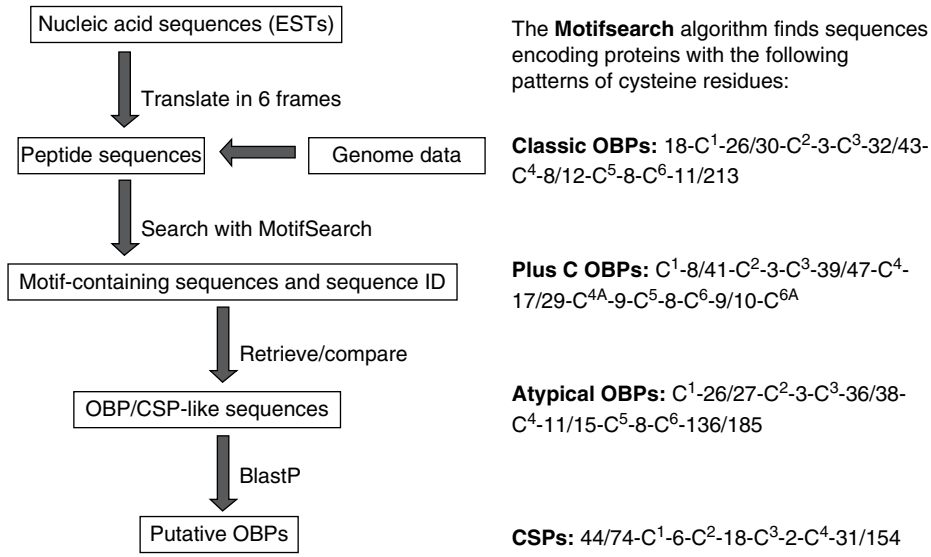

Fig. 2.1. Identification of sequences encoding putative odorant-binding proteins (OBPs) and chemosensory proteins (CSPs) in insects.

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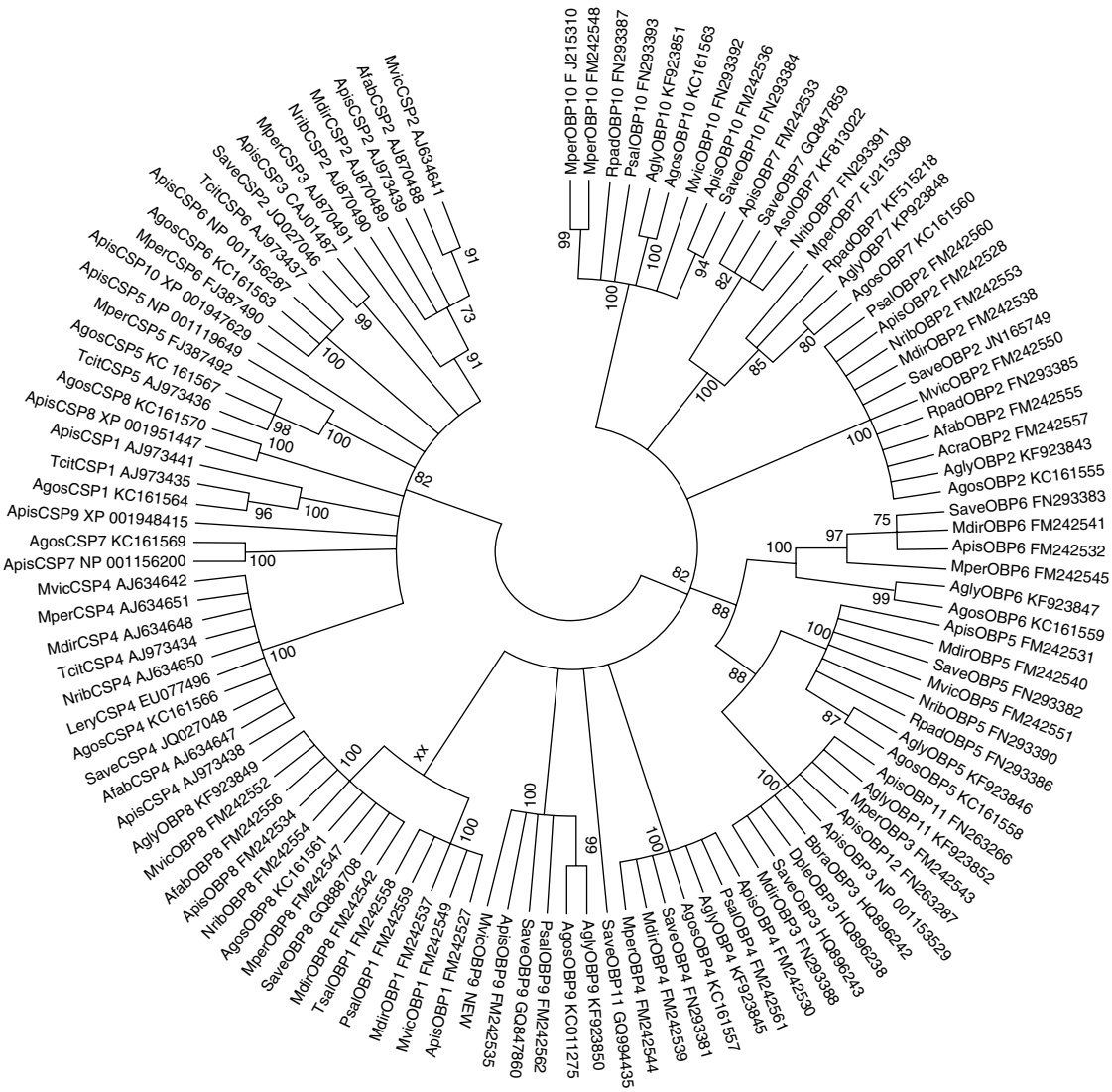

Fig. 2.2. Aphid OBPs and CSPs identified from genomic data sets. Acra = *Aphis craccivora*; Afab = *Aphis fabae*; Agly = *Aphis glycines*; Agos = *Aphis gossypii*; Apis = *Acyrthosiphon pisum*; Asol = *Aulacorthum solani*; Bbra = *Brevicoryne brassicae*; Dpla = *Dysaphis plantaginea*; Lery = *Lipaphis erysimi*; Mper = *Myzus persicae*; Mdir = *Metopolophium dirhodum*; Mvic = *Megoura viciae*; Nrib = *Nasonovia ribisnigri*; Psal = *Pterocomma salicis*; Rpad = *Rhopalosiphum padi*; Save = *Sitobion avenae*; Tcit = *Aphis* (*Toxoptera*) *citricidus*; Tsal = *Tuberolachnus salignus*.

other research on aphid olfaction and their interactions with host plants and predators (Tagu *et al*., 2010; Sun *et al*., 2011; Vandermoten *et al*., 2011; Ahn *et al*., 2012; Savchenko *et al*., 2013).

Once a semiochemical has been intercepted by OBPs or CSPs or diffused into the lymph, it has to trigger the behavioural response by interacting with odorant receptors (ORs). The identification of ORs and gustatory receptors (GRs) was done for *A. pisum* in 2009 and showed that in this aphid there has been large gene family expansions and adaptive evolution of the receptors (Smadja *et al*., 2009). Then Smadja *et al*. (2012) used high-throughput sequencing and screening for divergence under selection at 172 loci to identify a handful of loci with high differentiation among

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host races of *A. pisum* and corresponding to ORs and GRs, a first step in understanding ecological speciation.

Pickett *et al.* (2012) have discussed how using the new genomic approaches to understand insect molecular recognition may allow the exploitation of reception and detection as tools for the deception of pests and beneficial insects in pest control strategies.

Aphid–Plant Interactions During Feeding

The way aphids locate suitable host plants and feed on them is discussed above and in Chapter 9, this volume. However, one area that is particularly important for aphids to be crop pests is that they are able to suppress plant defences and feed, causing both direct damage and the transmission of plant viruses. The way in which aphids overcome the defence mechanisms has become a very active area of research, which has benefitted greatly from genome/genomic approaches, especially for the identification of 'effectors'. It has been assumed that the interaction between aphids and their host plants is functionally analogous to plant–pathogen interactions, and Carolan *et al.* (2011) used a dual transcriptomic-proteomic approach to generate a catalogue of candidate effector proteins from the salivary glands of *A. pisum*, showing that many of the proteins had been characterized previously in phytopathogenic organisms (e.g. nematodes and fungi) and suggesting the evolution of common solutions to the plant-parasitic lifestyle.

Hogenhout and Bos (2011) predicted that tools for high-throughput effector identification and functional characterization in combination with RNAi would enable identification of effector/target combinations that could lead to novel strategies for pest resistance in plants. Since then, many *M. persicae* and *A. pisum* salivary proteins with a signal peptide necessary for functioning as an effector have been identified and some molecules such as MP10 and MP42 from *M. persicae* and C002 from *M. persicae* and *A. pisum* partially functionally characterized (Rodriguez and Bos, 2013). This work is now being extended to use high-throughput sequencing (Illumina) of salivary gland transcripts to identify the related effectors in another aphid species, *Macrosiphon euphorbiae* (Atamian *et al.*, 2013). In this study, transient expression of two of the candidate effectors in *Nicotiana benthamiana* was able to suppress the defences of the plant and increase the fecundity of the aphids feeding on the plant. More recently, sequencing of effector genes has shown that these effectors are fast evolving and are likely, under positive selection, to promote the colonization of specific plant species (Pitino and Hogenhout, 2013). Rodriguez and Bos (2013) have provided an overview of recent advances in aphid effector biology, acknowledging the role of genome and transcriptome data in this new and exciting area of research.

Growth and Development

The methods used to measure aphid growth and development and the limitations of using such measurements to predict field populations and likely pest status are discussed in Chapter 5, this volume. However, the understanding of the biochemical/molecular basis of development has grown recently as more genomics techniques have been applied. In a survey of developmental genes involved in fundamental processes such as body plan and organogenesis in *A. pisum*, Shigenobu *et al.* (2010a) reported that many gene duplications, gene losses and pathway modifications had occurred in several families involved in development. This is a rare occurrence in animal genomes and the authors speculated that there might be a role in the generation of different morphology, life cycles and polyphenism. Basic helix-loop-helix (bHLH) proteins play a role in developmental processes in a wide range of higher organisms, and Dang *et al.* (2011) identified 54 bHLH genes in *A. pisum* belonging to 37 gene families and with orthologues in other insects, although the precise role in the regulation of insect/aphid development remains to be elucidated. Li *et al.* (2013) intriguingly showed that family-B G protein-coupled receptors (known to play a vital role in growth and development) had, in insect evolution, undergone species-specific expansions and episodic duplications.

Of course, it is known that many hormones play a role in the control of development and reproduction, and Christiaens *et al.* (2010) identified *A. pisum* genes encoding P450s, responsible for the biosynthesis of 20-hydroxyecdysone (controls and coordinates development in insects), and nuclear receptors thought to mitigate the effect of 20-hydroxyecdysone on the transcription of genes involved in moulting/metamorphosis.

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Immunity

To be a 'successful' species, any insect must be able to defend itself against a range of parasites/pathogens, and this may be especially true for pest insects that have to survive in the crop, where the nature of the monoculture may favour the location of hosts by parasites and where biological control agents may be deployed. To do this, insects have an innate immune system involving melanization, phagocytosis and the synthesis of potent antimicrobial peptides/polypeptides that are secreted into the haemolymph. It is known that the insect system shares many of the basic characteristics of the mammalian acute phase response, especially at the level of controlling gene expression, where similar *cis*-regulatory and inducible transactivators appear to play key functions. However, there is evidence that aphids have a reduced antibacterial defence, with *E.coli* K-12, usually cleared from the haemolymph in other insects, growing exponentially in *A. pisum* and killing them within a few days (Altincicek *et al*., 2011). In this respect, it is interesting that the first annotation of the immune and stress genes in the *A. pisum* genome showed that this aphid appeared to be missing genes present in other insects and thought to be critical for the recognition, signalling and killing of microbes (Gerardo *et al*., 2010). The authors of this study recognized that the limitations of the aphid immune system might be aphid specific, perhaps as a result of their association with microbial symbionts facilitating their survival without strong immune protection. The role of symbiont-mediated defence in *A. pisum*, which protects against parasitic wasps and fungi, and that such non-immunological defences may be important in interacting with immune system-based defences, is discussed by Parker *et al*. (2011). Vilcinskas (2013) has suggested that insect immunity genes can be lost when alternative defence strategies, with a lower fitness penalty, have evolved. This might apply to aphids that have co-evolved with their symbionts (see later) and where their phloem-feeding habit may make them less likely to ingest microbial pathogens. The lack of immunity-related genes in aphids has been discussed by Vilcinskas (2013), who suggested three hypotheses to explain this: (i) a diet limited in microbes; (ii) the symbionts supply antibacterial defences; and (iii) aphids invest in 'terminal reproduction' rather than immunity following a bacterial challenge.

Virus Transmission

Many aphids are considered to be important crop pests but do little direct feeding damage; rather, it is their ability to transmit viruses that affect crop plants that makes them able to do serious damage to crop yields. This is true for many virus–aphid–crop combinations and involves a variety of transmission modes (Chapter 15, this volume). In the UK, aphids transmitting sugar beet, brassica and cereal viruses are among the most important crop pests. Aphid proteins putatively involved in virus transmission have been identified, and can act as biomarkers for transmission competence (Cilia *et al*., 2011a). For *Schizaphis graminum* (greenbug), nucleotide and EST database searches have been used to show that some of their biomarkers are conserved in two aphid species and in the whitefly, *Bemisia tabaci* (Cilia *et al*., 2012), suggesting that it is possible to have easily identifiable markers for the ability to transmit viruses. This has a potential practical application for predicting if the insect will be an efficient vector and therefore needs to be controlled in crops. There have been many studies of aphid proteins/peptides thought to be involved in virus transmission, but to date many have not been validated. For example, it has been suggested that a chaperonin, GroEL (synthesized in aphids by a symbiont), binds to virus in the haemolymph and facilitates virus transmission, but Bouvaine *et al*. (2011) have failed to detect it in aphid haemolymph, fat body or gut and conclude that it is unlikely to contribute to transmission. More recently, Tamborindeguy *et al*. (2013) have used PCR amplification and sequencing to show that in *S. graminum* both cyclophilin A and B proteins interact with the *Cereal yellow dwarf virus* that it transmits and are important but not sufficient to mediate virus transport from the hindgut lumen to the haemocoel.

Aphid Control, Insecticides and Resistance

The control of aphids using chemical aphicides on a range of crops is considered in Chapter 18, this volume, and the resulting problems of the aphids evolving resistance to these compounds is detailed in Chapter 19, this volume. There is no doubt that aphids are one of the best-studied systems for studying the development of resistance, and latterly this has been greatly facilitated by having genomic resources.

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Indeed, some of our most detailed understanding of how increased metabolism and changes in the genes encoding insecticide targets can give rise to resistance comes from aphid studies.

One of the most important pest aphids is *M. persicae*, and its development of resistance to a range of compounds has been well documented. This included the early identification of a gene amplification conferring high levels of organophosphate-detoxifying esterases long before the advent of genomic resources (Field *et al.*, 1988). Subsequently, cloning techniques were used to identify the mutation responsible for modified acetylcholine esterase (AChE) conferring resistance to carbamates (Nabeshima *et al.*, 2003; Andrews *et al.*, 2004) and mutations in the sodium channel responsible for pyrethroid resistance (Martinez-Torres *et al.*, 1999; Eleftherianos *et al.*, 2008). A more detailed study of genes encoding potential insecticide-degrading enzymes and genes encoding ion channels in aphids had to await the sequencing of the *A. pisum* genome (Dale *et al.*, 2010; Ramsey *et al.*, 2010b). Since then, microarray analysis has been used to show that the amplification of a cytochrome P450 gene is associated with moderate resistance to neonicotinoid insecticides in *M. persicae* (Puinean *et al.*, 2010), and arrays coupled with target site sequencing have been used to show that very high-level resistance results from a single point mutation in the gene encoding the B subunit of the nicotinic acetylcholine receptor (Bass *et al.*, 2011). The identification and cloning of the gene encoding the sodium channel in *M. persicae* has also allowed the elucidation of differential resistance to different pyrethroids (Burton *et al.*, 2011) and to molecular models predicting which mutations affect which pesticide (Davies *et al.*, 2008).

A microarray study of genes up- or down-regulated in three genotypes of *M. persicae* has shown that in response to a carbamate (targeting AChE), sensitive aphids up-regulated 183 genes (including detoxifying enzymes), aphids with a mutation conferring resistance to pyrethroids up-regulated 17 genes and aphids with pyrethroid and carbamate resistance up-regulated only 7 (Silva *et al.*, 2012). The authors concluded that the genotypes have varying transcriptional plasticity and can assemble different phenotypes depending on the selection pressures.

Thus, genomic techniques have played a major role in understanding insecticide resistance in aphids and elucidating the basis of selectivity of compounds for insect versus mammal and between insect species. Our recent study of the aphid sodium channel, using genome resources (Amey *et al.*, 2015), has shown that it has unique and interesting properties that differentiate it from the channel found in other insects (Fig. 2.3), and this may provide opportunities for the design of new compounds aimed specifically at aphids. It is to be hoped that this approach will extend to other insecticides as their interactions with their targets become better understood.

Another indirect effect on aphid control has come from the use of our knowledge of the mutations underlying resistance to develop high-throughput screens for monitoring the occurrence and spread of resistance in field populations. For example, Roy *et al.* (2013) documented changes in insecticide resistance in French populations of *M. persicae* over a decade, and van Toor *et al.* (2008) looked at insecticide resistance in *M. persicae* in New Zealand. At Rothamsted Research, we have made wide use of such diagnostics to inform stakeholders of resistance issues using articles in the 'trade press' (e.g. Harrington *et al.*, 2009).

An alternative to conventional insecticide use that has been adopted for the control of some pest species has been the use of plants expressing *Bacillus thuringiensis* (Bt) delta endotoxins, especially Cry1Ac and Cry3Aa. However, these are not particularly effective against Hemipteran insects (Li *et al.*, 2011). Chougule *et al.* (2013) used a range of genomic/molecular techniques to show that the insertion of a 12-amino acid gut-binding peptide from *A. pisum* into one of three loops of the Bt toxin Cyt2Aa gave enhanced binding and toxicity to both *A. pisum* and *M. persicae*, thus retargeting the toxin to Hemiptera and potentially allowing a wide use of Bt technology to control crop pests.

Symbiosis

That aphids benefit from the presence of symbiotic bacteria is well established and almost certainly has allowed aphids to evolve and adapt over evolutionary history. Thus, the role of symbionts is important for understanding aphids as crop pests. Genomics has contributed greatly to our understanding of this relationship. An early examination of the *A. pisum* genome showed that, for many biosynthetic pathways, important genes are missing and this is possible because of

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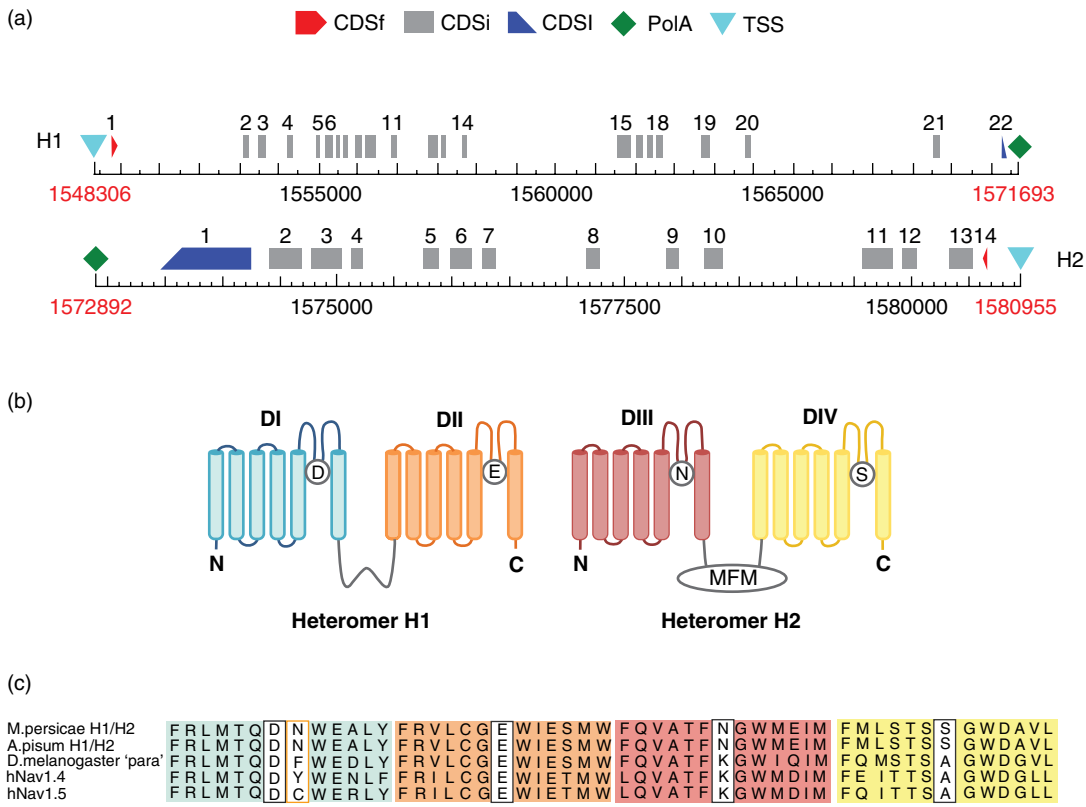

Fig. 2.3. Analysis of aphid voltage-gated sodium channels. (a) FGENESH (Softberry) gene prediction of the coding region for the *Myzus persicae* channel on the genome scaffold showing that, unlike other insects, aphid channels are encoded by two heteromers, H1 and H2. CDSf = first (starting with start codon) coding exon; CDSi = internal exon; CDSl = last coding segment; PolA = position of polyadenylation; TSS = position of transcription start (TATA-box position). (b) Each heteromer making up the channel consists of two 6TM domains, with the approximate position of the fast inactivation particle 'MFM' motif on heteromer H2 highlighted. The aphid channel also has an unusual ion selectivity filter DENS (not DEKA), which may make it a non-selective cation channel. (c) Sequence alignments of the S6 segments of aphids, fruit fly and human TTX-sensitive (Nav1.4) and -resistant (Nav1.5) channels. The selectivity filter sequences are highlighted (dark grey frames). Of particular note in relation to TTX insensitivity in aphids is the substitution within DI of an aromatic residue (phenylalanine or tyrosine) with a non-aromatic asparagine residue (orange framed residues), making aphids (in contrast to all other insects) insensitive to this toxin. The DIII asparagine in the DENS motif also contributes to TTX insensitivity in aphids.

complementation by gene products from the aphid primary symbiont *Buchnera aphidicola*; for example, the purine-recycling genes (Ramsey *et al*., 2010a) and genes encoding steps in amino acid synthesis (Wilson *et al*., 2010). The latter showed that the biosynthetic pathway was shared between the aphid and the symbiont, allowing aphid control over the symbiont, and maybe accounting for the successful partnership. This sharing of intermediates requires a close association provided by the bacteriocytes that harbour the symbionts and function as specialist organs of amino acid synthesis (Hansen and Moran, 2011), with recently evolved secretion proteins mediating the symbiosis (Shigenobu and Stern, 2013) and an expanded superfamily of amino acid transporters that function at the interface between the aphid and the bacteriocyte (Price *et al*., 2011). Genomic studies using microarrays have shown that *B. aphidicola* induces a defensive immune response in non-host cells that does not occur in host cells, supporting the view that the symbiosis

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is at least partly involved in the reduced immune response seen in aphids (Douglas *et al*., 2011).

As well as the primary symbiont, *B. aphidicola*, aphids harbour many other facultative symbionts, and again genomics have played a role in understanding these relationships. *Serratia symbiotica* is a recently evolved facultative symbiont that provides tolerance to heat stress, and gene expression studies have shown that it does this with little change in host gene expression (Burke and Moran, 2011). Sequencing of the genome of *S. symbiotica* has shown that it has been subject to massive genomic decay, presumably associated with its transition from a free-living to a symbiotic lifestyle.

Other facultative symbionts, *Candidatus* Regiella insecticola and *Candidatus* Hamiltonella defensa are thought to be involved in protecting aphids from natural enemies and fungal attack (Degnan *et al*., 2010; Parker *et al*., 2013), and genomic studies that reveal these interactions are important for understanding how aphids defend themselves and potentially avoid control strategies in crops. It is also interesting that another symbiont, *Wolbachia*, which has the potential for biological control in insects but has always been thought to be absent in aphids, has now been identified in many aphid populations and, based on 16S rRNA sequences, aphids appear to have two new supergroups of the bacterium along with two previously known supergroups (Augustinos *et al*., 2011).

Thus, symbionts are very important in determining aphid lifestyle and their potential as crop pests, and this is considered in much more detail in Chapter 6, this volume.

Conclusions

This chapter aims to give a very broad overview of areas where genomics has contributed to understanding aspects of aphid biology, ecology, behaviour and evolution, which in turn have played important roles in the way aphids have colonized crops and achieved pest status. In some areas, especially in understanding insecticide resistance, host location and plant–aphid interactions, it is to be hoped that such studies will aid future crop protection strategies, both in the better use and design of conventional chemical control and in the development of novel ways of preventing aphids from reducing crop production.

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3 Population Genetic Issues: New Insights Using Conventional Molecular Markers and Genomics Tools

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Introduction

Aphids as pests of crops and their adaptations

Aphids are highly variable morphologically, genetically and behaviourally. It is this large pool of variation that has allowed them to be such globally successful pests of agriculture, horticulture and forestry, not only by damaging plant vigour by tapping into their phloem sap, often as large colonies, but also by transmission of plant pathogenic viruses. This can have huge consequences for the economics of healthy plant maintenance and production consequent upon attack by aphids.

Worldwide, these small herbivores are estimated to cause tens of millions to billions US$ of yield loss per annum (Blackman and Eastop, 2000; Allard *et al*., 2003; Kim *et al*., 2008; Dedryver *et al*., 2010), while in the UK, damage to cereals alone can be worth around £120 million annually (Tatchell, 1989). As a direct result of the huge economic losses caused by aphids, a variety of pesticides has been used against them over the past 50 years or so, initially in the glasshouse, later in the field, such that around 20 major pest species worldwide have become resistant to these chemicals (Chapter 19, this volume). This relatively rapid adaptation is undoubtedly due in large part to the potentially astronomical rate of reproduction of aphids (Dixon, 1998) and the concomitant enhanced level of mutation (as a result of 'genetic inflation', i.e. large numbers of largely genetically identical clonal copies of the genotype bearing a particularly favourable mutation, say an insecticide resistance one, such that this is much more amenable to positive selection). Such diversity is evidence that variation is the chief clue to understanding the biology and success of aphids.

The rapid adaptation of certain pest aphids, such as the cereal aphid *Schizaphis graminum* (greenbug), in breaking the induced resistance mechanisms of their plant hosts is further evidence of their formidable attributes as pests. Aphids have been around since the Triassic Period, 250–200 MYA (Eastop, 1986; Grimaldi and Engel, 2005), and have been successful in the long 'arms race' with plants. They have evolved several adaptive life-cycle strategies and widened their host-plant range. Furthermore, they can, in the asexual phase of the life cycle, produce vast hordes of offspring in a very short space of time (Dixon, 1989; Harrington,

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1994) and, relying on mutation alone, tackle and often overcome many diverse ecological challenges.

Variety and adaptation are also enhanced with their:

- wide morphological (e.g. wingless and winged) and colour polyphenisms
- phenotypic plasticity (some of which may ultimately have a genetic basis)
- intimate associations internally with endosymbiotic bacteria of various kinds
- interactions with different species of guard ants
- different behaviours in terms of migration and dispersal
- chemical defences, including alarm pheromones and host-plant kairomones
- induction of winged morphs as a function of stress (overcrowding and predators/parasitoids)
- intimate genetic–biochemical relationships with their host plants (e.g. galling in some species) and hymenopterous parasitoids (probably enhancing metapopulation structuring in some species; e.g. tansy aphids and their specialized parasitoids; Loxdale *et al*., 2008, 2011c; Nyabuga *et al*., 2010)
- the evolution of defensive (soldier) castes bearing specialized morphologies in certain species of gall-forming aphids (Foster, 2002).

For these reasons, aphids are clearly 'insects for all seasons', an attribute directly related to their great ecological/evolutionary flexibility. They are continually at the cutting edge of ecological adaptive change and, unlike many other insects and other animals, have superior potential and abilities in terms of evolution just because of their powers of mutational change, aided by their phenomenally rapid asexual propagation.

What the use of molecular markers in aphid studies has so far revealed

For much of the past century, the true nature of aphids was largely unknown, and in some cases wrongly interpreted, by pioneers working in the field of aphid ecology, including life cycle and modes of dispersal. With the advent of molecular markers, initially allozyme markers, more recently DNA markers, huge strides have been made in our greater understanding of the life of these insects, both from a fundamental as well as an applied standpoint. Since the turn of the millennium, the suite and repertoire of molecular technologies has increased, enhanced by the rapidly declining costs of DNA sequencing, along with the sheer speed of this. This has allowed further advances to be made, more especially in the field of functional genomics. Here, the sequence and nature of the genes themselves can be examined, such that the very protein and phenotypic physiological/biochemical expression of these genes can be elucidated.

In the past, effectively the pre-genomics era, the main and most commonly used molecular markers available in aphidology were either protein based, and hence expression products of the coding genes, especially allozymes, or DNA fragments of the genome – for example, mitochondrial and/or nuclear resolved using RAPD (random amplified polymorphic DNA), RFLP (random fragment length polymorphism) or AFLP (amplified fragment length polymorphism) techniques – or were relatively simple non-coding DNA sequences such as spacers of the ribosomal DNA (rDNA) region of the chromosome (the nuclear-encoded ribosomal RNA genes), i.e. ITS (internal transcribed spacer) and IGS (intergenic spacer) and mini- and microsatellites (Loxdale and Lushai, 1998, 2007). There is, naturally, a continuity between these relatively simple molecular markers and knowing in detail the sequence of large regions of the DNA and chromosomes, perhaps the entire genome, and how these sequences determine the biology of the insects concerned. It is a gradation both of technology and of our understanding that derives therefrom. It is a seamless journey from non-coding sequences and genes to the full sequence itself, and in the future, perhaps the near future, how the genes themselves are regulated. As such then, the advent of genomics has extended our ability from indirectly inferring population processes based on largely anonymous genetic markers to understanding the genetic basis of aphid ecology/biology and how it is shaped by natural selection. As a consequence, unknowns related to aphid biology that have intrigued and mystified generations of aphidologists are being elucidated quickly, such that our knowledge base, and hence our ability to understand and perhaps control these insects in a more rational, targeted manner, will also continue apace.

The way forward: new genomics approaches to studying aphids

Because of the rapid evolution of insecticide resistance and plant resistance gene breaking by pest

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aphid species, such control has never been more important. It requires thorough background knowledge of the population ecology and dynamics of aphids, their biological associations and interactions, including genomic interactions, with their endosymbionts, and natural enemies including pathogens (viruses, bacteria and fungi) and arthropod predators and parasitoids. Only then will aphid control on a wide and lasting scale be feasible, rather than the control measures of today, which usually involve short-term 'stop-gap' approaches (e.g. spraying with chemical toxins). These ignore the fact that evolution continues regardless, often rapidly in insects because of their short lifespans/reproduction rate and environmental flexibility.

Here, we explain how molecular markers have been used and continue to be used to understand aphid life cycles, including population structure and dynamics and overwintering. Without repeating all the discoveries concerning these topic areas as outlined earlier (Loxdale and Lushai, 2007), we refer briefly to the major thrusts and findings using 'conventional' (i.e. non-genomic) molecular technology, more especially allozymes, mitochondrial DNA markers and mini- and microsatellites, and then move on to the new areas exposed and unravelled by the employment of more sophisticated genomics approaches, the fruits of rapid DNA sequencing. By such means, we show how the use of even simple molecular tools can provide valuable insights into key aspects of aphid biology related to life cycle and aerial movement in particular. As for the other aspects of aphid biology revealed using genomics approaches, notably the genetic/biochemical/physiological mechanisms of insecticide resistance, of endosymbiotic bacterial interactions, pathogen attack, host-plant resistance-breaking phenomena, interactions with host-plant kairomones and feeding behaviour and physiology, these are explored fully elsewhere in this volume. Taxonomic issues, including the separation of closely related species, especially of pest importance, are described in Chapter 1, this volume. We refer only to aphid bacterial endosymbionts, for example *Buchnera*, etc. (Douglas *et al*., 2003), where they relate specifically to host-plant adaptation (Zytynska and Weisser, 2016), rather than to their fundamental biology, phylogeny in relation to plant evolution (Baumann *et al*., 1995; Clark *et al*., 2000; Von Dohlen and Moran, 2000; Degnan *et al*., 2010; Nováková *et al*., 2013) or formerly assumed association with aphid carotenoid-based pigmentation (Jenkins *et al*., 1999). Very interestingly, more recent studies show that translocated genes (carotene desaturase) from a fungus are undoubtedly involved in the expression of carotenoid-based colour in aphids (Moran and Jarvik, 2010), an ancient association pre-dating the divergence of adelgids and aphids (Nováková and Moran, 2012).

Identification of Species

In the past, aphids could be discriminated satisfactorily, even as nymphs, using fluorescent pigment profiles (Henderson *et al*., 1976) or allozyme banding profiles (e.g. for blackberry (*Rubus*)-feeding aphids; Loxdale and Brookes, 1989). Aphid species are now usually separated using molecular (DNA) markers, more especially a 658-bp fragment from the *5′* region of the mitochondrial cytochrome c oxidase 1 (COI) gene (Foottit *et al*., 2008), the so-called bar-coding gene fragment. Using this approach, the authors found that 96% of 300 species representing 130 genera were well discriminated, with only about 0.2% sequence variation within species. The authors conclude, 'Despite the complex life-cycles and parthenogenetic reproduction of aphids, DNA barcodes are an effective tool for identification'.

Identification of Clones

Asexual lineages of aphids are commonly termed 'clones'. This has two interpretations. First, clones are the asexual offspring deriving from the original asexual stem mother (fundatrix morph) that hatched in the spring from the overwintering sexually produced egg. In life-cycle scenarios where asexual aphids overwinter in the mobile stages, or even when oversummering on alternative hosts (Loxdale *et al*., 1993; Burd *et al*., 1998; Anstead *et al*., 2003; Puterka *et al*., 2010; Weng *et al*., 2010), clones may persist for a long time, maybe years or even decades, and rise to high frequencies in the field (Fenton *et al*., 1998; Vorburger *et al*., 2003a; Piffaretti *et al*., 2013). Clones founded from such asexual members may also be maintained in the laboratory for decades (van Emden, 2009). However, it is unlikely that clones as such are immortal, just because selection pressures will not remain constant over time and will eventually eliminate particular lineages (Wilson *et al*., 1999; Vorburger, 2006), including

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insecticide-resistant aphids bearing different resistance mechanisms that are also subject to fitness costs of one sort or another; for example, climatic, hymenopterous parasitoid attack, etc. (Fenton *et al*., 2010). A second interpretation is that members of a so-called clone are genetically identical throughout their genomes. Ideas of such genetic identity cannot be true, even on theoretical grounds. It is well established that DNA is liable to constant mutational events due to a plethora of ultra-fast molecular mechanisms, including point mutations, errors of DNA repair, insertions, deletions, etc. (Loxdale, 2010).

It is now well documented, using both RAPD and AFLP markers, that phylloxerids and aphids show widespread and rapid mutational changes, even within a very few generations of testing (Lushai *et al*., 1997, 1998; Vorwerk and Forneck, 2007; Loxdale *et al*., 2013; Fig. 3.1). The use of aphid-specific AFLP primers makes it unlikely that such variation derives from extra-genomic sequences, for example viruses, bacteria and ingested plant chloroplast DNA (Vorwerk and Forneck, 2007; see also Lushai *et al*., 1997), and direct sequencing supports this contention (Vorwerk and Forneck, 2007). In the case of *Daktulosphaira vitifoliae* (vine rootstock aphid or grape phylloxera), the sequencing of 37 selected polymorphic bands revealed that the majority (32) derived from non-coding regions, the remaining five apparently from 18S rDNA sequences (Vorwerk and Forneck, 2007). It is probable that each individual is genetically different from its clone mates at some point throughout the large genome of aphids of around 530 Mb (IAGC, 2010; Loxdale, 2008a,b, 2009; Loxdale *et al*., 2013). The continuous production of mutations throughout the aphid genome at rates $>10^{-6}$ per gene per generation, certainly in non-coding regions that are known to be subject to fast mutational changes (Vorburger *et al*., 2003a; Wilson *et al*., 2003; Loxdale, 2009), means that strict genetic identity is highly unlikely anyway (Lushai and Loxdale, 2002; Loxdale and Lushai, 2003).

Because the clone is a dynamic evolving entity (Lushai *et al*., 2003), a new term is preferable to clone, with its connotation of strict genetic fidelity. The term 'clonotype' as a euphemism for multilocus genotype (MLG) has been suggested for asexual lineages derived from a common asexual stem mother (fundatrix) and showing continuous mutational changes, but it is hardly elegant and it will be difficult now to overturn entrenched views in this area, especially in the public eye (Martens *et al*., 2009). Another term that we hereby coin is 'clan', which refers to 'A division of a tribe tracing descent from a common ancestor' (www.thefreedictionary.com/clan) and hence perhaps describes better the true nature of the genetically diverging clone mates within the conventional viewed clonal colony derived from a single asexual foundress.

Another discovery of particular interest when discussing clonal genetic fidelity, found using RAPDs, is *inter*morph (winged and wingless asexuals, winged male and wingless female sexual forms), *intra*clonal genetic variation in *Sitobion avenae* (English grain aphid) and *Rhopalosiphum padi* (bird cherry–oat aphid), reared under strict conditions of clonal hygiene (Lushai *et al*., 1997). Such variations may relate to transposon effects (Loxdale, 2008a,b), or perhaps to DNA methylation events between the genomes of the two morphs that differentially affect the primer sites and hence primer binding (Srinivasan and Brisson, 2012). The ~250-bp band in *S. avenae* discriminating wingless from winged asexuals showed >97% homology with an unknown band as detected from the full genome sequence of *Acyrthosiphon pisum* (pea aphid) (Walther Traut, unpublished; Fig. 3.2). Hence, the band is not an artefact (virus, bacteria, fungus, etc.) but a true aphid genomic band. Further to this, recent studies of the chromosome karyotype of *Myzus persicae* (peach–potato aphid) have revealed that within certain asexual lineages tested (2n = 12–14), *inter*embryo, *intra*clonal genetic variation is present, due to fission events between the X (sex) chromosome and autosomes 1 and 3 (Monti *et al*., 2012). Thus again, concepts of the clone as an unchanging entity are untenable and, rather, it is seen to be a potentially dynamic entity, even at the level of gross chromosomal changes. Such changes could lead to changes of host plant choice and even incipient speciation events, such as in the case of *Myzus antirrhinii* (antirrhinum aphid) (2n = 13 or 14), which may have diverged from *M. persicae sensu stricto* (2n = 12). This probably occurred due to a chromosomal fission event that prevented members of the newly mutated population breeding back into the original parental population as a result of chromosomal non-disjunctions on the metaphase plate during meiosis (Blackman and Paterson, 1986). As a consequence, the antirrhinum aphid is essentially an asexual species (Foottit, 1997).

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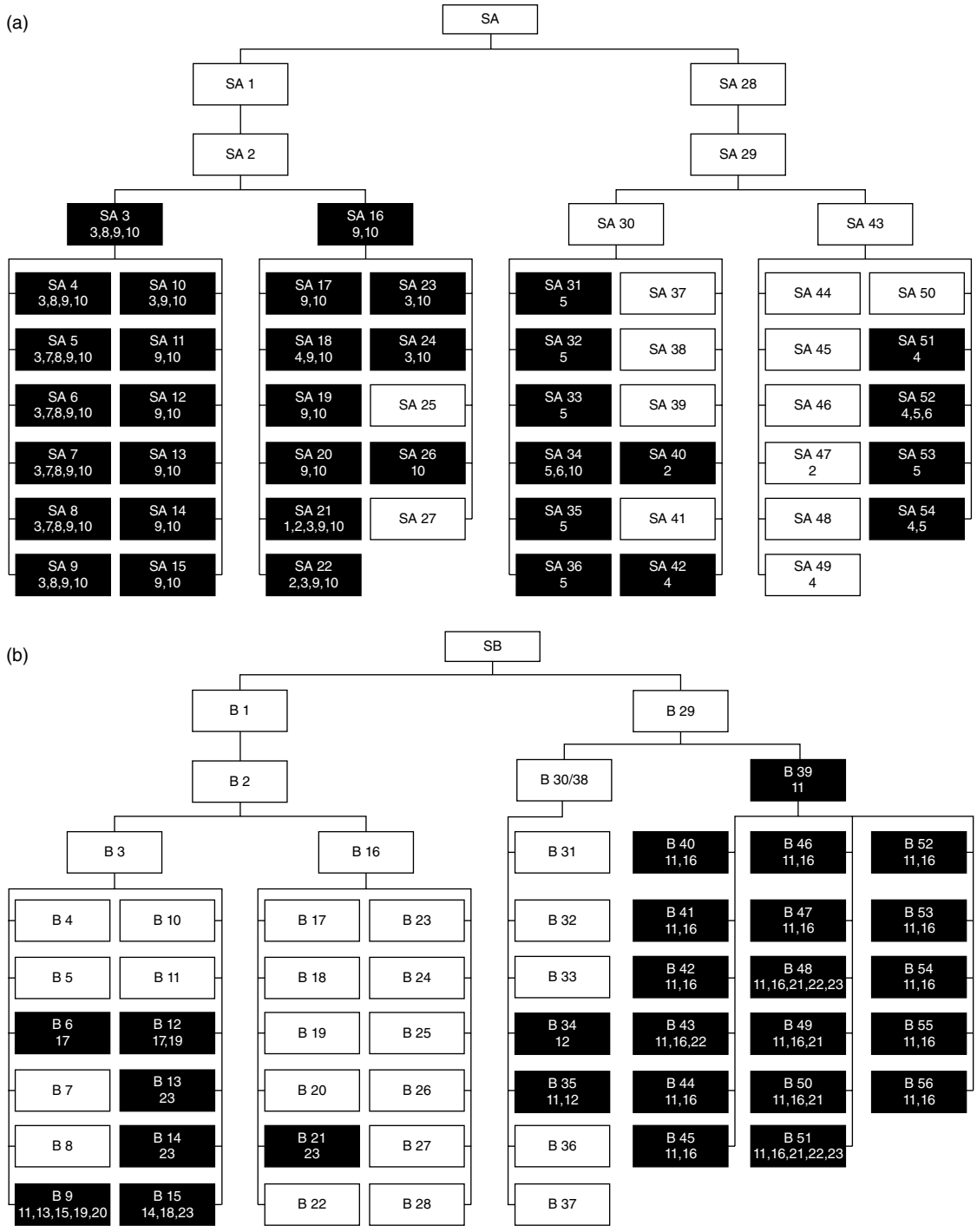

Fig. 3.1. Descendants of two *Sitobion avenae* asexual stem foundresses, (a) SA and (b) SB, reared over five generational cycles, showing mutations revealed using AFLP markers. Black boxes indicate mutated individuals; numbers refer to mutations listed in Table 2 of original paper. (From Loxdale *et al*., 2013; figures reproduced with permission of the *Bulletin of Entomological Research*.)

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Fig. 3.2. Result of BLAST search of 248-bp RAPD-PCR amplified sequence, originally published in Lushai *et al*. (1997), from an asexual lineage (E3) of wingless *Sitobion avenae* (and missing from winged individuals of the same lineage), revealing one excellent match (241/248 = ~ 97% homology) when compared with the published reference sequence of the *Acyrthosiphon pisum* (pea aphid), strain LSR1 in the NCBI (National Center for Biotechnology Information) database available since 2010 (unplaced genomic scaffold, Acyr_2.0 Scaffold 675; Sequence ID: ref NW_003384164; Length: 179099; Number of Matches: 1; http://www.ncbi.nlm.nih.gov/) (*cf.* also IAGC*,* 2010).

Loss of sexual reproduction is not unique to aphids, and seemingly has occurred in several phyla. Recently, analysis of the genome of a bdelloid rotifer, *Adineta vaga* (an asexual species), showed that this organism was unable to resume conventional meiosis. However, several gene conversion features were described, a process that might limit the effect of deleterious mutation accumulations (Flot *et al*., 2013). Concerning aphids, the available genome sequence of *A. pisum* is derived from a sexual lineage, so such investigations are not yet possible. However, comparing genome structures of sexual and asexual lineages in the pea aphid, or sequencing genomes of asexual aphid species, might highlight molecular mechanisms associated with genetic variation in clonal individuals and elimination of deleterious mutations in the absence of meiosis.

Host-plant Adaptation

Considering the genetic variability of aphids, both molecular and chromosomal (Blackman, 1980, 1981; Blackman and Eastop, 2000, 2007; Monti *et al*., 2012), as well as their intimate dependence on plants, it is not surprising that aphids are known to show host plant-related population divergence. This often marks the beginning of true speciation and seems to occur sympatrically (Peccoud *et al*., 2009a), although allopatric mechanisms are also possible (Jousselin *et al*., 2013).

Cereal aphids

Of karyological differences, a good example concerns the two chromosomal forms of *Rhopalosiphum maidis* (corn leaf aphid) infesting maize and sorghum (2n = 10 and 12, respectively; Brown and Blackman, 1988). This aphid is essentially an asexual species (Blackman and Eastop, 2000) and, like the antirrhinum aphid, the chromosomal forms may be considered as sympatric host-adapted species, or at the very least, races.

At a purely molecular level, aphids of the genus *Sitobion* have proved illuminating in terms of the process of sympatric speciation. Loxdale and Brookes (1990a) noted, using allozymes (glutamate oxaloacetate transaminase, GOT), that in the holocylic *Sitobion fragariae* (blackberry–cereal aphid), certain GOT genotypes (bearing the S (slow) allele)

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occurred at high frequency (>0.58) within certain local subpopulations in southern England, while appearing virtually absent from the primary overwintering host *Rubus fruticosus* (bramble) in the same areas sampled. This suggested that these particular genotypes represented asexual genotypes that remained permanently all year round on the secondary host, grasses, in this case cocksfoot (*Dactylis glomerata*). Thus, some kind of asexual population divergence appeared to be occurring in these otherwise morphologically identical genotypes (Victor Eastop, unpublished), which ultimately related to the host plant, certainly the secondary host, and may have had a chromosomal basis, although karyotype was not investigated. De Barro *et al*. (1995a), using RAPD markers, were able to separate genotypes partially into cocksfoot- and wheat-preferring forms (see also Wilson *et al*., 1999). Loxdale and Brookes (1990b) had already shown that the *Sitobion* found on cocksfoot were predominantly *S. fragariae* (f >0.90), rather than the largely anholocyclic sister species, *S. avenae*. It is probable that *S. avenae* evolved from *S. fragariae* with the domestication of cereals; certainly, both are morphologically very similar and identical in terms of chromosome number (2n = 18) (Blackman and Eastop, 2000).

Sunnucks *et al*. (1997), using microsatellite markers, showed that aphids on the two hosts sampled in the UK, cocksfoot and wheat, displayed host-specific alleles at high frequencies, along with intermediate forms. Examination of mitochondrial DNA (mtDNA) haplotypes showed that introgression (hybridization) had occurred between the two *Sitobion* species, with some level of asymmetry (25/31 cases), suggesting that winged males of *S. avenae* had mated mainly with wingless sexual females of *S. fragariae*, the former species rarely reproducing sexually, although it can do occasionally under suitable short day length, low temperature conditions, but always on cereals and grasses (Poaceae) (Hand, 1989; Llewellyn, 2000; Simon *et al*., 2002). Lushai *et al*. (2002), using RAPDs and a Latin square arrangement of plant hosts sown in the field (wheat, barley and two species of grass), were able to demonstrate host preference of winged asexual forms coming into the crop early in the growing season in the UK; these forms bear more highly developed sensory organs for host localization compared to the wingless forms (Powell *et al*., 2006; Peccoud and Simon, 2010). Haack *et al*. (2000) have also demonstrated, using microsatellites, a clear host preference for *S. avenae* in the field in France, and the existence of specialist and more generalist genotypes, the latter perhaps encouraged by modern agricultural practices.

In North America, molecular work has been performed to discriminate the biotypes of the important economic pest of cereals, the greenbug, using the 1.2-kb portion of the cytochrome oxidase I mitochondrial gene (Shufran *et al*., 2000). In addition to the nine known biotypes (B, C, E, F, G, H, I, J and K), three others were included (i.e. biotype A (NY), a sample collected from Great Plains wild rye (*Elymus canadensis*) (CWR), and an isolate from Germany (EUR). Three clades were shown to exist. Clade 1 comprised the biotypes (C, E, K, I, J) normally found on sorghum and wheat and considered as agricultural pests. The other two clades are rarely found on crops. Another rare biotype (H), found outside the three clades, was suspected of being another *Schizaphis* species. Generally, there were few base substitutions between these biotypes. This pioneering work was followed up by Anstead *et al*. (2002). Using 12 previously sequenced *S. graminum* clones, they confirmed the existence of the three clades. Although they failed to find a correlation between biotype and mtDNA (one biotype was even found among all three clades, suggesting exchange among clades of genetic material conditioning for crop virulence, or the sharing of a common ancestor), there was a relationship between plant host and mtDNA haplotype, as shown in the earlier study by Shufran *et al*. (2000). It is probable that such host races evolved before the introduction of modern agriculture in the USA in recent historical times (Anstead *et al*., 2002).

Zhang *et al*. (2012) have used a combination of mitochondrial and microsatellite markers to reveal that the host shift of *Diuraphis noxia* (Russian wheat aphid) to cultivated cereals can be traced back to a single mitochondrial haplotype approximately 7500 years ago, when cultivated cereals were first planted in this aphid species' area of origin in north-central Asia. A subsequent study on global populations confirmed that all populations currently found on cereals can be traced back to this single genotype (Zhang *et al*., 2014).

Pea aphid

Based on pioneering work by Via (1991), the pea aphid has become one of the best-understood examples of host specialization in phytophagous

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insects. The host races specialized on clover and lucerne found in North America are maintained by genetically based trade-offs in performance on these plants. Further work has shown that this extends to many more different host plants in the pea aphid's native European range (Ferrari *et al*., 2008). Interestingly, this pervasive host specialization seems to be promoted by the pea aphid's genetic architecture, in that loci with antagonistic effects on performance on different hosts are linked to loci that produce assortative mating through habitat choice (Hawthorne and Via, 2001). More recently, several studies employing microsatellites to quantify genetic differentiation have shown that in the pea aphid species complex, sympatric speciation has seemingly occurred in the various host-adapted forms (11 races and species) of the aphid infesting cultivated and wild Leguminosae (Frantz *et al*., 2006; Peccoud *et al*., 2009a; Peccoud and Simon, 2010). In addition, the role of bacterial endosymbionts in host-plant adaptation is now understood in more detail for pea aphids (Peccoud *et al*., 2009b, 2014a; Henry *et al*., 2013). Different host-adapted forms preferring their own natal plant species and trade-offs preventing the optimal use of multiple host plants enhance selection against migrants and reduced fitness of hybrids between forms. Peccoud *et al*. (2014b) have indeed demonstrated that hybrids between different biotypes are often less fit than their parents, but it depends on the divergence between the parents of the hybrids. Accordingly, the males of the various forms also prefer the wingless sexual females of their own particular hosts, probably enhanced by pre-zygotic barriers, more especially the correct mix of female-emitted sex pheromone constituents (Knäbe, 1999; Goldansaz, 2003).

The fact that males of some host-preferring forms are wingless presumably goes a long way to promoting host specialization. Divergent selection and reproductive isolation leave a genetic signature: Via (1999) showed, using allozymes, that in the pink and green lucerne- and clover-preferring forms of the pea aphid, asymmetry was found in terms of host preference, probably related to trade-offs and selection against hybrids formed of sexual reproduction. In further work (Via and West, 2008), involving 40 AFLP markers and five sequence-tagged co-dominant markers of the chromosomal regions around the quantitative trait locus (QTL) controlling host acceptance and use, very limited introgression was observed at genomic regions linked to loci under divergent selection. As a consequence, large parts of the genome are extensively 'hitchhiked' during host selection, such that interpopulation divergence is promoted, while at the same time rates of inter-race recombination are limited throughout large portions of the genome. The genetic and genomic architectures of host specialization traits in the pea aphid have also now been tackled using genomic resources for population studies. Jaquiéry *et al*. (2012) sampled pea aphid populations on three different host plants and used more than 300 microsatellite markers to identify 11 loci that showed high genetic differentiation in correlation with host-plant origin. This study was recently enlarged to eight other pea aphid biotypes, finally to reduce to four the number of microsatellite loci still under differentiation for the 11 biotypes (Nouhaud *et al*., 2014).

Cotton aphid or melon aphid

Host specialization in *Aphis gossypii* (cotton aphid or melon aphid) has been studied in global populations using microsatellite markers (Carletto *et al*., 2009), showing that the host plant is a stronger determinant of genetic structure than geographic distance. The strong association with host plants is reversible, however, whether by selection (Wu *et al*., 2013) or by the presence of vacant niches due to geographic isolation from host-specific lineages (Chen *et al*., 2013). The ecological specialization involved in these and similar examples of host adaptation in aphids marks the cutting edge of the evolutionary process and is undoubtedly occurring sympatrically, although some initial degree of allopatric separation encouraging population divergence cannot be ruled out. If sympatric modes are at work, then these are against the views of Mayr (1963), who considered such mechanisms unlikely, but strongly support other work in, for example, stick insects of the genus *Timema* (Nosil *et al*., 2002) and danaid butterflies (Smith, 2014).

Peach–potato and tobacco aphids

Myzus persicae is often described as being a highly polyphagous insect, attacking plants in 40 families worldwide (Blackman and Eastop, 2000). However, it may be that this apparent 'generalism' (Loxdale *et al*., 2011a) is illusory and that *M. persicae* is in reality a species complex comprising numerous morphologically similar cryptic species or subspecific

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forms ('biotypes' *sensu* Eastop, 1973), which may ultimately be discriminated using modern high-resolution molecular markers, more especially sequencing. If it really can imbibe the sap from so many plant species and deal with the numerous antifeedant secondary plant compounds encountered, many, such as alkaloids, highly toxic, then perhaps this is a striking form of specialism rather than generalism, and that the aphid has evolved enzymatic and other mechanisms to deal with these (Loxdale *et al*., 2011a; Chapter 9, this volume). In this light, it is of interest that Vorburger *et al*. (2003b) failed to find experimental support for the more frequent occurrence of general purpose genotypes (GPGs) in terms of geometric mean fitness across different host plants in obligate asexual as opposed to cyclical parthenogenetic forms of this species. Thus, there was no evidence for the assumption that long-term parthenogenesis would select for broader ecological tolerances (Lynch, 1984). Certainly, there is evidence for specialization in the *M. persicae* complex exemplified by the nicotine-feeding subspecific form, *Myzus persicae nicotianae* (Blackman, 1987; Chapter 1, this volume).

Population genetic studies of the aphid in Greece using microsatellite markers, with data analysed using Bayesian approaches, revealed a greater divergence between aphids in tobacco-growing regions compared to non-tobacco-growing regions, irrespective of reproductive mode (Margaritopoulos *et al*., 2007a). Populations could be split into groups corresponding with *persicae*, and holocyclic and anholocyclic *nicotianae,* while genetic distance analysis showed strong regional differentiation but marked year-on-year stability, indicating low interpopulation migration. Interestingly, this level of population genetic differentiation, regionally depending on the presence or absence of the host, tobacco, is suggestive of assortative mating between *M. persicae s.s*. and *M. persicae nicotianae*. Indeed, parallel physiological studies have revealed prezygotic barriers to gene flow, which reinforce the isolation of the taxa. Thus, besides differences in the daily rhythm in which sexual females release sex pheromone, and the fact that this coincides with the searching activity of the taxa-specific winged males, these were generally more attracted to their own conspecific females rather than the alternative females (Margaritopoulos *et al*., 2007a,b). Hence, while the genetic level of population differentiation has generally been found to be low, mechanisms are in place promoting divergence, ultimately to the level of full speciation. This is another example of apparent sympatric speciation, and of males being preferentially attracted to their own specific females via sex pheromones.

All these studies outline the dynamic nature of host adaptation within populations of aphids, showing that evolution continues apace, both within the agroecosystem, and hence of importance to humankind, and without. The basis of this evolution is the variability found within natural populations of aphids, variability that may be selected and hence become common, or even dominant, within and among populations.

Life Cycle in Relation to Climate

Another important aspect of the variability of aphids, one that directly impacts on aphids as pests of crops, is life-cycle variation. Aphids are famed for their complex and various life cycles (Chapter 4, this volume).

Some holocyclic aphids like *Drepanosiphum platanoidis* (sycamore aphid) and *Macrosiphoniella tanacetaria* (tansy aphid) are monoecious, remaining on the same host throughout the year, oviparae of the latter species laying overwintering eggs after mating on the dying stems of the host plant in the autumn (Massonnet, 2002; Massonnet *et al*., 2002; Loxdale *et al*., 2011b,c). In one species, *Acyrthosiphon svalbardicum* (Svalbard endemic aphid), which feeds exclusively on mountain avens (*Dryas octopetala*) on the Svalbard Islands (Spitzbergen) of the High Arctic, following egg hatch in the spring, the fundatrix gives rise directly to sexual morphs as well as a few asexual females. These in turn produce a third generation comprising more sexual morphs, which can increase the number of overwintering eggs, if conditions allow. This life cycle is especially adapted to the adverse conditions often pertaining during the short growing season in the Arctic (Strathdee *et al*., 1993; Hullé *et al*., 2008).

The life-cycle polymorphisms of aphids have been shown to correlate broadly with geography, and hence ultimately climate. Blackman (1974) demonstrated that holocycly in *M. persicae* was confined mainly to regions with severe winters and anholocycly to temperate or even subtropical regions. The type of life cycle predominating in an aphid population leaves a population genetic signature, which in turn allows some inference about reproductive modes from genetic marker

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data (Balloux *et al*., 2003). Despite the many asexual generations during the growth season, the genetic structure of a holocyclic population is virtually indistinguishable from that of populations that exclusively reproduce sexually (Sandrock *et al*., 2011). If parthenogenetic overwintering predominates, on the other hand, aphid populations will be characterized by a reduced genotypic diversity as well as deviations from Hardy–Weinberg (H–W) and linkage equilibria (Halkett *et al*., 2005). For example, Simon *et al*. (1999), using allozyme markers and with assessment of the population frequency of heterozygosity and deviations from H–W expectations at a range of polymorphic loci (relating to random mating), found that *S. avenae* formed a south–north cline across France, again with holocylic forms mainly in the colder north of the country, anholocyclic forms in the warmer south. Llewellyn *et al*. (2003) found a similar clinal pattern with *S. avenae* in the UK. Similar patterns were observed in France (Dedryver *et al*., 2001). Guillemaud *et al*. (2003), studying *M. persicae* in France, also found a relationship between life cycle and climate, again with holocyclic forms in regions with severe winters and anholocyclics the opposite (see also Vorburger *et al*., 2003b). Last, Martinez-Torres *et al*. (1996, 1997), exploring mitochondrial DNA haplotype in *R. padi*, found a clear correlation between certain haplotypes and geographic region across France. Thus, for example, haplotype I, a marker from a predominantly anholocyclic form of the aphid, was predominant in milder regions and only occurred on the secondary host/s (Poaceae), whereas haplotype II, and the rarer haplotypes III and IV, all found in holocyclic clones, occurred at higher frequency in regions with more severe winters. Thus, there is ample evidence from both nuclear and mitochondrial genetic markers of a relationship between life cycle and climate.

In order to tackle the genetic determinants of asexual reproduction, Jaquiéry *et al*. (2014) developed a quantitative approach to identify genetic divergent loci between holocyclic and androcyclic (male producing) populations, at a genome-scale level in the pea aphid. First, they developed segregating populations in the laboratory and mapped a single recessive locus (QTL) on the X (sex) chromosome controlling obligate asexuality. Second, a microsatellite screen of wild anholocyclic and holocyclic populations led to the identification of genetically divergent loci, also located on the X chromosome and co-localized with the previously identified QTL. This 10-cM region corresponds to several non-aligned scaffolds; it is still too early to pinpoint putative genes related to the reproductive mode in the pea aphid, but this trait is probably governed by a small number of genes.

Earlier, Harrington *et al*. (2007) had shown a relationship between the date of first capture of winged *M. persicae* in the Rothamsted Insect Survey (RIS) 12.2-m high suction-trap network in the UK (Chapter 16, this volume) and the preceding mean January and February temperatures. Furthermore, as aforementioned, wingless virginoparae were known to be able to survive cold winter temperatures under certain circumstances, for example, under a blanket of snow, such aphids being known to have a fair degree of cold tolerance (Chapter 7, this volume). However, in such cold conditions, the vast majority of aphids overwinter as eggs and therefore, if it is accepted that this is the major reason for sexual reproduction in aphids, in addition to some degree of mixing of variation between lineages (Loxdale, 2008a,b, 2009), then these insects are surely 'slaves of their environment' (Loxdale and Lushai, 1999). Thus, the distribution of the various life-cycle morphs is to some large degree sorted by a process of positive selection over many generations and, as with photoperiod (Smith and McKay, 1990; Loxdale *et al*., 1993), there is probably strong negative selection against aphids moving too far away from their natal habitat. If this is so, it marks an environmental constraint against overly long-distance aerial movements of aphids, above and beyond the other ecological constraints such as host-plant dependence- that is, not moving away from regions where a suitable host is available (Loxdale, 2008a).

Spatial and Temporal Dynamics of Aphids, Including Short- and Longer-distance Aerial Movements

Wool *et al*. (1978) were the first to demonstrate molecular genetic variation in aphids- in this case, a collection of asexual lineages of *M. persicae* held in the laboratory and tested using a range of allozyme markers. Thereafter, such markers were applied to field populations of aphids, especially by Loxdale and co-workers and Simon and co-workers (e.g. Loxdale *et al*., 1985; Simon *et al*., 1999). They found widespread genetic heterogeneity at various spatial scales, either in the UK and/or mainland Europe, and that even in species with a sexual

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phase, morphs were not equally distributed across the landscape, including in terms of life-cycle morph, as mentioned above. Furthermore, they found species-related levels of population genetic variation and divergence, possibly reflecting selection and/or genetic drift differentially acting upon different subpopulations (e.g. Wilson *et al*., 1999), or that such variation was predominantly a function of aphid flight behaviour.

It is known from wind tunnel experiments on flying aphids (Hardie, 1993) that different aphid species show different responses during the early flight period. Species differ in their initial attraction to white-light targets (representing the sky), relating to the initial migratory phase, while they differ too in the later response to green targets (representing the plant host), relating to host-seeking behaviour, as aphids descend below the boundary layer of still air (Taylor, 1974) and actively search for suitable hosts using both visual and olfactory cues (Loxdale *et al*., 1993). Even above the boundary layer and when borne on the wind above their slow flight speed in still air, aphids are still actively flying (Taylor, 1965; Loxdale *et al*., 1993). When so carried, they are theoretically capable of travelling long distances. However, their available fuel (lipids) is limited and they usually attempt to maximize their chances of landing on a suitable host and successfully reproducing at the earliest opportunity. If their landing behaviour is disturbed when flying over bright reflecting surfaces such as water, sheets of aluminium foil and perhaps rocky terrain and deserts, roads and buildings, etc., then landing is inhibited and hence delayed (Loxdale *et al*., 1993).

As with birds, not all aphid species show the same migratory urge or ability. Even within some species such as *Aphis fabae* (black bean aphid), there are local fliers and more long-distant fliers (Cammell, 1981; Kidd and Cleaver, 1984, 1986). Other aphids, such as the sycamore aphid, show trivial flights around the canopy of their tree hosts as well as more long-distance flights (Dixon, 1969; Wynne *et al*., 1994). Last, within a species such as *R. padi*, which is both holocylic and heteroecious, a polyphenism is known in terms of flight behaviour: gynoparae searching for the primary host *Prunus padus* tend to fly higher than virginoparae searching for the secondary host, Poaceae (Tatchell *et al*., 1988). This probably reflects the distribution of the host; grasses and cereals are generally abundant over large geographical areas, whereas the primary host occurs most often as single, widely separated individual plants (*P. padus* is not uncommon, but is widely dispersed; Tatchell *et al*., 1983).

The behaviour is most certainly reflected in the comparative genetic patterns found within and between the different aphid species tested using allozyme and nuclear DNA markers; that is, IGS (rDNA) and mini- and microsatellite markers. This in turn reflects host abundance such that aphids which infest locally common plants tend to fly significantly less far than those species with widely dispersed primary or secondary hosts, as suggested above in the case of *R. padi* and *P. padus*, or whose host (perhaps a crop plant) is ephemeral and either becomes unsuitable due to senescence (e.g. grasses and cereals in midsummer) or is actively removed (due to cropping). In such cases, the aphid species in question has no choice but to disperse, possibly long distance. With aphid species with a locally abundant but isolated host, effectively forming 'islands of resource' (e.g. tansy plants, *Tanacetum vulgare*), there may be strong selection against distance movement of winged aphids away from their natal host plants (Massonnet and Weisser, 2004; Loxdale *et al*., 2011c). It is interesting in this context that males of some aphid species without host alternation are wingless, presumably reflecting selection against male dispersal; for example, *Metopeurum fuscoviride* (pink tansy aphid) (Loxdale *et al*., 2011c; Fig. 3.3). After all, the risk of not finding an appropriate host plant is high for winged aphids (Ward *et al*., 1998; Klueken *et al*., 2012). It was discovered in the pea aphid that male wing formation was polymorphic and under the simple genetic control of the biallelic aphicarus (*api*) locus (Caillaud *et al*., 2002; Braendle *et al*., 2005a,b). This implies that the relative frequencies of winged and wingless males may respond to selection for or against dispersal relatively quickly. Indeed, Frantz *et al*. (2009) reported that pea aphid host races occurring on perennial plants produced higher frequencies of wingless males than pea aphids from annual host plants, on which the ability to disperse was likely to be more important (Frantz *et al*., 2009, 2010).

Such causative reasons undoubtedly shape the flight behaviour of migrating aphids in turn, and ultimately govern the population genetic structure of aphids. Hence, the major cereal pest, *S. avenae*, which is predominantly anholocyclic in the UK and much of Western Europe, shows rather similar genetic patterns as observed using allozymes (homogeneity of allele frequencies; small genetic

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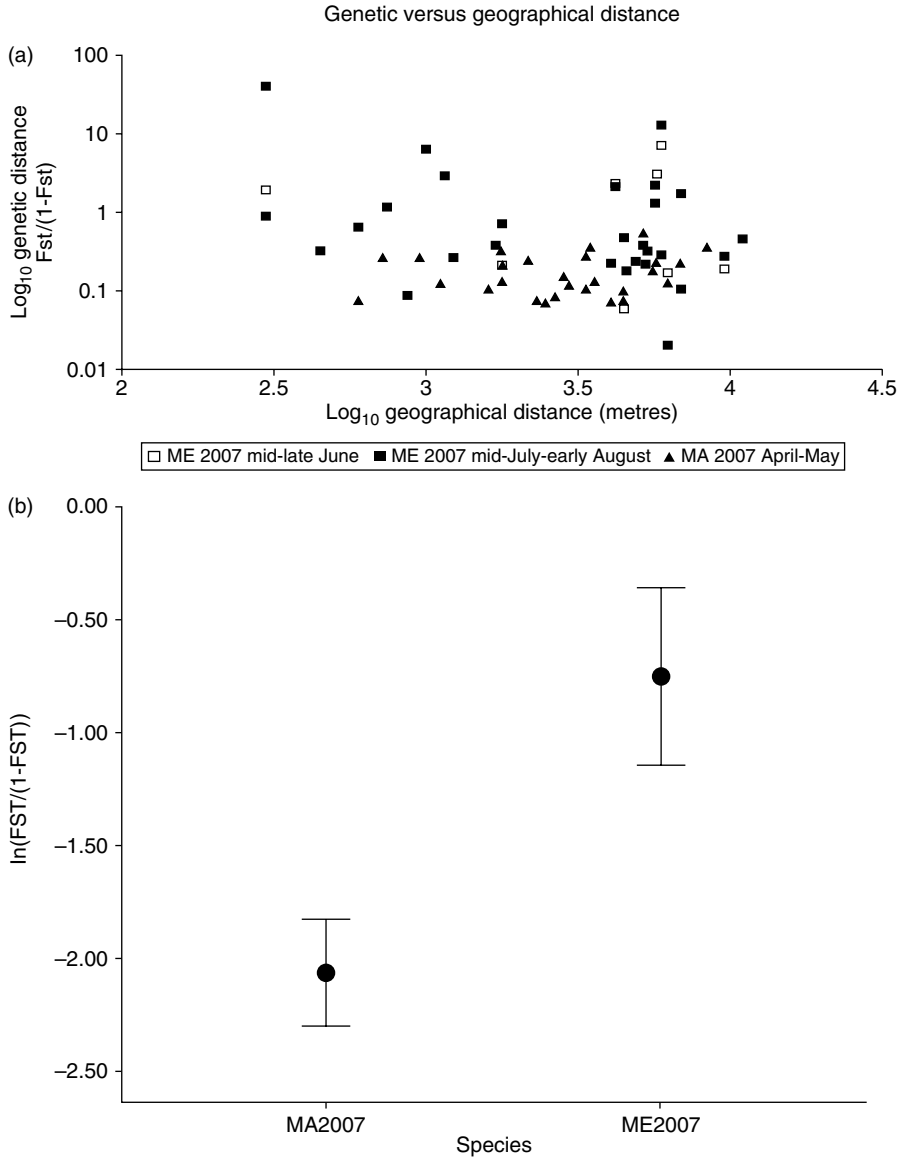

Fig. 3.3. (a) Isolation by distance (IBD) graph showing $\log_{10}$ genetic distance [as *F*st/(1 – *F*st)] versus $\log_{10}$ geographical distance (metres) in two specialist tansy-feeding aphid species, *Macrosiphoniella tanacetaria* (MA) and *Metopeurum fuscoviride* (ME) studied using polymorphic microsatellite markers at small spatial scales (≤ 16 km) in Jena, Germany. For MA, only the larger spring (late April to mid-May) samples were tested, whereas for ME, only the two larger summer (mid- to late June) and late summer (mid-July to early August) samples were used. (b) Relative 'migratoryness' of tansy aphids as measured after analysis of covariance, plotted as ln[*F*st/(1 – *F*st)] versus MA and ME. In essence, these graphs reveal that while neither species shows obvious IBD over the spatial scales examined, ME is clearly less migratory over the spatial scales tested than MA; that is, it shows a relatively higher level of genetic distance. This may relate to the fact that MA produces winged spring and summer asexual migratory females as well as winged sexual males in the autumn, whereas while ME produces winged spring and summer asexual migratory females, the autumn males are wingless, a fact appearing to isolate further the local subpopulations compared with MA within the two respective species metapopulations. (From Loxdale *et al*., 2011a; figures reproduced with permission of the *Biological Journal of the Linnean Society*.)

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distances even over large geographical distances (~ 800 km); Loxdale *et al*., 1985), and this is broadly confirmed using microsatellites, including small values of *F*st (i.e. mostly ≤ 0.05; Llewellyn *et al*., 2003). This aphid, highly adapted to cultivated cereals, especially wheat (as demonstrated by De Barro *et al*., 1994, 1995b, using the $(GATA)_4$ probe and Vialatte *et al*., 2005, 2007, using microsatellites), has little choice but to move on when the crop is harvested in late summer. In contrast, its holocyclic sister species, *S. fragariae*, shows genetic heterogeneity over even small spatial scales (<50 km) (Loxdale and Brookes, 1990a), suggesting it is less migratory, a view supported by its relative rareness in 12.2-m high RIS suction traps at peak abundance compared to *S. avenae* (about tenfold less common; e.g. Woiwod *et al*., 1988). *Sitobion fragariae* also showed stable GOT genotype frequencies when measured over a 5-year period, revealing that local subpopulations were apparently not greatly perturbed by the influx and efflux of winged migrants from outside the sampled area.

Other migrating pest species studied include *S. graminum* in the USA, tested using IGS markers; in this species, a clear lack of population structuring within maize and sorghum fields sampled suggests a tendency towards long-distance aerial movements (Shufran *et al*., 1991). Similarly, studies on *R. padi* using both allozymes (Loxdale and Brookes, 1988) and microsatellites (Delmotte *et al.,* 2002) argue that this species is broadly a long-distance disperser, especially during its autumnal quest to find the primary host, *P. padus*. This contrasts with *Phorodon humuli* (damson–hop aphid), which seems to undergo relatively short-distance movements (≤30 km) between its primary host, *Prunus* spp., especially sloe (*Prunus spinosa*), and wild and commercially grown hops (*Humulus lupulus*), in and around the hop gardens of Hereford and Kent in England, in studies involving the use of allozyme markers, including carboxylesterase markers associated with insecticide resistance (Loxdale *et al*., 1998). Furthermore, in this case, there seems to be an asymmetry in the duration of migration in the spring movements from *Prunus* to hops compared with the autumn movements from hops to *Prunus*, the former being of longer duration and hence greater distance (Loxdale *et al*., 1998), broadly supporting earlier suction-trap studies (Taylor *et al*., 1979). *Myzus persicae*, which host alternates between peach (*Prunus persica*) and numerous secondary hosts, especially crops (brassicas, sugar beet, etc.), appears to show an intermediate migratory urge, studies using microsatellites suggesting a migratory ambit below about 50 km (Wilson *et al*., 2002; Guillemaud *et al*., 2003; Vorburger *et al*., 2003a). Again, this broadly supports earlier suction-trap studies (Taylor, 1977).

Gall aphids are interesting in that they have very inbred populations within the gall itself, as well as soldiers with modified morphology for defending the colony from attack by arthropod predators and parasitic wasps (Foster *et al*., 2000). The entire biological scenario is broadly supportive of Hamiltonian kin selection (Hamilton, 1964a,b), although one might well ask why such defensive strategies are not more prevalent among asexually reproducing organisms, including aphids other than gall-forming species, if they are as closely related to one another as still generally supposed (but see the section above on clones). What can be said is that besides showing all the signatures of significant inbreeding, including deviations from H–W equilibrium and linkage disequilibrium, colonies of gall-feeding aphid species tend also to show little indication of panmixia and intergall mixing (Hebert *et al*., 1991; Martinez *et al*., 2005). On the contrary, the colonies seem mainly to be self-contained genetic units and with little evidence of gene exchange (gene flow) between gall demes, a fact that suggests that inbreeding in these insects, as in aphids generally, may not be the terrible affliction it is often assumed to be in many animals (Loxdale, 2002), more especially among conservationists, for example, of rare and endangered butterflies (Saccheri *et al*., 1998).

In the studies using co-dominant molecular markers (i.e. allozymes or microsatellites), it has often been found that asexual populations show severe deviations from H–W expectations (due to the multiplication of particular genotypes/MLGs within asexual lineages), often with an excess of homozygotes or heterozygotes and linkage disequilibrium in the case of MLGs (Loxdale *et al*., 1985; Loxdale and Brookes, 1990a; Simon *et al*., 1999; Wilson *et al*., 1999; Delmotte *et al*., 2002; Guillemaud *et al*., 2003; Llewellyn *et al*., 2003; Rubiano-Rodríguez *et al*., 2014; discussed by Halkett *et al*., 2005; Loxdale and Lushai, 2007). The value of such data is that they provide an indication of the presence of asexual propagation, or even sexual reproduction with little obvious sign of perturbation due to migration, thus indicating that the subpopulations examined are genetically stable and probably

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not mixing much with other conspecific aphids from farther afield (Loxdale *et al*., 1998). For any given species, on plotting observed genotype numbers per locus versus expected genotype numbers, assuming the population samples taken to be in accordance with H–W expectations (hence a line with a 45 degree slope), deviations from the line reveal the presence of cryptic asexual genotypes within an apparently holocyclic population (Loxdale and Brookes, 1990a; Miller, 2000, Miller *et al*., 2003). Arnaud-Haond and Belkhir (2007) also provide a useful method for assessing the level of asexuality via calculation of the index, *psex*.

Metapopulations

It can be argued that perhaps all aphid species populations are metapopulations (Loxdale *et al*., 2010; Loxdale and Weisser, 2011). This is because these are often confined as colonies to single plants, the plants being separated such that once the initial winged foundress has landed and started reproducing on a suitable plant, the likelihood that wingless aphids, assuming they fall off the plant, can walk and find another plant is limited in terms of spatial scale, although some individuals do so successfully (Harrington and Taylor, 1990).

These considerations apart, some aphid species do appear to have 'classical' metapopulation structure (Hanski, 1998, 1999), whereupon individual colonies are subject to colonization and extinction events. Good examples include the tansy-feeding aphids, *M. tanacetaria* and *M. fuscoviride*, the latter an ant-attended species. The two species show different distributions on the natal plant and different behaviours. They also have somewhat different life cycles/morphs, although both are monoecious and holocyclic, colonies being formed in isolated stands of the host plant, which grows on poor soils, often at disturbed sites such as along railway tracks and waste ground (Massonnet, 2002; Massonnet *et al*., 2002; Massonnet and Weisser, 2004; Loxdale *et al*., 2011c). *Macrosiphoniella tanacetaria* tends to inhabit the new flush leaf growth and later flowering crown of the plant, whereas *M. fuscoviride* generally infests the stems. Perhaps because it competes with *M. fuscoviride*, ants tend to kill *M. tanacetaria* when encountered (Loxdale *et al*., 2011c; Mehrparvar *et al*., 2014). Perhaps, in turn, this explains why the former ant-guarded species rarely falls from the plant, whereas colonies of the latter readily fall when alarmed. *Macrosiphoniella tanacetaria* has winged males and asexual females, and wingless sexual and asexual females, while in *M. fuscoviride*, both sexual forms are wingless, although the asexual females can be winged (Hille Ris Lambers, 1939). The fact that the *M. fuscoviride* males are wingless impacts on the population structure and dynamics of this aphid compared with *M. tanacetaria*. Thus, while both species have very heterogeneous population genetic structuring (e.g. Massonnet *et al*., 2002; Massonnet and Weisser, 2004; Loxdale *et al*., 2011c), with even subpopulations in close proximity displaying high *F*st values (average ≥ 0.15), suggesting rather little interdeme gene flow, the values of divergence of *M. fuscoviride* are higher than those of *M. tanacetaria*, undoubtedly reflecting the difference in life cycle (Fig. 3.3). Probably, migration is confined to within a few kilometres in both species. Certainly, in *M. tanacetaria* there was no evidence of isolation by distance (IBD) effects over small spatial scales (Massonnet *et al*., 2002; Loxdale *et al*., 2011c), although such were noticed at greater distances (average 470 km; Massonnet and Weisser, 2004). Locally, *M. tanacetaria* populations were seen to exhibit some degree of genetic change throughout the growing season (decline in genetic variability with some degree of turnover of alleles), the former probably reflecting bottlenecking of populations in late summer, the latter relating to local intercolony movements, especially by winged males in the autumn originating from different colonies (Loxdale *et al*., 2011b). The reduced migratory ambit is probably related to the fact that the widely scattered plant resources (clumps of tansy plants) are difficult for the winged migrants to locate within the heterogeneous environment, and hence there has been strong selection over time against long-distant movements.

Superclones … or Superclans?

Work by Fenton *et al*. (1998) on the population genetic structure of insecticide-resistant lineages of *M. persicae* in Scotland showed that one genotype in particular (clone J) tended to dominate fields of potatoes and brassicas over a large area. Later work (Kasprowicz *et al*., 2008) using a suite of six polymorphic microsatellite markers on preserved 12.2-m suction-trapped or field-collected aphids, collected in Scotland over a 10-year period, and of known insecticide-resistance status, were shown to

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comprise predominantly of long-term asexual clones. Interestingly, of 1497 individuals analysed, 14 clones (denoted A–N) comprised over 98% of the collection. Accordingly, some lineages were especially abundant, while most were widespread on all the plants surveyed. In particular, two clones showed distinctive features: clone L was found only in the north-east of Scotland, while clone E occurred predominantly on brassica crops. The authors concluded that this confined distribution related to some degree of local adaptation in these particular genotypes (Kasprowicz *et al*., 2008). The predominance of asexuality in Scottish populations is generally considered to relate to the general scarcity of the primary host, peach, in this region (Fenton *et al*., 2003).

Such widespread 'superclones' have also been detected elsewhere (Table 3.1), e.g. in the invasive *Aphis nerii* (oleander aphid) (Harrison and Mondor, 2011) in the southern USA and *M. persicae* in south-eastern Australia (Vorburger *et al*., 2003a), while Piffaretti *et al*. (2013) showed that the globally distributed H2 lineage of *Brachycaudus helichrysi* (leaf-curling plum aphid), was dominated by just eight asexual genotypes. The study on *A. nerii* assessed genetic diversity with five polymorphic microsatellite loci over a 2-year period within and among three populations separated by small (100 km) and large (3700 km) geographic distances on two host-plant species – oleander (*Nerium oleander*) and milkweed (*Asclepias* spp.). Amazingly, genotypic variation was absent in all populations, each population comprising a single MLG, while the genetic composition of one population changed completely between the 2 sampling years. Not surprisingly, there was no evidence of sexual reproduction; nor was there any molecular signature of host races in aphids infesting the two hosts. In the study on *M. persicae*, aphids were collected at several sites in south-eastern Australia and surveyed using seven microsatellites. The distribution of life-cycle types correlated with climatic conditions, obligate asexuals residing in warmer climes, holocyclic forms in areas with colder winters (see the section above on life cycle), as well as with the availability of the primary host plant (more holocyclic genotypes in areas with peach orchards). Genotypic diversity was seen to increase in proportion to the number of cyclical parthenogens in a sample, since these represented unique genotypes; in contrast, the obligate parthenogens often showed multiple copies as a result of 'genetic inflation', that is, reproduction of asexual genotypes. Of these obligate asexuals, two were found to be especially abundant and widespread, that is, 24% and 17.4% of the entire collection, respectively (Fig. 3. 4). As with the two common *S. avenae* genotypes found by Haack *et al*. (2000) on wheat in France (see the section above on host-plant adaptation), both of these highly successful *M. persicae* genotypes were present in the majority of all collection sites.

The predominance of so-called superclones in aphid populations is by no means universal. It appears to be particularly common in populations recently introduced to areas outside the aphid's native range with a climate permissive of parthenogenetic overwintering. A good example is Chile, where several introduced pest aphids exhibit extremely low clonal diversity, such as *S. avenae* (Figueroa *et al*., 2005), *M. persicae* (Fuentes-Contreras *et al*., 2004) and *A. pisum* (Peccoud *et al*., 2008). This raises the question of whether superclones are really 'super' in the sense that they rise to high frequencies because they are favoured by natural selection (or anthropogenic selection by insecticides, for example), or whether they represent historical contingencies (i.e. first one there). The relatively rapid turnover of abundant clones in some populations (see below) would seem to support the former explanation. Under more 'normal' circumstances, superabundant clones seem to be observed less commonly. Loxdale *et al*. (2010) plotted the number of MLGs for *M. tanacetaria* and *M. fuscoviride* collected from tansy in Jena, Germany, and *S. avenae* caught in the field and in suction traps in the UK against copy number (number of MLG repeats). Surprisingly, regardless of whether the aphid was holocyclic (the tansy aphids) or largely anholocyclic (English grain aphid), similar negative exponential graphs were produced, showing that most colonies in these three species sampled at different places and times and by different means comprised mainly unique or small numbers of genotype copies (MLGs), trailing away to small numbers of genotypes comprising larger numbers of copies. In other words, most samples tested were highly genetically variable, arguing that due to selection and/or genetic drift, the lifetime of clones was brief, and that aphids did not show a lack of variation but rather appeared to have a wealth of it, regularly created by sexual recombination or by mutation to produce new variants.

If this interpretation is correct, and certainly it agrees broadly with the findings of Haack *et al*.

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Table 3.1. Aphid populations frequently comprise highly abundant and geographically widespread genotypes that reproduce by obligate parthenogenesis ('superclones'). The table includes examples of studies in which microsatellite analysis indicated the presence of such clones by the frequent sampling of individuals with identical multilocus genotypes (MLGs).

Species	Study area	*G*/*N*	*N*	Relative frequency of most common clone (%)	Reference
Acyrthosiphon pisum	Chile	0.037	432	46.8	Peccoud *et al*. (2008)
Aphis gossypii	Cameroon	0.009	1176	74.0	Brevault *et al*. (2008)
	Tunisia	0.020	559	37.9	Charaabi *et al*. (2008)
	Australia	0.014	936	40.4	Chen *et al*. (2013)
	Worldwide	0.012	3615	31.9	Carletto *et al*. (2009)
Aphis nerii	Southern USA	0.006	319	84.3	Harrison and Mondor (2011)
Brachycaudus helichrysi H2	Worldwide	0.036	224	34.8	Piffaretti *et al*. (2013)
Daktulosphaira vitifoliae	South-east Australia	0.125	361	31.9	Corrie *et al*. (2002)
Diuraphis noxia	Iran	0.133	376	31.6	Dolatti *et al*. (2005)
Melanaphis sacchari	Worldwide	0.004	1333	43.4	Nibouche *et al*. (2014)
Myzus persicae	Greece and southern Italy	n/a	482	19.7	Blackman *et al*. (2007)
	Scotland	0.042	188	25.0	Fenton *et al*. (2005)
	France	0.063	255	85.9	Zamoum *et al*. (2005)
	Victoria, Australia	0.437	167	24.0	Vorburger *et al*. (2003a)
	New Zealand	0.319	72	36.1	van Toor *et al*. (2008)
Myzus p. nicotianae	Chile	0.029	35	100.0	Fuentes-Contreras *et al*. (2004)
	Worldwide	0.160	430	14.4	Fuentes-Contreras *et al*. (2004)
Rhopalosiphum padi	France	0.135	1306	55.2	Gilabert *et al*. (2009)
	Australia	0.053	510	62.7	Valenzuela *et al*. (2010)
Sitobion avenae	North-west France	0.585	808	14.9	Dedryver *et al*. (2008)
	Chile	0.042	1042	35.9	Figueroa *et al*. (2004, 2005)
	Britanny, France	0.262	867	36.9	Haack *et al*. (2000)
	Great Britain	0.461	356	10.1	Llewellyn *et al*. (2003)
	England (southern)	0.328	238	26.5	Llewellyn *et al*. (2004)
Sitobion miscanthii	Australia	0.007	555	73.5	Sunnucks *et al*. (1996)
	China, Beijing area	0.315	143	18.2	Wang *et al*. (2008)
Sitobion n. fragariae	Australia	0.008	121	100.0	Sunnucks *et al*. (1996)
Tuberolachnus salignus	Europe and North America	0.024	660	34.2	Aradottir *et al*. (2012)

Notes: *G*/*N* = the number of different MLGs in the overall sample divided by sample size, a simple measure of clonal diversity; *N* = sample size; n/a = not available.

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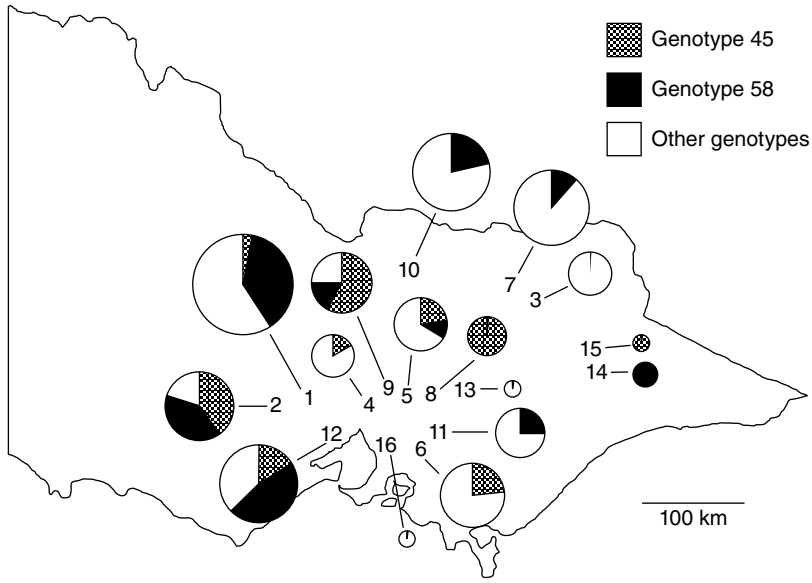

Fig. 3.4. Distribution and relative frequencies of the two most abundant and geographically widespread microsatellite multilocus genotypes of *Myzus persicae* across 16 locations in Victoria, south-eastern Australia, in 2002, showing that 'superclones' can predominate in aphid populations. Pie areas are proportional to sample size. (From Vorburger *et al*., 2003a; figure reproduced with permission of *Molecular Ecology*.)

(2000) that dominant genotypes are rare in *S. avenae* field collections, it may be that clonal competition (Stewart, 1996) is generally more intense than imagined and that, for most genotypes, they are indeed 'here today, gone tomorrow'. If that in turn is true, it is further evidence for the adaptive clonal genotype (Lushai *et al*., 2003) and against notions of multi-purpose genotypes; that is, that 'one clone fits all' – a view dismissed by Vorburger *et al*. (2003b). One or a very few genotypes may thrive for a while, but even in the case of the insecticide-resistance genotypes of *M. persicae*, it is clear that the turnover of particular resistance genotypes is rather quick. This is due to various selective pressures, including the fact that aphids with particular resistance mechanisms have pleiotropic fitness costs, expressed especially when spraying ceases (Chapter 19, this volume). Mostly, genotypes are monitored over a few years; we have no idea how particular genotypes fare over hundreds or thousands of years or more. This may be evidence for Red Queen-like processes occurring within natural aphid populations as individuals and closely related colonies, perhaps sometimes whole populations of briefly favoured (selected) clones, strive to keep apace genetically with a plethora of rapidly evolving predators, parasitoids and pathogens (see the section above on host-plant adaptation and also Loxdale *et al*., 2008, 2010; Loxdale and Weisser, 2011). In the end, variability is surely all, and the outstanding success of aphids must be accorded with this and not invariability.

This is a broadly analogous argument on the 'specialism' versus 'generalism' debate; if it were really true that generalists exist, why are there not a few hundred such generalist insect species globally rather than the million or so (probably many more) that we actually observe, especially in the tropics (Loxdale *et al*., 2011a)? The reason is that the world is a dynamic place and is forever changing, and living organisms must adapt accordingly to a complex, heterogeneous world with continuously unfolding ecological scenarios. A particular aphid genotype may be good for a while, i.e. successful in an ecological- evolutionary sense, but it does not last forever. Probably, the instances of aphid superclones mentioned here relate to the relative stability of agroecosystems, with their large areas of genetically closely -related crop monocultures. But this is not the 'real world', in the sense that nature has a free hand and most probably, despite the best efforts of humans to

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control ecological processes, even superclones cannot withstand the march of time.

Tracing the Origin of Aphid Genotypes

Several studies have attempted to trace the origin of particular aphid species or genotypes, including with respect to chromosome karyotype, but this is not an easy thing to do. For example, Hales (1993) was able to show from karyological evidence that certain insecticide-resistant genotypes of *M. persicae* had their origin in Europe and were transported to Australia probably during the past 50 years or so, undoubtedly by human agency.

Because insecticide-resistance mutations have been identified in several aphid species, they are often employed as potential indicators of the origin of aphid clones. It is important that this is done in combination with genome-wide markers, since identical resistance mutations are likely to arise independently in different genetic backgrounds (Anstead *et al*., 2005). Combinations of insecticide-resistance and microsatellite markers have been used effectively to monitor invasions of insecticide-resistant *M. persicae* genotypes into the UK (Fenton *et al*., 2005), as have microsatellites to track *M. persicae s.s*. and *M.p. nicotianae* globally (Margaritopoulos *et al*., 2009). No studies have yet used insecticide resistance successfully to trace the exact origin of aphid genotypes, but a global study is ongoing to trace the origin of the recently discovered M918L *s-kdr* mutation in *M. persicae* (Bass *et al*., 2014).

Microsatellite markers have been used to trace the prospective origin of New World populations of *M. persicae nicotianae* (Zepeda-Paulo *et al*., 2010). Bayesian analysis identified the most likely invasion scenario, which included a single introduction from Europe or Asia and a subsequent introduction from North America to South America. Liu *et al*. (2010) used a phylogenetic analysis of AFLP markers to investigate the relationship between North American and global *D. noxia* populations, which suggested that multiple introductions into North America had taken place. Because these invasions have occurred on an ecological (i.e. short) timescale, both these studies relied on markers with high mutation rates (microsatellites, AFLPs) that were not ideal for determining the source of incursions (Estoup and Guillemaud, 2010). Zhang *et al*. (2014) reconstructed the global invasion history of the Russian wheat aphid on cereals using a combination of microsatellite markers and gene sequences from the obligate symbiont, *Buchnera aphidicola*, which accumulated mutations much faster than aphid mitochondrial or nuclear genes (Fig. 3.5). Using a Bayesian computational approach, they were able to identify two independent global invasion pathways, pointing to human-assisted movement between continents (Zhang *et al*., 2014).

Detecting Foreign Bodies in Aphids Using Molecular Markers

Initially, allozyme electrophoresis was used to detect the presence of the larvae of hymenopterous parasitoids (Bracondiae: Aphidiinae; Fig. 3.6) within the bodies of their aphid hosts. The technique was not able to monitor the egg stage of the parasitoid, so it was liable to underestimate the true percentage of parasitism within natural aphid field populations. Even so, using a previously produced electrophoretic 'key' to the common species within the cereal agroecosystem in the UK (Castañera *et al*., 1983; Walton *et al*., 1990a), Walton *et al*. (1990b) were able to determine successfully the percentage parasitism of braconids attacking adult *S. avenae* within wheat fields in southern England, mostly by *Aphidius rhopalosiphi* and at levels of <40%. Later, using winged asexual adult aphids caught in suction traps, it was shown that the approach could be used to detect parasitoids within their flying hosts and revealed that parasitoids could be carried to the new-founded colony, such parasitized aphids often producing a few offspring before succumbing to the effects of parasitism (Walton *et al*., 2011; Derocles *et al*., 2014a). Traugott *et al*. (2008) used polymerase chain reactions (PCR) involving specific primers sensitive enough to detect a single parasitoid egg. Using this technique, they were able to detect endoparasitism by a total of 12 parasitoid species, again in *S. avenae*, including nine primary and three hyper- or secondary parasitoids. As with allozymes, over the growing season just under 20% were found to be parasitized, the proportion of parasitized aphids increasing monotonically over time until the host population crashed. Of the parasitized aphids, around 4% carried the DNA of two species of hyperparasitoid. Nine combinations of primary parasitoids within a single host were found, but only 1.6% of all screened aphids were parasitized by more than one hyperparasitoid. The authors

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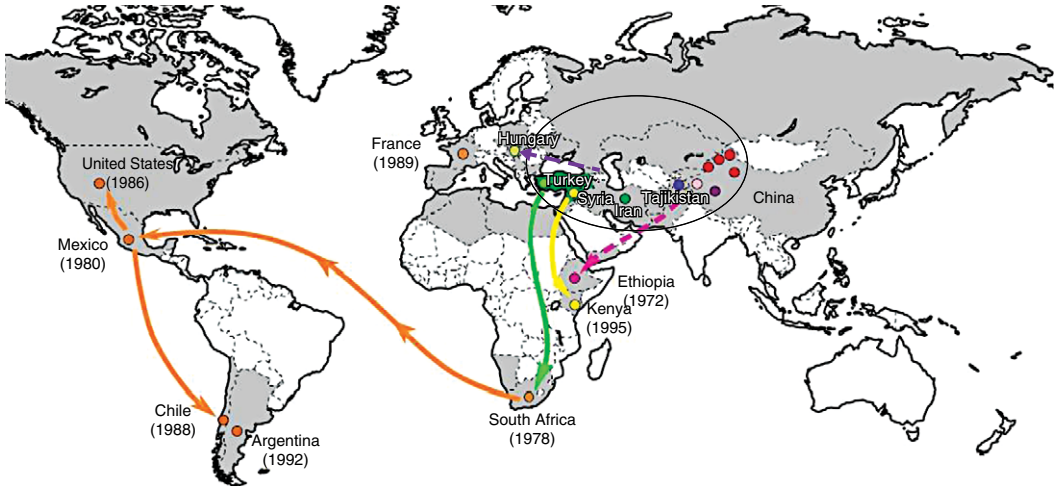

Fig. 3.5. Putative global invasion routes of Russian wheat aphid, *Diuraphis noxia*, starting in its native range in south-western and mid-Asia (area circumscribed by ellipse). Grey shading indicates countries where RWA has been reported, while the coloured dots indicate sampling sites. The green highlighted region in the Middle East is the assumed source of invasive clones. The solid arrows show the independent invasion pathways from the Middle East to Africa, the dashed arrows the possible native range extending to Ethiopia and Hungary. The year of first detection is given for selected countries. Distributions of the various RWA genotypes found were determined from the analysis of ten polymorphic microsatellite markers, two sequenced mitochondrial haplotypic markers (cytochrome oxidase I (CO1) and a continuous fragment centred on NADH dehydrogenase subunit 6 (ND6), including partial NADH subunit 4 L, two tRNA genes, total ND6 and partial cytochrome B) and three sequenced endosymbiont genes from the *Buchnera aphidicola* genomes: two from plasmids, TrpEG pseudogene and LeuBC, and one from genomic DNA, ddlB pseudogene (see Zhang *et al*., 2014). (Figure reproduced with permission of *Molecular Ecology*.)

Fig. 3.6. A female parasitoid wasp, *Lysiphlebus fabarum*, injecting an egg into an apterous third instar of *Aphis fabae*. (© Photograph by Christoph Vorburger.)

outline the potential of this approach in parasitoid food web research, a potential far greater than the less flexible allozyme systems of the previous two decades. This potential has recently been exploited by Derocles *et al*. (2014b) using rRNA 16S gene sequencing.

Molecular approaches have also been used successfully to detect entomophthoralean fungi in the bodies of their aphid hosts (e.g. using allozymes; Wilding *et al*., 1993) and, more recently, the presence of facultative endosymbiotic bacteria in aphids, and their role in host-plant adaptation has been explored in detail, especially by Simon *et al*. (2003) using 16S rDNA markers. The fact that aphids are very important plant-virus vectors can also be explored using molecular genetic approaches. Thus, in the case of *R. padi*, it is the wingless and winged asexual forms that overwinter on Poaceae successfully as live aphids that carry, and hence potentially transmit, barley yellow dwarf virus (BYDV), not the winged adult forms (exules) deriving from eggs hatching in the spring and migrating from the primary woody host bird cherry (*P. padus*) to Poaceae, including cereal crops. These life-cycle types can be differentiated readily using both chemical–visual approaches (Lowles, 1995), as well as molecular techniques, i.e. sequence characterized amplified regions (SCAR bands) (Simon *et al*., 1996; Terradot *et al*., 1999).

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Aphid Genomics

The first aphid genome was published in 2010, for the pea aphid (IAGC, 2010; Tagu *et al*., 2010; Chapter 2, this volume). This 530-Mb genome has been sequenced, partially assembled and annotated thanks to a community effort of the International Aphid Genomics Consortium (IAGC). Knowledge of the genome has a range of applications; for example, in evolutionary biology and phylogenetics (the history of species), the functioning of the genomes (What are the genes? What do they encode for? When are they active? What do they do?), the interplay with microorganisms (all eukaryotes are chimeras with bacteria) and the genetic diversity within the species. With allozymes and microsatellites, etc., only a very small portion of the otherwise large genome of aphids is surveyed. This may give a very biased and inadequate view of what is going on at the genomic level. The advantages of getting a sequenced, assembled and annotated genome are numerous. First, the number of markers and putatively polymorphic markers is enormous: the use of single nucleotide polymorphisms (SNPs) allows searching for genetic diversity with thousands of markers, and thus covering and describing at a high fidelity the genetic variations within populations, and even within an individual (allelic variation). This can be obtained by re-sequencing at low coverage the genomes of different populations to check, by mapping/alignment to the reference genome, the portion/bases of the genomes that show polymorphisms. Even now, such comparison of populations by re-sequencing can be performed in the absence of a reference genome (Quillery *et al*., 2014). Second, covering a whole annotated genome (even partially) allows choosing markers within genes or functional elements (markers supposed to be 'under selection') and markers within intergenic zones (supposed to be 'neutral'), depending on the application needed (phylogeography will use neutral markers but association genetics will prefer selected markers). Third, markers can be chosen as uniformly (or not) distributed on the different chromosomes, and can also discriminate sexual chromosomes from autosomes (Jaquiéry *et al*., 2013). Fourth, detected polymorphism can be correlated immediately with annotated gene elements whose putative functions can be assigned, in order to make the link between genotype and phenotype (such as in the identification of genes responsible for QTLs).

But what does a genome reveal in terms of the ecological adaptation of aphids? Several observations made of the genome structure and composition have allowed the revisitation of key physiological or development elements involved in aphid biology (pea aphid for the time being) in terms of sensing the abiotic and biotic environment. Catalogues of odorant-binding proteins (Zhou *et al*., 2010) and gustatory receptors (Smadja *et al*., 2009) and plant detoxification processes (Ramsey *et al*., 2010), as well as neuropeptides and neurohormones (Huybrechts *et al*., 2010), give the full complement of genes acting in the chemosensory apparatus of the pea aphid, gene families that often evolve quickly due to the diversity of the numerous effectors/ligands in the environment (pesticides, plant and natural enemy odours or volatiles). This description has now been used to understand the functions that are under selection, for instance, in host adaptation (see above), as well as sensing abiotic factors such as photoperiod (Cortés *et al*., 2010). Nutrition is complex in aphids since the diet is very restricted (phloem sap), lacks essential amino acids and suffers from the overconcentration of sugars (for which a duplication of sugar transporter genes has been noted; Price *et al*., 2010): the complex interplay with the obligatory symbiont *B. aphidicola* has been deciphered by comparing the whole gene complement of the host (the pea aphid) and the symbiont, and by examining the sharing of enzymatic activities between the two partners (Wilson *et al*., 2010; Hansen and Moran, 2011). Both *B. aphidicola* and the aphid genome contribute to the synthesis of several amino acids, but the pea aphid lacks genes involved in tyrosine degradation and arginine biosynthesis. This division of labour clearly impacts on the intimate relationship between the two partners, and probably contributes to the finely balanced equilibrium or control of this essential nutritional symbiosis. This has to be viewed in light of another specific observation: the pea aphid genome lacks a series of genes involved in the immunodeficiency pathway (IMD) (Gerardo *et al*., 2010), which might be related to the presence of a large number of bacteria (primary and secondary symbionts) in different body parts of the pea aphid.

Clearly, a general feature of the pea aphid genome is a large duplication, even expansion in many cases, of gene families (Huerta-Cepas *et al*., 2010), with a high number of predicted genes (>34,000) compared to other arthropods (with the exception of *Daphnia*).

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The causes of these expansions are unknown, and this concerns gene sequences only, not all genomic duplication. It involves many different gene families and, in some instances, such as the microRNA or piRNA machinery, duplicated copies diverged under positive selection from the original copies, and the copies have different expression profiles (Fig. 3.7), suggesting that new functions of these duplicated copies have been acquired (Jaubert-Possamai *et al.*, 2010; Lu *et al.*, 2011). A survey of natural populations to check the occurrence of sequence diversity within these gene family members needs to be performed to correlate finally their presence with ecological adaptation. In addition, this trend has to be checked in other aphid genomes to measure the specificity or generality of this observation.

The high number of predicted genes in the pea aphid genome was not expected. The challenge

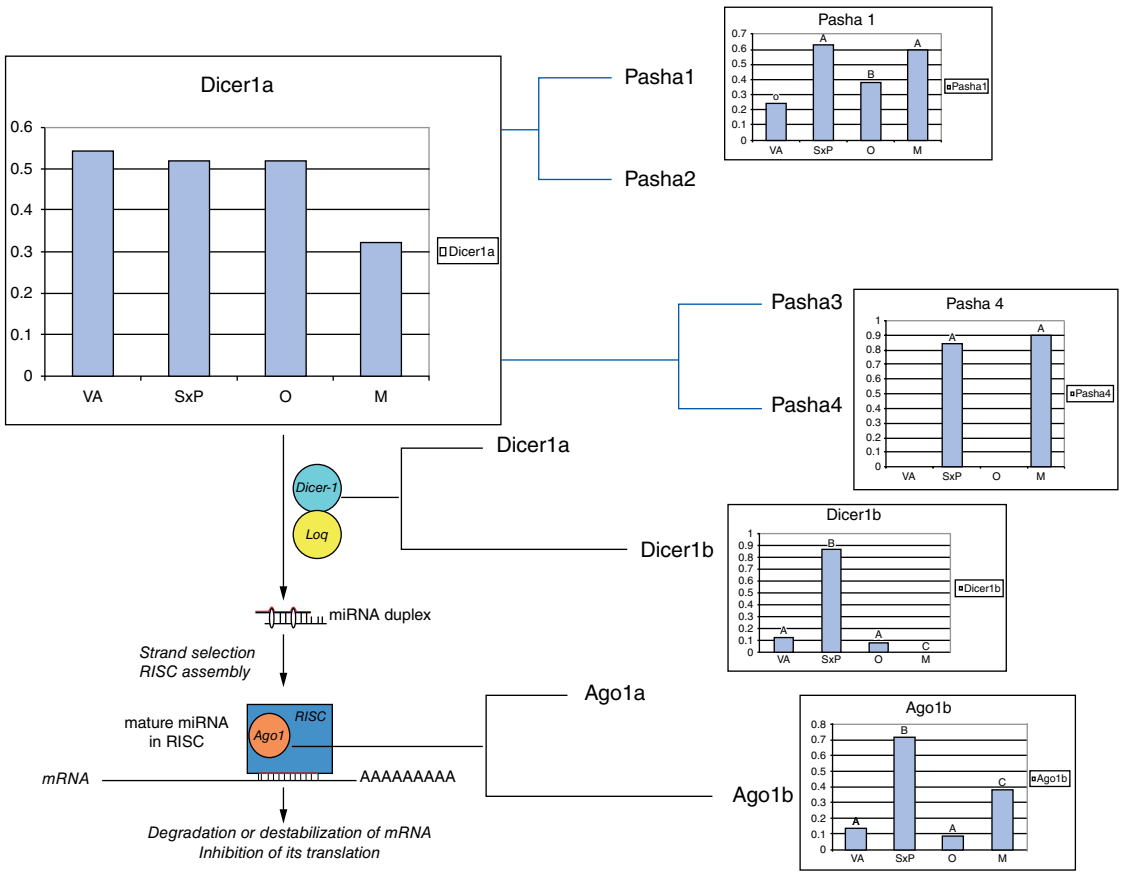

Fig. 3.7. Duplication of genes involved in the microRNA machinery in the pea aphid genome: differential expression of the divergent copies. Dicer1, Pasha2, Pasha3 and Ago1 are genes encoding proteins involved in different steps of the microRNA maturation. In the pea aphid, these genes are duplicated. In each case, one copy is very similar to the conserved copy in other insects (such as Dicer1a, Pasha2, Pasha3 and Ago1a), whereas the second copy is very divergent and sometimes with traces of positive selection (e.g. Ago1b), suggesting the acquisition of a new function. The conserved copies have a similar mRNA level of expression in different sexual morphs of the pea aphid: males (M), sexual females (= oviparae) (O), parthenogenetic females under long photoperiod (VA) and parthenogenetic females under short photoperiod (Sxp). However, the divergent copies have different mRNA expression profiles in these different morphs. For instance, Pasha1 and Pasha4 are more expressed in Sxp and M than in O and VA; Dicer1b is more expressed in Sxp than in the other morphs; Ago1b is more expressed in Sxp and M. This suggests that duplication of genes was followed in the pea aphid by diversification of expression profiles that could be related with diversification of functions. (*cf.* Jaubert-Possamai *et al.*, 2010.)

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now is to identify the functions of all these genes, mostly because a large number of the sequences recorded are so-called 'orphan' sequences, that is to say, with no homologous sequences in other species. Several hypotheses can be proposed: such duplications are neutral in terms of function; however, they may represent an added cost for the cell in terms of maintenance during cell division and DNA maintenance. These duplications might also be related to the high plasticity of the pea aphid to react to its environment; it is intriguing that such large numbers of orphan genes have also been found in *Daphnia*, which also develops a series of plastic traits (Colbourne *et al*., 2011). Thus, functional analyses and/or population diversity studies might help in the future to characterize the function of these 'new' genes and their putative implication in the ecological adaptation of aphids to their environment.

The upscaling of markers and genotyping possibilities allowed by genome sequencing and resequencing is now readily available in many laboratories worldwide, essentially because the price of DNA sequencing has decreased dramatically year on year, and throughput meanwhile is increasing in parallel. However, the 'smartness' of a population genetic experiment does not rely primarily on the techniques used for the detection of polymorphisms (even if it can help) but rather on the strength of the sampling processes and statistical treatments involved. So, population geneticists still need to keep their basic expertise in sampling and statistics. Ultimately, upscaling in terms of throughput depends completely on the capacity of a given laboratory to analyse genome sequences using bioinformatics, with connection to data centres able to store, calculate and display data, as well as strong connections with people suitably expert in bioinformatics.

In the case of aphid genomics, sequence data are made publicly available to the aphidological community at AphidBase (Legeai *et al*., 2010; available at http://bipaa.genouest.org/is/aphidbase/). AphidBase is a centralized bioinformatic resource that has been developed to facilitate community annotation of the pea aphid genome by the IAGC.

In conclusion, aphid population genetics enters a new era where the scientific questions remain the same as before but can be investigated by much more powerful techniques enabling the description and analyses of polymorphisms. The first genome available for these approaches was that of *A. pisum*. Already, several new aphid genomes have been published or are in progress, such as for *Diuraphis noxia* (Nicholson *et al*., 2015), *Myzus persicae* (Mathers *et al*., 2017), *Aphis glycines* (Wenger *et al*., 2017) and the grape Phylloxera, *D. vitifoliae* (unpublished).

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4 Life Cycles and Polyphenism[1]

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Introduction

Aphids display a diverse range of relatively complicated life cycles associated with seasonal changes and the ephemeral availability of suitable host-plant material. The life cycle is divided into stages characterized by one or more specialist phenotypes/morphs. Each of these morphs has a specific function that is necessary for the completion of that stage of the life cycle. Typical aphid life cycles have morphs that specialize in sexual and/or parthenogenetic reproduction, population dispersal/migration and surviving less favourable climatic or nutritional conditions. Not all morphs of pest species infest crop plants. How these life cycles, and related morphs, influence the likelihood of aphids becoming crop pests, when at least one host plant has economic significance, and the importance of the different life cycles for applied entomology are reported here.

Different aphid life cycles can have significant implications for the effect an aphid can have on crops. For example, the life cycle may determine whether a species is likely to encounter crops, and the number of different crops likely to be encountered during a year. Also, the population density of an aphid species depends, in any one year, on factors such as temperature and natural enemies, but the relative importance of these factors depends on the aphid's life cycle. The morph of a particular aphid species infesting a crop also influences the degree of damage the aphid will inflict. For example, wingless parthenogenetic morphs reproduce at a rate up to 70% greater than their winged counterparts (Noda, 1959; Dixon and Wratten, 1971), although obviously their capacity for long-range movement is removed. It is therefore important to understand the life cycles and morphs of aphids to determine if and how a species will damage a crop, and to assess and effect control measures.

The major types of aphid life cycle and the different morphs associated with each stage of the cycle are examined first. Factors that induce the production of the morphs that cause damage to crops are then discussed. Finally, the significance of life cycle and polyphenism in determining the pest status of an aphid species is considered, together with implications for forecasting and controlling aphid populations. Examples come mainly from aphid groups, in particular the Aphidinae and Eriosomatinae, which contain the most important pests, although the life cycles of other aphid taxa are considered when they provide useful comparisons.

Types of Life Cycle

There are two major types of aphid life cycle based on how the insect utilizes host plants: host alternating (heteroecious) and non-host alternating (monoecious, or autoecious). Host-alternating aphids live on one plant species in winter (primary host – usually woody plants), migrate to an unrelated plant species (secondary host – usually herbaceous plants) in spring/summer and migrate back to the primary host in autumn. Sexual reproduction gives rise to eggs that are laid on the primary host after males and sexual females (oviparae) have mated. Aphids that interrupt parthenogenesis with sexual reproduction in this way are termed holocyclic, whether

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heteroecious or monoecious. Non-host-alternating aphids remain either on the same host species or utilize closely-related host species throughout the year; that is, they can sexually produce eggs on the same group of host plants that is fed on by all of the parthenogenetic generations. Some aphid species reproduce continuously by parthenogenesis and never produce an egg stage, and these are known as anholocyclic. Some species show both holocycly and anholocycly in different clonal representatives, and some essentially heteroecious species have clones that appear to be anholocyclic, do not reproduce sexually and thus circumvent the need for host alternation (e.g. *Myzus persicae* (peach–potato aphid); Blackman, 1974). In addition, there are androcyclic clones that produce only the males of the sexual generation (e.g. *M. persicae*; Blackman, 1974). No extant aphid species reproduces solely by sex, although this is generally agreed to be the ancestral mode of reproduction (Moran, 1992). The life-cycle types are elaborated upon in this chapter, and their importance in determining the pest status is discussed. There are important crop pests using all life-cycle strategies.

Host-alternating aphids

Host-alternating/heteroecious aphids are often more economically important than non-host-alternating species, as the secondary hosts are usually herbaceous species, and frequently a crop plant. For this reason, and because of their unusual life cycle, these aphids have been particularly well studied, even though they represent approximately only 10% of aphid species. Despite its comparative rarity, host alternation is widespread across aphid groups, being found in four of the eight subfamilies of the Aphididae (the Aphidinae, Anoeciinae, Hormaphidinae and Eriosomatinae) (Shaposhnikov, 1981), suggesting that this life-cycle strategy in aphids has evolved several times.

A generalized host-alternating life cycle for the subfamily Aphidinae is shown in Fig. 4.1. Typically, mating occurs in autumn on the usually woody, primary host plant. Eggs are laid and overwinter as the diapausing stage. In spring, the eggs hatch and normally give rise to sequential generations of two highly fecund, apterous (wingless) morphs, the fundatrix, or stem mother, which give birth to the fundatrigenia generation. The latter produce the alate (winged) spring migrants, which fly to the secondary host, where they reproduce parthenogenetically. After several parthenogenetic generations throughout the summer, winged males and gynoparae are produced, and these migrate back to the primary host. The gynoparae produce oviparae on the primary host, which then mate with the males and produce the overwintering eggs. There are many variations on this general theme. For example, the eggs of *Brachycaudus helichrysi* (leaf-curling plum aphid) hatch in autumn and the fundatrix overwinters. The number of generations between egg hatch and the appearance of the winged spring migrants is variable in some species and may depend on the nutritional quality of the primary host.

The fundatrix usually has reduced sensory apparatus and restricted movement. It generally has shorter legs, cauda, siphunculi and, frequently, antennae with fewer antennal segments than other morphs. Depending on the species, the fundatrix can be winged, wingless, or brachypterous (possessing non-functional vestigial wings), and the fundatrices generally have more ovarioles in their gonads, associated with high rates of reproduction (Wellings *et al*., 1980; Leather and Wellings, 1981). The bodies of fundatrices are more rounded than those of the other parthenogenetic morphs, and can be many times larger. Much of this morphology again is associated with achieving a high reproductive rate, which can, in extreme examples, be 20 times greater than that of later occurring parthenogenetic generations (Hille Ris Lambers, 1966). The fundatrigeniae also have a high reproductive rate and a similar morphology. These two morphs result in the production of large numbers of spring migrants. Of these spring migrants, it has been estimated that only 0.2–1% succeed in locating a host (Taylor, 1977; Ward *et al*., 1998). The high reproduction on the primary host (by the fundatrix and fundatrigeniae) and later in the life cycle on the secondary hosts (by other parthenogenetic females) offset the potentially huge losses incurred during flight to new hosts (Kundu and Dixon, 1995). The coexistence of abundant plants that are suitable for colonization at different times of the year and the ability of aphids to produce a number of highly reproductive generations in quick succession have resulted in some 600 aphid species exploiting host alternation (Kundu and Dixon, 1995).

During the summer on the secondary host, several parthenogenetic generations develop. It is this phase of the life cycle that generally causes damage to crops. Within these generations, there is frequently further polyphenism that is induced either by

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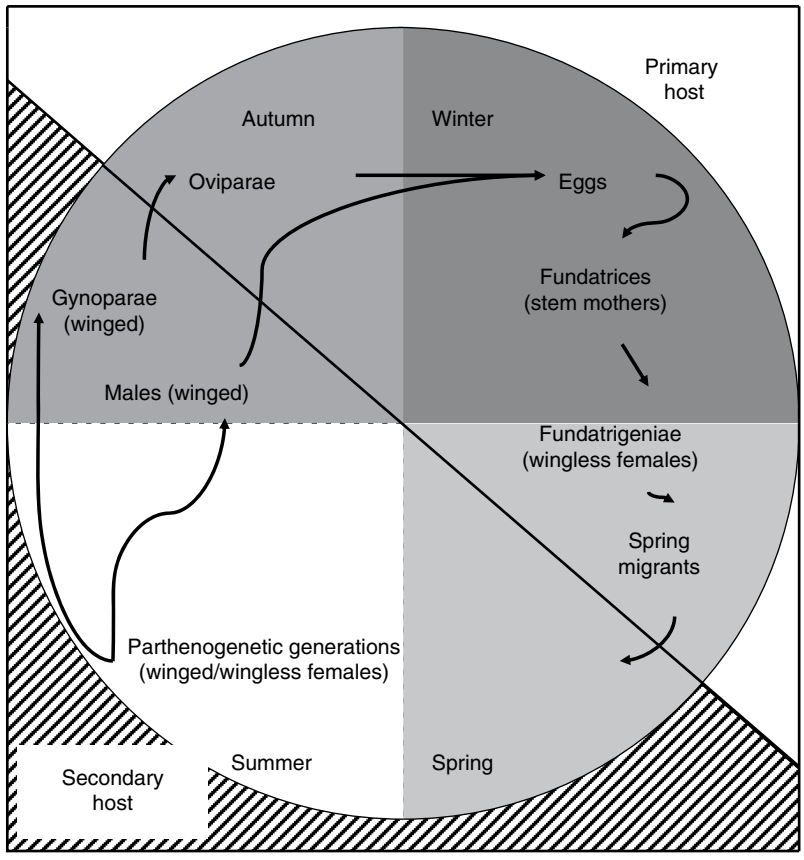

Fig. 4.1. A generalized life cycle of a host-alternating (heteroecious) aphid.

environmental factors or by direct genetic control, the latter depending on the generation. For example, in the Aphidinae, the first generation of individuals produced on the secondary host is usually wingless and often has shorter appendages and sometimes fewer antennal segments than individuals in the second and subsequent generations. These characteristics resemble those of the fundatrix, indicating a greater investment in reproduction at the expense of other capabilities. This is associated with a low predator pressure early in summer, and as natural enemy populations are low but increase during the summer, the increasing investment in sensory and movement functions may afford some avoidance behaviours (Lang and Gsodl, 2001).

Aphids readily colonize new environments, such as newly-emerging crops and annual plants, and rapidly increase in abundance, which predisposes them to become pests and results in them being difficult to control. Their ability to increase numbers rapidly may also enable them to modify plant metabolism to improve host quality for themselves and subsequent generations (Prado and Tjallingii, 1997; Williams *et al*., 1998). Such positive feedback is well known in galling aphids, but may also be a factor promoting the rapid population growth of non-galling aphids on crops (e.g. Dixon and Wratten, 1971).

Polyphenism in parthenogenetic wingless morphs is most marked in galling aphids. The fundatrices of these aphids often have reduced appendages and sensory apparatus, and similar morphs are produced again after migration to the summer host. Enclosure within a gall makes it advantageous for aphids to maximize reproduction, as they are somewhat protected. Many of the species of Pemphiginae and Hormaphidinae produce soldiers, which are typically early-instar nymphs and often reproductively sterile and morphologically and behaviourally specialized to defend the occupants

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of a gall. Surprisingly, these small and fragile soldiers, which are often present in large numbers, are very effective at protecting colonies against a wide range of insect natural enemies (Stern and Foster, 1996), and can even repair galls damaged by caterpillars (Kurosu *et al*., 2003). Such species are, however, generally not very important as crop pests and thus will not be considered further here.

Gynoparae and males are usually winged and, when adult, differ in host-plant preference from their mothers and the spring migrants, preferring their primary rather than secondary host (Powell and Hardie, 2001; Tosh *et al*., 2003). In the Aphidinae, the morphological differences between the winged parthenogenetic morphs and gynoparae are relatively small and generally restricted to the antennae (e.g. number and distribution of rhinaria; Hardie, 1980a). There are, however, phenotypic differences in flight behaviour, with the initial flight period of winged virginoparae readily interrupted by plant-like visual stimuli and gynoparae undergoing long initial periods of upwardly directed flight – gynoparae showing a true migratory behaviour (Nottingham and Hardie, 1989).

The production of males and gynoparae often is temporally separated, which results in the offspring of the gynoparae, the oviparae, co-occurring in time with males. Oviparous females show little polyphenism and are either similar in size to the apterous parthenogenetic females produced in summer, or are smaller (Dixon *et al*., 1998). Males are always winged in host-alternating species and fly from the secondary to the primary host, locating the oviparae using sex pheromones (Pettersson, 1970; Dewhirst *et al*., 2010). The oviparae and males mate to produce one or more eggs. These may be laid on the host, or occasionally (e.g. in the Fordini), the oviparae die with a single egg inside their bodies. The eggs remain dormant and hatch when determined by genetic and environmental factors such as photoperiod and temperature (Via, 1992; Komazaki, 1995).

The evolutionary origins of host alternation have been the subject of much debate (Moran, 1992; Dixon, 1998). There are two main opposing hypotheses, the adaptive (or complementary) and the maladaptive (or fundatrix constraint) hypotheses. The adaptive hypothesis assumes that the significant losses incurred during migration (Taylor, 1977; Ward *et al*., 1998) are outweighed by the increased fitness in summer compared to that if the aphid had remained on the primary host (Kundu and Dixon, 1995). The maladaptive hypothesis (Dixon, 1998) assumes that the fundatrix is so highly adapted to the primary host that the aphid has to return to the primary host (which is usually, but not always, phylogenetically older than the secondary host), as the fundatrix cannot survive on the secondary host. While this debate is academic with respect to pest status, the idea central to both hypotheses is that the population growth rate on herbaceous plants in summer is significantly greater than it would be if the aphid remained on the primary host (Kundu and Dixon, 1995).

Non-host-alternating aphids

Many monoecious aphids live only on trees and are unlikely to be agricultural pests, but can be (Evans *et al*., 2002). Others, such as *Acyrthosiphon pisum* (pea aphid) and *Sitobion avenae* (English grain aphid) live only on herbaceous hosts or grasses, and therefore may be found on crops throughout all or part of the year. Many of the monoecious species that now live only on herbaceous plants have evolved from heteroecious species that no longer utilize their primary host. A diagram of the monoecious life cycle is shown in Fig. 4.2. The same morphs generally are involved in the monoecious life cycle as are found in the heteroecious life cycle, and their characteristics are largely as described above for heteroecious species. However, the specific forms involved in spring and autumn movement between alternate hosts are not necessary. Here, only the particular characteristics of the morphs of monoecious species that differ from those of the corresponding morphs of heteroecious species are discussed.

The fundatrices of monoecious species are unlike those of most heteroecious species in being more similar to other apterous morphs of the species. For example, the fundatrices of heteroecious species generally are more rotund and can have five times as many ovarioles as individuals of the following generation, whereas in most monoecious species, the number of ovarioles and their morphology may differ only slightly between the two morphs. The high degree of specialization of heteroecious fundatrices may be associated with the tendency to gall, to various degrees, their primary host in spring.

The summer generations of monoecious species display similar characteristics to those of heteroecious species, capable of wing/wingless polyphenism depending on population density and/or nutrition.

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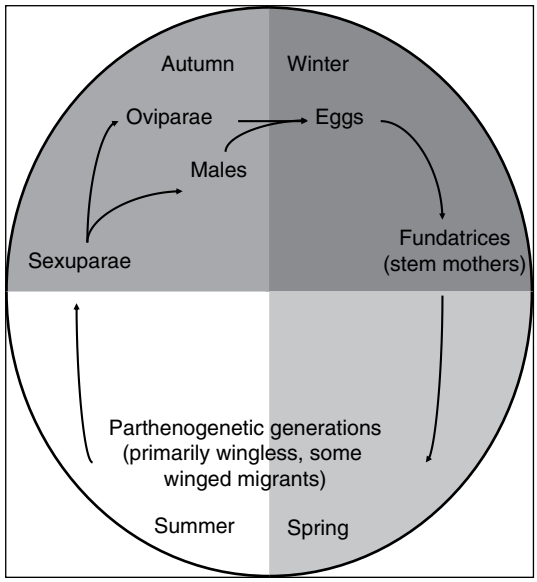

Fig.4.2. A generalized life cycle of a non-host-alternating (monoecious) aphid from the subfamily Aphidinae.

The sexual forms, males and oviparae, are produced in autumn and tend to be produced by the same mother (often apterous and termed sexupara). Males are genetically winged or wingless, depending on species or clone and mating results in the production of overwintering eggs.

Two-year life cycles

Some aphids within the tribes Fordini and Hormaphidini do not have the annual life cycles described above. They exhibit biennial life cycles during which galls are produced on one of the host plants. Some of these galls remain closed for over a year before producing winged morphs that move to another host. Such life cycles are not discussed in detail here as these species are rarely of economic importance.

Holocyclic and anholocyclic life cycles

The life cycles described above, host alternation, non-host alternation and 2-year life cycles, are termed holocyclic; that is, they are 'complete' in that the aphids undergo sexual reproduction, produce eggs and go through a viviparous, parthenogenetic phase. However, aphids do not always complete such life cycles. Under specific circumstances, some can survive throughout the year reproducing parthenogenetically. This is termed anholocycly and can be particularly important in agricultural ecosystems. In these life cycles, the aphids survive the winter as mobile parthenogenetic females, although in temperate regions they frequently suffer exceptionally high mortality (Harrington and Cheng, 1984; Leather, 1993; Williams *et al*., 2000).

Anholocyclic life cycles are found most frequently where the geographical range of an aphid is greater than that of its primary host plant. For example, the increase in the proportion of anholocyclic clones of *Rhopalosiphum padi* (bird cherry–oat aphid) in the UK from north to south is associated with a decline in the abundance of its primary host, bird cherry (*Prunus padus*). Another notable example is *M. persicae*, a major pest of many broad-leaved crops in northern Europe. The primary host of *M. persicae* is peach (*Prunus persica*), which is uncommon in the UK. As a result, *M. persicae* infrequently completes its full life cycle in the UK and overwinters on a large number of secondary hosts in the mobile stages (Williams *et al*., 2000). Although mortality is considerable (Harrington and Cheng, 1984; Leather, 1993), enough adults survive the winter to colonize crops in spring in sufficient numbers for the species to become a significant pest. Sheltered environments and milder climatic conditions can also influence winter survival and anholocyclic life styles.

Anholocycly is not confined to heteroecious species of aphids; approximately 3% of all aphid species are entirely anholocyclic throughout their range (Blackman, 1980). The summer and winter hosts of anholocyclic species are usually herbaceous.

For species to survive periods of adverse environmental conditions other than as eggs, specialist morphs may be produced (see below), or the adult females may adopt particular behavioural strategies (Dean, 1974; Dewar and Carter, 1984; McLeod, 1987). However, winter mortality of mobile morphs is generally much greater than that of eggs, as eggs are significantly more tolerant of low temperatures (Leather, 1993). The largest cause of mortality of eggs is frequently predation rather than low temperature.

There are clones of aphid species that have life cycles that are intermediate between anholocycly and holocycly. These clones produce only males or oviparae, but not both. For example, some clones

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of *M. persicae*, *S. avenae* and *R. padi* that pass the winter in the mobile stages produce males, but not oviparae. This is termed androcycly (Blackman, 1974; Simon *et al*., 1991; Helden and Dixon, 2002). This allows the ability to survive the winter in the parthenogenetic form to be passed through the sexual phase, creating genetic variability in continuously essentially parthenogenetic lines.

Factors Determining the Production of Different Morphs

For an aphid to progress from one stage of its life cycle to another, or to escape/counter untoward environmental conditions, it must respond to environmental or genetic cues either to produce offspring of a particular morph or for the early-instar nymphs to develop into a specific morph.

Determination of sexual morphs

Males and oviparae in temperate regions characteristically appear in autumn. In the case of host-alternating (heteroecious) aphids, however, asexual winged morphs are produced at this time on the secondary hosts and fly back to the primary host, where they produce either oviparae only or both oviparae and males. Those that produce only oviparae are called gynoparae and those that produce both sexes (i.e. in Pemphiginae, Hormaphidinae and Anoeciinae) are called sexuparae. That is, they appear in autumn and give birth to the sexual morphs and, therefore, although asexual, are included in this section.

The switch from parthenogenetic reproduction to the production of sexual morphs is determined by a number of environmental and genetic (intrinsic) factors that are similar for both heteroecious and monoecious species. As early as the mid-1800s, it was known that, given suitable conditions, aphids could continue indefinitely to reproduce parthogenetically. This led to the conclusion that environmental factors were involved in the production of sexual morphs.

Environmental determination

Marcovitch (1923, 1924) first demonstrated that photoperiod was important in the induction of sexual morphs, suggesting that short day lengths were associated with their production. Aphids were the first animals shown to respond to day length, shortly after photoperiodism had been demonstrated in plants (Garner and Allard, 1920). Thus, as day length influences the growth of plants, which in turn affects the diet of aphids, it was not until some 40 years later (Lees, 1961a, 1964) that the effect of photoperiod was unequivocally demonstrated to have a direct influence on aphids. Lees (1963) also demonstrated that the stimulus for the production of sexual morphs was actually the length of the dark period, rather than length of the light phase.

Temperature is also an important factor in the induction of sexual morphs. Sexual morphs are produced at shorter night lengths (longer day lengths) at lower temperatures, resulting in sexuals being produced earlier in the year when autumns are cool (Dixon and Glen, 1971), although slower development at lower temperatures also influences phenology. Lees (1963) calculated that for *Megoura viciae* (vetch aphid) a 5°C rise in temperature increased the length of the dark period required to induce sexual morph production by 15 min. Thus, there is some temperature compensation to allow an accurate prediction of calendar date; that is, *c*. a 5-day delay in the production of sexuals for a 5°C rise in average temperature. It is also of interest that the photoperiodic mechanisms for ovipara and male determination in the pea aphid, *A. pisum,* are different (Lees, 1990).

The host plant itself can also play a role in the induction of sexual morphs. This has been demonstrated both for root-feeding aphids, such as *Pemphigus bursarius* (lettuce root aphid), which cannot be influenced directly by day length, and foliage feeders, such as *Aphis farinosa* and *Dysaphis devecta* (rosy leaf-curling aphid). These species produce sexual morphs when plant growth ceases, regardless of day length (Hille Ris Lambers, 1960; Forrest, 1970). Root-feeding aphids such as *Pemphigus betae* (sugar beet root aphid) also produce sexual morphs in direct response to a decrease in temperature, regardless of day length (Moran *et al*., 1993).

Intrinsic factors

When aphids emerge from eggs in the spring, the conditions experienced by the first few generations in terms of day length and temperature may be similar to those experienced by aphids in the autumn. However, an intrinsic 'interval timer' has been shown to delay the production of sexual morphs

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(Bonnemaison, 1951; Lees, 1961b). For example, the offspring of *M. viciae* fundatrices do not produce sexual morphs for 80–90 days, even when reared in conditions optimal for sexual morph production (Lees, 1960). In *Eucallipterus tiliae* (lime aphid) and *Drepanosiphum platanoidis* (sycamore aphid), the proportion of sexual morphs produced in each generation gradually increases; even when environmental conditions are kept constant (Dixon, 1998).

The occurrence of males of some pest species in spring is relatively common in the UK; for example, in the case of *Brevicoryne brassicae* (cabbage aphid) and *Metopolophium dirhodum* (rose–grain aphid) (Taylor *et al*., 1998). This is contrary to what one would expect if an intrinsic timer prevented the early production of sexual morphs. As the occurrence of males in spring is more common after mild winters, this phenomenon is likely to be due to virginoparae from androcyclic clones surviving the winter rather than to virginoparae from holocyclic clones that passed the winter in the egg stage. As the interval timers of the mothers of spring males seem not to be operating, such timers may only operate immediately after the egg stage.

Determination of asexual winged morphs

The determination of winged morphs has long been known to be associated with crowding and the nutritional status of plants. The adaptive significance of this is clear, as under either of these conditions the production of winged morphs would presumably increase the chances of clonal survival as it facilitates escape from poor or depleted resources.

Crowding

Wadley (1923) was first to demonstrate experimentally that crowding was associated with the production of winged morphs. The stimulus appears to be physical contact between individual aphids (Johnson, 1965). A series of experiments in the 1960s showed that winged morphs could not only be induced by forcing individual aphids to come into contact with each other, but also by a range of physical stimuli including touching the abdomen with an inert object (Johnson, 1965; Lees, 1967).

However, not all aphid species respond in this manner, or at least do not have the same degree of sensitivity to such stimuli. Experiments with *M. persicae* show that this species does not always increase production of winged morphs in response to crowding (Williams *et al*., 2000). Müller *et al*. (2001) postulated that this might be due to non-gregarious species such as *M. persicae* being less responsive to the crowding stimulus than the more gregarious species such as *Aphis fabae* (black bean aphid) and cereal aphids. This may be because, for less gregarious species, the crowding stimulus is rarely present in the wild. Müller *et al*. (2001) surveyed 32 studies testing the influence of crowding on wing production in aphids. Experiments tended to show no increase in winged morph production when aphids were crowded in usual field-like conditions compared to isolated individuals. Evidence for aphids producing more winged morphs when crowded was strongest when aphids were reared in laboratory conditions that ensured physical contact between individuals. This suggested that, while physical contact was a clear stimulus for winged morph production, more gregarious species seemed to be more responsive to such a stimulus. It is also noteworthy that the crowding effect can be maternal/prenatal, and operate via the mother, or postnatal and solely depend on conditions that young-instar larvae experience, or a combination of both, depending on species (Müller *et al*., 2001).

Nutrition

The nutritional quality of a plant has also long been known to be associated with winged morph production (e.g. Wadley, 1923; Bonnemaison, 1951; Mittler and Dadd, 1966; Dixon and Glen, 1971). Artificial diets have been used to determine the effect of particular nutrients, such as folic acid (Raccah *et al*., 1973), sugars (Raccah *et al*., 1972), vitamins (Mittler and Kleinjan, 1970), amino acids (Mittler and Dadd, 1966; Dadd, 1968; Mittler and Sutherland, 1969; Leckstein and Llewellyn, 1973; Harrewijn, 1976), antibiotics (Mittler, 1971) and chemical 'tokens' or 'apterous promoting principles' (e.g. lithium) (Harrewijn, 1978) on the induction of winged morphs.

While these studies show that certain dietary components are important for wing induction in parthenogenetic generations, it is the overall diet quality and/or crowding that is likely to determine wing dimorphism. It is clear that when nutritional quality is poor, the production of winged morphs can be advantageous. This is supported by many studies (Mittler and Kleinjan, 1970; Sutherland and Mittler; 1971; Harrewijn, 1973, 1976; Mittler,

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1972), although not by others (Mittler and Dadd, 1966; Dadd, 1968; Mittler and Sutherland, 1969; Schaefers and Judge, 1971; Harrewijn, 1973, 1976; Leckstein and Llewellyn, 1973; Schaefers and Montgomery, 1973; Williams *et al*., 2000) (see Müller *et al*., 2001, for a review of these studies). The contradictory nature of these results may arise because the advantage of winged morph production is dependent on the predictability of current and future habitat quality. Such predictability is seen on an annual basis in trees, where the nutritional quality for aphids is high in spring, low in summer and high again in autumn (Kundu and Dixon, 1995). This cycle of nutritional quality also occurs in individual leaves of annual plants, where aphids have high growth and reproduction rates on very young and senescing leaves but not on mature leaves (Fig. 4.3) (Kennedy *et al*., 1950). The relative success of a strategy of 'sitting out' the period of poor nutritional quality in a reproductive diapause or a strategy of producing winged morphs and moving depends partly on the risk associated with finding a better host. The latter depends on factors such as the abundance of the host plant, the degree of polyphagy of the aphid species and the likely future quality of the current host.

Natural enemies, pathogens and mutualists

The induction of winged morphs by natural enemies and pathogens is a relatively new area of research, but one that has significant implications in the context of aphids as crop pests (see Chapter 10, this volume). The extent to which natural enemies induce or inhibit wing morph production would have implications for potential biological control strategies. Aphids spread plant pathogens, especially viruses, and therefore any influence on morph induction would influence disease epidemiology.

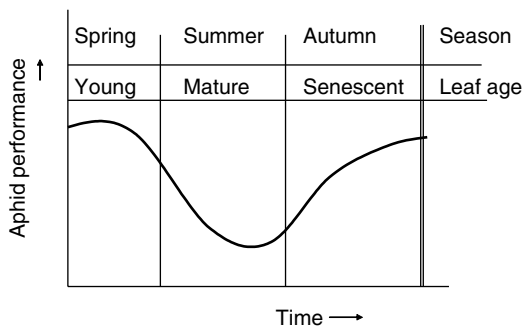

Fig. 4.3. The host quality of individual leaves of herbaceous plants during the summer and of trees for monoecious species. (From Kennedy *et al*., 1950; Kundu and Dixon, 1995.)

Most species of aphid are attacked by parasitoids. Early aphid instars are more susceptible to parasitoid attack than later instars, with, in the former case, the aphid being killed shortly before the parasitoid larva pupates prior to reaching adulthood. A few studies have assessed the influence of parasitoid attack on wing induction in individual aphids, the consensus of these studies being that parasitization inhibits the production of wings (Johnson, 1959; Liu and Hughes, 1984; Christiansen-Weniger and Hardie, 1998, 2000). The mechanism of reducing winged morph production is most likely to be through the composition of the calyx fluid released by the parasitoid into the haemolymph of the aphid during oviposition (Hardie and Christiansen-Weniger, 2001; Kati and Hardie, 2010).

While there is no evidence that aphids increase the production of winged morphs when attacked by parasitoids, there is evidence of them doing so when attacked by predatory beetles. This has been observed in *A. pisum* when attacked by ladybirds (Dixon and Agarwala, 1999; Weisser *et al*., 1999), although not when two other aphid species, *A. fabae* and *M. viciae*, were attacked by the same predatory species. This is likely to be due to these aphids having evolved other mechanisms that reduce their vulnerability to predators. For example, *A. fabae* is frequently ant attended (see below), and both species are unpalatable to natural enemies (Hardie, personal observations).

If aphid-vectored plant pathogens were to increase the production of winged morphs in an aphid population, then this would facilitate distribution of the pathogens, and clearly would have implications for epidemiology. The relationship between virus infection in plants and winged morph production has been studied in many crops. The aphids, *M. persicae*, *S. avenae*, *R. padi* and *Aphis gossypii* (cotton or melon aphid), have all been shown to increase their production of winged morphs when feeding on virus-infected plants (Macias and Mink, 1969; Gildow, 1980; Williams, 1995). However, it is unclear whether this is due to incidental changes in the nutritional quality of the phloem sap available to the aphids (Williams, 1995) or to virus particles more directly affecting the aphid's wing development mechanism.

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Interactions between plant pathogens and aphid parasitoids have also been reported. Thus, while a circulative, non-propagative virus can be transmitted more efficiently by parasitized vectors, the presence of the virus in the aphid host results in delayed parasitoid development, higher mortality and reduced oviposition by female parasitoids in viruliferous hosts (Christiansen-Weniger *et al*., 1998). The presence of parasitoids can increase the spread of non-persistently transmitted plant viruses, most likely by disturbing viruliferous aphids (Hodge *et al*., 2011).

The indirect role that mutualistic ants may have in reducing the production of winged morphs by mitigating the influence of ladybird attack (Dixon and Agarwala, 1999; Weisser *et al*., 1999) has already been mentioned. Ant attendance may also directly reduce the production of winged morphs (El-Ziady and Kennedy, 1956; El-Ziady, 1960; Seibert, 1992) by improving the health of the colony by reducing fungal growth through the removal of honeydew (Way, 1963) and by stimulating feeding (El-Ziady, 1960). However, ant attendance in annual crops is rarely observed, and therefore its significance in this context is likely to be minimal.

Other factors

Temperature may influence the morph of asexual generations, with higher temperatures tending to favour the production of wingless forms (e.g. Johnson, 1966; Lees, 1967; Schaefers and Judge, 1971; Liu, 1994). However, temperature is considered to modify the effects of crowding or nutrition in determining a change in morph rather than acting directly (Müller *et al*., 2001).

Diapausing morphs

Diapausing nymphal and adult morphs of aphids occur in summer (aestivation) and winter (hibernation), but this happens infrequently in pest species. As mentioned above, the nutritional quality of many woody hosts is poor for aphids during the summer months. Non-host-alternating species that remain on a woody host throughout the year have adopted numerous strategies to survive during the summer. For example, when the growth of its host slows down, *D. platanoidis* produces adults with poorly developed gonads and a large fat body to sustain them through the summer, when food quality is poor and crowding often acute (Dixon, 1975). Other species produce more morphologically distinct aestivating morphs. For example, *Periphyllus testudinaceus* produces morphs that are flattened and covered with plates that protect them from natural enemy attack. Many of these morphs are much smaller than other stages of the life cycle, and this may afford them some protection from natural enemies. The aestivating morphs of *Thelaxes dryophila* are sufficiently small to conceal themselves in the forks of leaf veins.

Hibernating morphs are termed hiemalis. These tend to have similar characteristics to aestivating morphs, such as large fat bodies and low reproductive capacity (Judge, 1967; Sutherland, 1968).

Eggs offer a robust overwintering diapause stage and are particularly well adapted to survive periods of low temperature, and clearly, once laid, they have no further nutritional requirements. For example, the eggs of *Rhopalosiphum insertum* (apple–grass aphid) can survive temperatures of –40°C (James and Luff, 1982). In addition, the termination of egg diapause and subsequent hatching are triggered by similar cues to those triggering the onset of plant growth in spring (Lushai *et al*., 1996; Ro *et al*., 1998). Thus, eggs are a very effective way of surviving winter in temperate regions.

The cues for the production of these diapausing stages vary. For example, in *P. bursarius*, temperatures of 10°C and short days stimulate the production of the hiemalis in the laboratory (Phillips *et al*., 2000). A combination of food quality, crowding and genetic factors produces the aestivating morphs in *D. platanoidis* (Dixon, 1972b).

Colour polymorphism

The colour of aphids can be due to pigmented internal tissues, pigmentation, or sclerotization of the cuticle or waxy exudates like those of *B. brassicae*. Colour either can be genetically fixed or environmentally triggered. Environmentally determined colour variation within a clone is usually reversible if conditions go back to their previous state.

Temperature and season are frequently associated with changes in aphid colour. For example, the highly colour-polymorphic *A. gossypii* is pale green at 25°C and dark green or dark brown at 12°C. Similarly, *D. platanoidis* develops dark pigmented dorsal bands on its abdomen when reared at low temperatures and red forms develop at high

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temperatures. Although this is tempered by genetic factors, as the offspring of fundatrices are green regardless of temperature, the influence of temperature becomes apparent only in later generations (Dixon, 1972a). Frequently, different morphs of the same species are also a different colour. For example, in *R. padi*, fundatrices are emerald green and fundatrigeniae are dark brown. The sexual morphs of many species are often a different colour from virginoparae.

Photoperiod influences the colour of *S. avenae*. The red form produces a larger proportion of green offspring when reared under short day lengths and low light intensities compared to the high proportion of red offspring produced under the reverse conditions (Markkula and Rautapää, 1967). Crowding can also induce colour change. The red form of *A. pisum*, for example, becomes pale green when reared under crowded conditions for a number of generations (Müller, 1961).

The nutritional quality of the diet can influence aphid colour. Green *M. persicae* produce pink offspring when reared on poor-quality hosts (Williams *et al*., 2000), and red *M. persicae* produce green offspring when crowded on poor diets (Ueda and Takada, 1977).

As little is known about the adaptive significance of different colour morphs, the implications for crop protection of environmentally determined colour polymorphism are not clear. However, when individuals of the same species can differ depending on environmental conditions, there are implications for the identification of pest species. Colour morphs can also be used to indicate 'stress' in an aphid population, for example in *M. persicae* (Williams *et al*., 2000), and therefore indicate when a population is likely to decline.

Colour within a species can be a genetic trait, as is well documented for *A. pisum*, *M. persicae* and various *Macrosiphum* species. The adaptive significance of genotypic colour difference is better understood than in the case of phenotypic colour variation, and may be useful for predicting the potential damage that may be caused by a colonizing aphid clone. For example, different coloured clones can have different reproduction rates, host preferences, feeding sites, tolerances of extreme temperatures, susceptibility to natural enemy attack, or other behavioural characteristics (Michaud and Mackauer, 1994; Battaglia *et al*., 2000; Weisser and Braendle, 2001; Dromph *et al*., 2002). However, why aphids often are not cryptically coloured is not clear, although tolerance of temperature extremes in pigmented aphids through their ability to absorb solar radiation and so increase their body temperature has been shown for some species (Markkula and Rautapää, 1967; Dixon, 1972b). Furthermore, brown forms of *S. avenae* are more protected against the damaging effects of ultraviolet radiation than are green forms (Thieme, 1997; Thieme and Heimbach, 1998). Colour has also been viewed as a form of defence from predators, either cryptic or warning (Stroyan, 1949; Losey *et al*., 1997).

Physiological control of polyphenism

It had long been proposed that as wingless adults resembled the young nymphal forms more closely than did the winged adults, the wingless adult was a neotenic form, and that wing dimorphism was likely controlled by a similar hormonal mechanism to nymphal/adult determination, namely by titres of juvenile hormone (JH) (Lees, 1966). However, later studies have proved somewhat contradictory, and while topical JH treatments affected 'successive' polyphenism (nymphal/adult progression) in *M. viciae*, it failed to affect 'alternative' polyphenism (the development of winged/wingless adults) in crowd-induced winged forms (Lees, 1977, 1980). The third instar was being most sensitive. More recent work (Ishikawa *et al*., 2013) repeated these studies on *Megoura crassicauda* (bean aphid) with similar results, but JH titre measurements indicated a slightly higher titre ($P < 0.01$) in third-instar insects developing towards wingless adults than the same instar developing towards the winged adult. However, topical JH inhibited wing development in short-day induced winged gynoparae of *A. fabae* when applied during the first and second instars, a period also sensitive to apterization by long days, and the resulting adults were apterized (an effect on successive polyphenism) rather than juvenilized (an effect on alternative polyphenism) (Hardie, 1980b). Juvenile hormone titres were also higher in aphids reared in long days than in short days (Hardie *et al*., 1985, and confirmed more recently Ishikawa *et al*., 2012). Discussions will continue on JH involvement in aphid alternative polyphenism, but the development of molecular techniques has begun to expand the understanding of the internal regulation of aphid polyphenism and this is discussed in Chapter 2, this volume.

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The Importance of Different Morphs for Crop Protection

Pest status

The importance of an aphid as a pest depends partly on how it damages a crop. If the damage is due to direct feeding, the morphs with the greatest reproduction rate cause the most damage. Apterous virginoparae can have up to a 70% greater reproductive output than their winged counterparts (Dixon and Wratten, 1971). Even among the Drepanosiphinae, parthenogenetic generations of which are always winged (Heie, 1987), morphs with reduced wings (brachypterous), which are incapable of flight, are more fecund than those with fully developed wings (macropterous) (Dixon, 1972c).

Virus transmission

Virus transmission is considered in detail in Chapter 15, this volume. The morphs most important for virus spread depend on the spatial scale being considered. Many viruses are brought into crops by winged aphids (primary infection), but the morph most important for spreading the virus within a crop (secondary spread) has been the subject of debate. Initially, winged aphids were considered to spread *Beet yellows virus* within fields of sugar beet (Watson and Healy, 1953). However, more recent work has shown that wingless aphids walking from plant to plant are more likely to be the major source of within-field virus spread (Ribbands, 1964; Jepson and Green, 1983; Williams *et al*., 2000). Molecular and immunological techniques that can detect virus particles in individual aphids (see Chapter 16, this volume) are now used to identify the morphs important in virus epidemiology. Furthermore, the quantity of virus can be measured using PCR techniques.

Forecasting

Forecasting aphid outbreaks is discussed in Chapter 16, this volume. However, it is worth mentioning here that the life cycle and factors affecting morph determination of aphids can have a significant impact on the ability to forecast the timing and severity of aphid infestation of crops. For anholocyclic aphids, the population size in spring and early summer, and therefore potential severity of crop damage during particularly susceptible growth stages, can be predicted from winter temperatures (Watson *et al*., 1975; Harrington *et al*., 1989, 1990). However, this is not the case for species that are holocyclic in the region of concern. The forecasting of many aphid pests that are holocyclic, and therefore overwinter as eggs, is more complex, as the winter mortality of such species is likely to be lower and certainly less dependent on temperature than that of anholocyclic species. However, the temperature in early spring, when the fundatrix and spring migrants are developing and reproducing, is more likely to be an important factor in determining the population size of such species in any particular summer. Several forecasts exist for holocyclic pest species, including *A. pisum* (McVean *et al*., 1999), *Phorodon humuli* (damson–hop aphid) (Jastrzebski and Solarska, 1998) and *A. fabae* (Way *et al*., 1981).

The Importance of Polyphenism in Determining Pest Status

The above is an account of polyphenism from an applied entomologist's point of view. However, to what degree is polyphenism associated with the pest status of aphids? By comparing the proportion of pest species in more or less polyphenic taxa, an attempt can be made to assess the role of polyphenism in determining the taxa's pest status.

Aphids can be compared with other insect taxa by determining the percentage of known aphid species that are pests with members of other taxa. For this analysis, an aphid pest is defined as a species listed by Blackman and Eastop (2000). These range from extremely well-known prolific pests such as *A. gossypii* to those where there is only one record of a species feeding on a crop. The list comprises 183 species, while Remaudière and Remaudière (1997) estimate that there is a total of about *c*.4700 aphid species. Therefore, about 3.9% of aphid species are pests (this excludes aphid vectors of non-persistent viruses that do not colonize the crop plant). This percentage was compared to that for the Order Lepidoptera, which comprises species that, like aphids, are predominantly herbivorous and thus have the potential to become crop pests. However, they are considerably less polyphenic than the aphids as adults, and only the larval stages inflict crop damage. It might be expected, therefore, that if alternative polyphenism is directly associated with aphids being such prolific pests, there would be proportionally fewer pests among the

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Lepidoptera than among the aphids. The number of lepidopteran species that are found on crops is approximately 6000 (Zhang, 1994). This figure includes a few beneficial species, although the majority of species listed, taken from the Arthropod Name Index (ANI) database of CABI, are pests. There are approximately 160,000 species of Lepidoptera worldwide (Barnard, 2011). Therefore, an estimation of the percentage of lepidopteran species that are pests is 3.8%. This is almost identical to the percentage of aphid species estimated to be pests.

To consider further the hypothesis that polyphenism predisposes aphids to become pests, each aphid genus with more than 30 species, with at least one species listed as a pest in Blackman and Eastop (2000), has been examined (Table 4.1). Host alternation might be used as a measure of polyphenism, as heteroecious species are generally more polyphenic than monoecious species. To reject the null hypothesis, it would be expected that heteroecious genera might have a greater percentage of pest species than monoecious genera. This is not the case, with 16% of heteroecious and 11% of monoecious species being pests ($\chi^2 = 3.75$; d.f. = 1; n.s.). The analysis suggests that the degree of polyphenism is not associated with pest status. However, it has to be noted that most host-alternating aphids are only pests on the secondary hosts during summer, not on the primary hosts, and the higher degree of polyphenism is associated with the host switch.

There are some 7000 species of plant cultivated as crops (FAO, 2016) and *c*.422,000 known plant species (*i*Plants, 2016); that is, some 1.7% of plants are crops. Thus, it appears that both aphids and lepidopteran pests are not distributed randomly across plants species but have taken the opportunity to exploit human agricultural endeavours. These data may, however, be biased in that many insect species remain to be identified and human resources will have concentrated on identifying pest species, which may thus be over-represented in the records currently available.

Conclusions

Although it is widely accepted that the pest status of aphids is associated with their high degree of alternative polyphenism, this does not appear to be so in relation to the proportion of species of aphid pests among the more polyphenic aphid taxa compared to the less polyphenic taxa. Further, comparison

Table 4.1. The percentage of aphid species that are pests for aphid genera with more than 30 species, at least one of which is listed in Blackman and Eastop (2000).

Genus	Number of species (approximate)	Number of pest species	Percentage pests	Predominant life cycle
Acyrthosiphon	100	12	12	Monoecious
Aphis	400	43	11	Heteroecious
Aulacorthum	50	8	16	Heteroecious
Brachycaudus	45	7	16	Heteroecious[a]
Dysaphis	100	16	16	Heteroecious
Greenidea	45	6	13	Monoecious
Illinoia	45	9	20	Monoecious
Macrosiphoniella	120	4	3	Monoecious
Macrosiphum	120	21	18	Monoecious[b]
Myzus	55	13	24	Heteroecious
Nasonovia	45	4	9	Monoecious[c]
Phylloxera	60	6	10	Monoecious
Pleotrichophorus	60	1	2	Monoecious
Prociphilus	50	2	4	Heteroecious
Schizaphis	40	5	13	Monoecious
Sitobion	75	17	23	Monoecious[c]
Uroleucon	180	9	5	Monoecious

Notes: [a]Mostly heteroecious, although some monoecious species are known. [b]*Macrosiphum* species are generally monoecious, although some, including important pest species such as *Macrosiphum euphorbiae*, are heteroecious. [c]Mostly monoecious, although some heteroecious species are known.

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with a less polyphenic non-aphid taxa indicates that a similar proportion of species are pests. However, in terms of the 'success' of individual aphid species as pests, the numbers/distribution/survival is undoubtedly influenced by their proclivity for polyphenism.

Aphids can damage crops in a number of different ways; for example, through toxins in the saliva injected into the plant, and directly by removing plant sap and indirectly by transmitting viruses. These types of damage can occur concurrently, caused by the same individual aphids. The more aphids present, the greater will be the direct damage. The most important factor in determining aphid abundance on a crop is the aphid's rate of population increase. In terms of virus damage, aphid abundance is not as important as the ease with which viruliferous individuals move from plant to plant. Therefore, the features of aphids that are the likely determinants of their pest status are their host range, prolific rate of reproduction and impressive powers of movement, which contribute to their abundance.

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5 Growth and Development

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Introduction

The growth and developmental rates of individual aphids have been studied extensively since the early investigations of Davis (1915) because they can be reliable indicators of future population growth rates (Leather and Dixon, 1984; Acreman and Dixon, 1989). In this chapter, we discuss the methods used to measure aphid growth and development, the relationships between these measures of aphid performance, and the reliability of using the results of such experiments to predict the performance of field populations of pest aphids.

Individual aphids frequently have extremely high growth and developmental rates, allowing populations rapidly to reach levels that are damaging to crop plants. Under optimal growth conditions, an individual aphid typically commences reproduction 7–10 days after it is born (Dixon, 1998). Such short development times are possible because newborn aphids contain the embryos of their first granddaughters. This 'telescoping of generations' means that an individual aphid has already completed two-thirds of its development before it is born (Dixon, 1998). Growth and developmental rates can be used to predict future fecundity because somatic growth and reproductive development occur simultaneously in the developing nymph, and thus can be affected simultaneously by any change in the rearing environment, although some exceptions exist.

Aphid growth and developmental rates are frequently measured in small-scale trials using single individuals, or small groups of similarly aged nymphs. In the first section of this chapter, the most commonly used measurements of aphid performance are described, with the relevant experimental techniques needed to investigate them. Factors that may affect the reliability of these approaches are then discussed, with a particular emphasis on studies that have investigated the relationships between the various measures of individual performance. Biotic and abiotic factors affecting the performance of individual aphids are outlined, and the need to control these in aphid performance studies is highlighted, as well as the potential limitations these represent when using laboratory-based studies to predict performance in the field.

Definitions

Aphid growth and developmental rates have been used extensively to predict the performance of aphid populations on crop plants because they correlate well with potential fecundity, achieved fecundity and the intrinsic rate of increase, r_m (Leather and Dixon, 1984; Dixon, 1990). Many aphid species show strong positive relationships between growth rates and potential fecundity (Lyth, 1985; Fereres *et al*., 1989). Similarly, adult size is frequently correlated with both potential fecundity (Dixon and Dharma, 1980; Kempton *et al*., 1980; Bintcliffe and Wratten, 1982; Llewellyn and Brown, 1985) and achieved fecundity (Leather and Dixon, 1984; Dixon, 1990, 1998).

'Growth' is defined here as an increase in aphid size; 'development' as the process of increasing reproductive maturity from birth to the first larviposition; 'potential fecundity' is a measure of the reproductive potential of an individual aphid – for example, the number of mature embryos contained

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in an adult; while 'achieved fecundity' is the total number of progeny produced by an adult. Potential fecundity may be a useful measure of aphid performance, as potential and achieved fecundity are frequently strongly positively correlated (Dixon and Wratten, 1971; Dixon and Dharma, 1980; Frazer and Gill, 1981; Leather and Dixon, 1984). Development rate and fecundity can be combined in the intrinsic rate of increase, r_m (Birch, 1948; Wyatt and White, 1977), an estimate of future population growth rates based on the performance of individual aphids.

Uses of aphid growth and developmental rates

The use of aphid relative growth rates to measure performance was initially suggested by van Emden (1969) as a means of measuring the direct effects of plant nutrition on aphid performance, without the confounding effects of maternal experience. Dixon (1990) and Leather and Dixon (1984) later demonstrated that relative growth rates and the intrinsic rate of increase, r_m (Wyatt and White, 1977), were strongly positively correlated (Fig. 5.1).

As a consequence, many authors have used mean relative growth rate (MRGR) or relative growth rate (RGR), defined below, when quick estimates of aphid performance are required; for example, to assess the resistance of plants to aphid attack (van Emden, 1969; Bintcliffe and Wratten, 1982; Givovich *et al*., 1988; Leszczynski *et al*., 1989; Wojciechowicz-Zytko and van Emden, 1995; Farid *et al*., 1998; Telang *et al*., 1999; Obopile and Ositile, 2010; Dahlin and Ninkovic, 2013), the quality of different growth stages of the host plant (Leather and Dixon, 1981; Ma and Bechinski, 2009), the effects of plant nutrition (Hosseini *et al*., 2010), the effects of temperature (Berg, 1984; Lamb *et al*., 1987), the effects of air pollution (Dohmen, 1985; Holopainen *et al*., 1997; Wu *et al*., 1997; Mondor *et al*. 2010) and the contribution of bacterial symbionts to aphid nutritional ecology (Adams and Douglas, 1997).

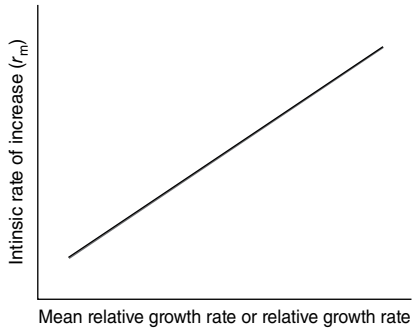

Fig. 5.1. Hypothetical relationship between aphid growth rates and the intrinsic rate of increase (r_m).

Similarly, the intrinsic rate of increase has been used to investigate the responses of individual aphids to changes in plant quality (Bintcliffe and Wratten, 1982; Lykouressis, 1984; Leszczynski *et al*., 1989; Obopile and Ositile, 2010), plant resistance (Dahlin and Ninkovic, 2013; Soffan and Aldawood, 2014), host nutrition (Nevo and Coll, 2001; Khan and Port, 2008; Hosseini *et al*., 2010; Stafford *et al*., 2012), temperature (Landin and Wennergren, 1987; Liu and Yue, 2000; Ma and Bechinski, 2009), drought stress (Sumner *et al*., 1986; Hale *et al*., 2003), atmospheric pollutants (Warrington *et al*., 1987; Awmack *et al*., 1997), host-plant virus infection (Fereres *et al*., 1989) and the sublethal effects of insecticide residues (Kerns and Gaylor, 1992).

Measurement of Aphid Growth and Developmental Rates

Growth rates

Most investigations of aphid growth rates have used living aphids to measure gain in fresh weight over a defined period, weighing the same individuals at the beginning and the end of the experiment (e.g. Banks and Macaulay, 1964; Tsitsipis and Mittler, 1976; Frazer and Gill, 1981; Kindlmann *et al*., 1992; Sunnucks *et al*., 1998; Manninen *et al*., 2000; Edwards, 2001; Mondor *et al*., 2010), although some authors, such as Lamb (1992), have used dry weight and have therefore used different individuals for each measurement.

Other investigations of aphid growth rates have taken advantage of the allometric relationships between aphid skeletal structure and size (Reddy and Alfred, 1981), using hind tibia length (Campbell, 1983) or antennal length (Varty, 1964; Murdie, 1969a,b). However, since the ratios of the sizes of some aphid body parts may change as the developing aphid grows (Varty, 1964; Dixon, 1987), such allometric relationships should be used with caution, unless used only within one instar and morph, e.g. apterous adults. Aphid growth rates are usually measured using individual aphids or small groups of aphids, often the progeny of a single female. Young (typically newborn) aphids

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are removed from their host plants, weighed on a microbalance and returned to the host plants for the desired time, after which they are removed and reweighed.

Aphid growth rates are a function of birth weight (Dixon *et al*., 1982; Carroll and Hoyt, 1986), as is weight loss when aphids are starved (e.g. Brough and Dixon, 1990). Since large aphids grow faster than small aphids (Dixon, 1998), measurements of aphid growth rates must correct for differences in initial weight. Both MRGR and RGR compensate for the increasing mass of the insect as it grows, since they are based on the logarithmic weight gain of the aphid.

The formula used to determine MRGR is based on an equation originally used by plant scientists (Radford, 1967):

$$\text{MRGR}\,(\mu g/\mu g/\text{day}) = (\log W_2 - \log W_1)/t_2 - t_1,$$

where W_1 = weight at the first weighing, W_2 = weight at the next weighing, $t_2 - t_1$ = the time (in days) between first (t_1) and second (t_2) weighings.

RGR is measured over the development time (D) of the aphid (i.e. from birth to the final moult, but before the onset of reproduction), and therefore takes the varying growth rate for different instars into account:

$$\text{RGR}\,(\mu g/\mu g/\text{day}) = (\log W_2 - \log W_1)/D.$$

There are experimental drawbacks associated with using MRGR or RGR to measure aphid performance. It is difficult to manipulate young aphids in the field and a very accurate microbalance is required to collect data. Newborn aphids can weigh as little as 30 µg (Dixon, 1998), and hence small inaccuracies in the measurement of initial weight can have large effects on the final value of MRGR or RGR because of the logarithmic nature of insect growth. A simple solution is to measure groups of aphids and use the average initial and final weights to determine growth rates. Although some aphid species appear not to be adversely affected by regular removal from their host plants (Newton and Dixon, 1990b), disturbance can have negative effects because aphids may take several hours to locate a suitable phloem element and commence feeding (Tjallingii, 1995; Diaz-Montano *et al*., 2007). Frequent disturbance may therefore lead to low estimates of aphid performance. The settling and feeding behaviour of aphids may also be affected by the treatment under investigation; for example, by components of host-plant quality such as concentrations of plant defensive metabolites (Zehnder *et al*., 2001), nutrient availability, and water stress (Ponder *et al*., 2001; Nowak and Komor, 2010) and by environmental factors such as elevated CO_2 atmospheres (Awmack *et al*., 1996). Feeding and settling behaviour may also vary according to the prior experience of the aphids used (Ramirez and Niemeyer, 2000), and even between individuals within a species (Bernays and Funk, 2000).

MRGR and RGR are, however, very simple and quick ways to investigate experimental treatment effects on aphid performance, since they may be measured over as little as 2 days (van Emden and Bashford, 1969; Adams and van Emden, 1972) and so represent a very attractive experimental procedure. Furthermore, the newly moulted adults produced after RGR is measured can be returned to the host plant to measure the fecundity achieved and r_m, or dissected to investigate treatment effects on potential fecundity.

Developmental rates

Developmental rates are determined by recording the period between particular events (for example, from birth to adult) and reporting the results as the reciprocal of the data. They can thus be used as a measure of performance (Berg, 1984; Carroll and Hoyt, 1986; Lamb *et al*., 1987; Lamb, 1992; Cabrera *et al*., 1995; Obopile and Ositile, 2010; Aqueel and Leather, 2011; Kos *et al*., 2015). Most aphids pass through four nymphal instars (Dixon, 1973) before moulting to the adult stage, although some species, such as *Rhopalosiphum nymphaeae* (water lily aphid), may have five instars, depending on rearing temperature (Rohita and Penman, 1983; Ballou *et al*., 1986). Measurements of development are particularly useful in studies investigating experimental treatment effects on aphids reared in field situations, as the aphids do not need to be removed from the host plant to be weighed. Instar duration may also be a useful measure, particularly in studies investigating the vulnerability of aphids to natural enemies that preferentially attack specific instars (Ives *et al*., 1999; Chau and Mackauer, 2001).

The reliability of development rate as a proxy of aphid performance is increased when used in conjunction with measures of fecundity. From this, the

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intrinsic rate of increase can be used to predict future population growth rates.

The intrinsic rate of increase, r_m

Birch's (1948) equation for calculating the intrinsic rate of increase of insect populations is usually replaced for aphids with the calculation of Wyatt and White, 1977, which relates the fecundity of an individual aphid to its development time. This much simpler calculation is possible because development time to larviposition in aphids is shorter than the ensuing reproductive period, and is advantageous with aphids since larviposition tends to become erratic in the later stages of reproduction.

$$r_m = (\ln Md \times c)/D,$$

where Md is the number of nymphs produced by the adult in the first D days of reproduction after the adult moult and D is the duration (in days) from birth to first larviposition. The constant, c, has a value of 0.738 and is an approximation of the proportion of the total fecundity produced by a female in the first D days of reproduction. It is obvious from this equation that a small change in development time will have a greater effect on r_m than an increase in fecundity of a similar magnitude. Although r_m has limitations (Awmack *et al.*, 1997), it is a favoured way of estimating population growth, as it is much easier than counting the thousands of aphids that are likely to occur in a real population.

While r_m includes both developmental and reproductive rates, and is often a more reliable measure of aphid performance than MRGR or RGR, it does have some limitations. r_m is a less sensitive measure of small, but biologically significant, changes in aphid performance (Lykouressis, 1984) and when treatments affect adult longevity but not development time (Sumner *et al.*, 1986). The fundamental assumption underlying the r_m equation is that a reproducing female will produce 95% of her progeny in the first D days of reproduction (Wojciechowicz-Zytko and van Emden, 1995). If this assumption is not met (for example, if a female dies after only a few days of reproduction), values of r_m overestimate the contribution of individual aphids to the growth of the population. Population growth rates of the pea aphid, *Acyrthosiphon pisum*, reared on *Vicia faba* (broad bean) and exposed to a neem-based insecticide, depended on the age at which the aphids were exposed to the insecticide. When individual *A. pisum* were exposed to this insecticide from birth, the population growth rates were negative. When, however, *A. pisum* were exposed as adults, there was no effect of this insecticide on r_m, highlighting the need to determine treatment effects on all aphid life stages (Stark and Wennergren, 1995).

Experimental Techniques

Aphid cages

Although the growth and development of individual aphids has been recorded under unrestricted field conditions (Cannon, 1984), most studies have used individual aphids reared in the laboratory or in controlled environments (van Emden, 1972; Dixon, 1998). Since newborn aphids are so small, it has become standard protocol to cage either an individual aphid or a group of aphids on the host plants.

The most commonly used aphid cage is the clip cage, originally designed by MacGillivray and Anderson (1957). Clip cages may range in size from those that cover a few cm^2 of the leaf to those that enclose whole leaves. As not all leaves used by aphids are flat, tubular cages based on gelatin capsules can also be used. These cages slip snugly over the entire leaf or stem, but can be opened easily without disturbing the occupants (Fisher, 1987). Alternatives to clip cages include gauze sleeves that can be used to confine aphids to specific parts of the plant (for example, stems). Whole plant cages, usually constructed of PVC tubes, open at the bottom and covered with gauze at the top, can be used to monitor colonies or aggregations of aphids that need free access to all or part of the plant (Markkula and Rautapaa, 1963).

Two clip cages, suitable for use on many crop species, are shown in Fig. 5.2. The Type I cage is the typical clip cage (MacGillivray and Anderson, 1957). The second cage (Type II) uses soft foam (Plastozote®, Watkins and Doncaster, UK) to minimize damage to the leaf surface and can also be supported with a standard plant stake, reducing strain on the leaf petiole, and can be opened without disturbing the aphids inside (Awmack, 1997; Huggett, 1997).

Disadvantages of aphid cages

Many clip cage designs have been criticized because they interfere with leaf gas exchange and may damage the leaf surface, changing leaf quality in

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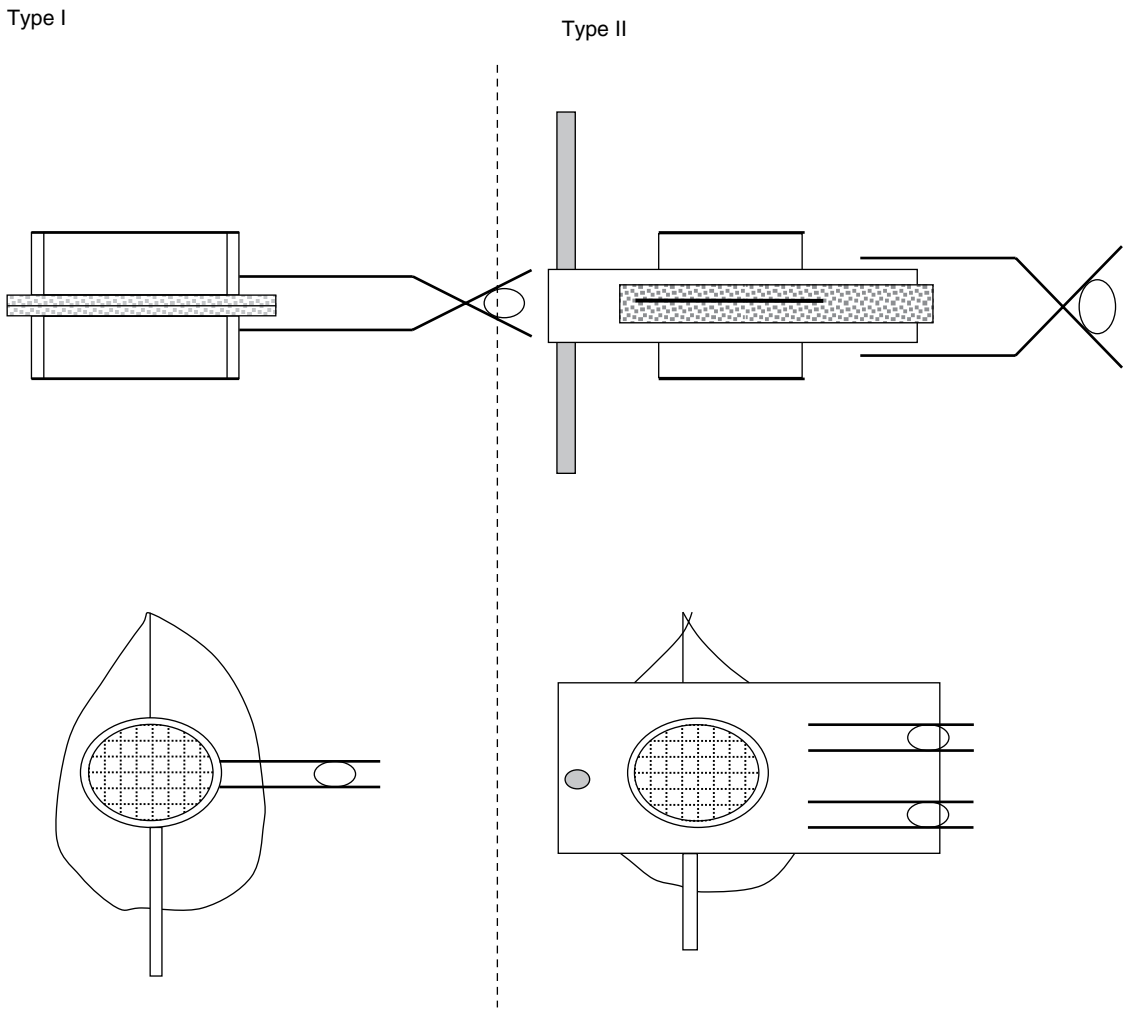

Fig. 5.2. Clip cages suitable for measuring aphid growth and development.

comparison with uncaged leaves (Crafts and Chu, 1999; Moore *et al*., 2003). The effects of larger cages on aphid performance have been documented from field experiments, as sunlight can be concentrated on to the plants, leading to temperatures within the cage that are considerably higher than ambient external temperatures (Woodford, 1973). In this case, large, muslin-covered frames may be placed over the plants to minimize fluctuations in microclimate. Alternatively, newer field cage designs involve coarser gauges to reduce microclimatic effects with the application of sticky glues to prevent movement in or out of the cages by small invertebrates (Thies *et al*., 2011).

A similar concern is that in a laboratory setting, aphid performance within cages may also not reflect the performance of uncaged aphids. Figure 5.3 shows the adult weight, development time and 7-day fecundity of *Rhopalosiphum padi* (bird cherry–oat aphid) reared without cages (control), in clip cages and in PVC tubes on oat seedlings (*Avena sativa* cv. 'Aster'). The data clearly show that clip cages and PVC tubes have an adverse effect on the adult weight of the aphids, and a small but significant effect on development time. The cages, however, had no significant effects on 7-day fecundity (S.R. Leather, unpublished). Adult weight and 7-day fecundity were positively correlated when the aphids were

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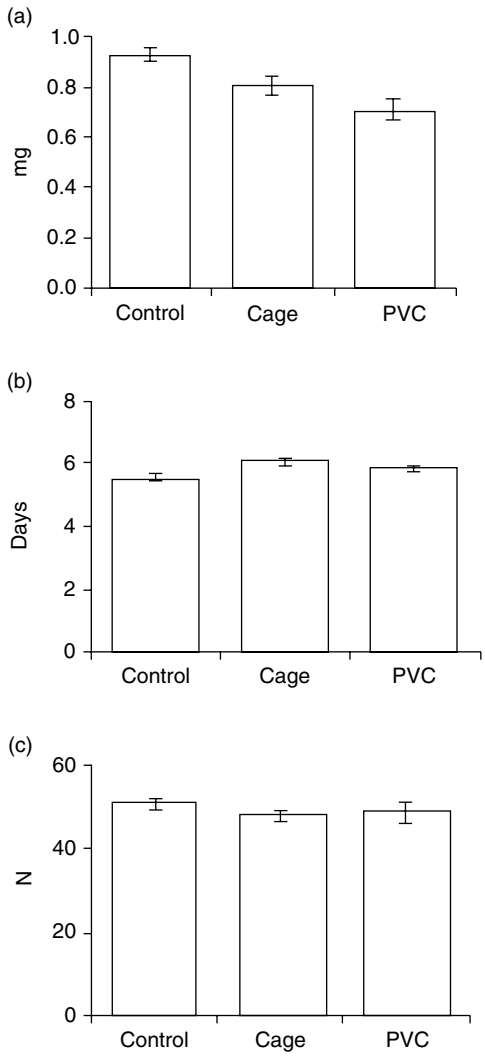

Fig. 5.3. Performance of *Rhopalosiphum padi* reared without cages, in clip cages and in PVC tubes on oat seedlings (*Avena sativa* cv. 'Aster'). (a) Adult weight (mg) ($F = 8.36$; df = 2.45; $P < 0.001$). (b) Development time (days) ($F = 6.10$; df = 2.45; $P < 0.001$). (c) 7-day fecundity ($F = 0.86$; df = 2.45; $P > 0.05$). All data are presented as the means of 16 replicates and are shown with ± the standard error of the mean.

reared in clip cages ($r^2 = 0.218$, $P < 0.05$) and PVC tubes ($r^2 = 0.417$, $P < 0.01$), but not when they were reared on uncaged control plants ($r^2 = 0.005$). Cages therefore affected not only the performance of *R. padi* but also the relationships between adult weight and potential or achieved fecundity. This example demonstrates clearly the problems inherent in comparing data collected using insect cages with data collected when the aphids are reared in more natural environments.

Limitations on the Use of Aphid Growth and Development Measures

While aphid growth and developmental rates often correlate with fecundity and intrinsic rate of increase and can be used to predict future fecundity (and hence population growth rates), some treatments affect the reliability of these relationships (Leather, 1988; Awmack and Leather, 2002). In this section, we discuss some examples where the assumptions of aphid relative performance measures are not met, and so their use as predictors of performance must be used with caution.

The reliability of size × fecundity relationships

Aphid size is determined predominantly by the quality of the larval host plant (Banks and Macaulay, 1964; van Emden and Bashford, 1969; Leather and Dixon, 1982; Acreman and Dixon, 1989; Gange and Pryse, 1990; Caillaud *et al*., 1994; Aqueel and Leather, 2011; Garratt *et al*., 2010), although the quality of the adult's host plant is also important (Markkula and Rouka, 1970; Watt, 1979; Leather and Dixon, 1981; McLeod *et al*., 1991) since aphids continue to mature offspring after the final adult moult. Some aphid species vary allocation of their resources between reproductive and somatic tissues, e.g. *Myzocallis boerneri* (Turkey oak aphid) (Sequeira and Dixon, 1996), *Drepanosiphum platanoidis* (sycamore aphid) (Douglas, 2000), *Megoura viciae* (vetch aphid) (Brough and Dixon, 1990) and *Sitobion avenae* (grain aphid) (Helden and Dixon, 1998). Thus, insect size may not necessarily be a reliable predictor of future fecundity (Leather, 1988; Mondor *et al*., 2010). Maternal effects (i.e. the host plant on which the parent of the reproducing aphid was reared) may also affect aphid size × fecundity relationships (Leather, 1989; Messina, 1993).

While there are generally strong and positive correlations between aphid growth and developmental rates and the intrinsic rate of increase, r_m, it has been shown that this relationship can vary with both the species of aphid under investigation and the growth stage of the host plant. Guldemond *et al*. (1998) demonstrated that the relationship between MRGR and r_m varied with both the species of aphid

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investigated (*Aphis gossypii* – cotton or melon aphid, or *Myzus persicae* – peach–potato aphid) and the growth stage of the host plant (chrysanthemum, *Chrysanthemum morifolium*). If experimental treatments affect such relationships (e.g. Kerns and Gaylor, 1992; Sarao and Singh, 1998), individual growth rates may not reflect population growth rates.

Variable growth, development and reproductive rates

Restricting measurements of aphid growth or fecundity to certain instars or periods of just 1 or 2 days and inferring performance or potential population increase from this can be convenient, but has risks. Aphid growth, developmental and reproductive rates are often not constant and may not respond to experimental treatments in the same way throughout the life of the aphid. Some aphid species, such as *S. avenae*, have high nymphal growth rates during early instars (Newton and Dixon, 1990b), while growth rates often decrease in later instars as the aphid switches resources to embryo maturation (Kindlmann and Dixon, 1989, 1992; Newton and Dixon, 1990b). Instar duration frequently varies, with the fourth instar being significantly longer than the first three (Kieckhefer *et al*., 1989; Araya *et al*., 1996; Dixon, 1998), particularly in the case of individuals destined to be alate (Newton and Dixon, 1990a). Many other insect groups show similar declines in growth rates as they develop (Scriber and Slansky, 1981). Treatments may therefore not affect all aphid instars equally, and early aphid instars may also be more sensitive to changes in the quality of their host plants than later instars. When *Schizaphis graminum* (greenbug) was reared on maize or sorghum cultivars, the host plant significantly affected the development time of the first and second aphid instars, but not the third or fourth (McCauley *et al*., 1990). Similarly, the development of first-instar *A. pisum* was slower on aphid-resistant red clover (*Trifolium pratense*) cultivars than on susceptible ones, but since later instars took less time to develop on resistant cultivars, the total developmental time was unaffected (Zeng *et al*., 1993).

van Emden found that a single value for MRGR gave a close fit to the weight increase of *M. persicae* throughout larval development (van Emden, 1969). However, in view of the previous paragraph, it would be wise to assess MRGR on aphids of similar age at the first weighing, and to do this early in nymphal development over a short interval of 2–4 days.

Changes in the reproductive rates of individual aphids may also affect the reliability of assumptions about the relationships between growth rates and adult size and fecundity, as not all aphids produce nymphs at a constant rate throughout their adult life. Zeng *et al*. (1993) showed that *A. pisum* produced more nymphs during the daytime than at night, demonstrating that measurements of fecundity must take place over at least 24 h. Many aphid species produce a rapid 'burst' of reproduction shortly after the final moult, and then show a reduced rate of reproduction for the remainder of their adult life (Dixon, 1998). Aphid reproductive strategies may also vary according to predictable changes in plant quality (Leather, 1987) or unpredictable environmental conditions such as starvation, crowding and predation (Leather *et al*., 1983; Ward *et al*., 1983; Gruber and Dixon, 1988; Brough and Dixon, 1990; Kouame and Mackauer, 1992; Muller *et al*., 2001; Kunert *et al*., 2005; Mehrparvar *et al*., 2013). The firstborn nymphs may not be representative of the entire progeny (Dixon *et al*., 1993) because birth order may affect subsequent performance. The firstborn nymphs of *A. pisum* are smaller than those born on subsequent days (Murdie, 1969b), but after about 7 days of reproduction, nymphal weight begins to fall and by 14 days the nymphs born are smaller than those born in the first 2 days. Similarly, firstborn *M. persicae* nymphs show greater cold hardiness than nymphs born later (Clough *et al*., 1990).

Decoupling development times and fecundity

Treatments that affect reproductive rates but not development times or growth rates also affect the reliability of r_m. *Sitobion avenae* (English grain aphid) reared on winter wheat at double-ambient CO_2 had greater fecundity than at ambient CO_2, but their development times were unaffected (Awmack *et al*., 1996). Similarly, *A. pisum* development time was unaffected by CO_2 and O_3, but subsequent aphid populations densities were (Mondor *et al*., 2010). In a similar experiment, when *Aulacorthum solani* (glasshouse and potato aphid) was reared on either broad bean or tansy (*Tanacetum vulgare*) at elevated CO_2, development time decreased and r_m increased on tansy but not on bean, while fecundity increased on bean but not on tansy (Awmack *et al*., 1997). In these examples, r_m is unlikely to be a reliable predictor of aphid population growth rates, as aphid fitness parameters

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appear to become uncoupled on exposure to this novel environment. The relationships between adult size and r_m may also become uncoupled if the aphid is exposed to starvation and resorbs embryos to release essential nutrients (Ward and Dixon, 1982; Brough and Dixon, 1990). Thus, a fundamental assumption underlying the r_m equation is that experimental conditions remain constant throughout the life of the aphid.

Factors Affecting Aphid Growth and Development

Aphid growth and developmental rates are affected by a wide range of both intrinsic and extrinsic factors such as diet quality (e.g. Watt and Dixon, 1981; Gruber and Dixon, 1988; Tsai and Wang, 2001; Vancanneyt *et al*., 2001), host nutrient supply (Hosseini *et al*., 2010), host resistance (Obopile and Ositile, 2010; Dahlin and Ninkovic, 2013), plant growth stage (Zhou and Carter, 1992; Ma and Bechinski, 2009), the abiotic environment (Kenten, 1955; Dean, 1974; Walgenbach *et al*., 1988; McVean and Dixon, 2001; Joschinski *et al*., 2015), maternal experience (Johnson, 1965; Dixon and Glen, 1971; Chambers, 1982; Kidd and Tozer, 1984) and maternal morph (Leather, 1989). In this section, some of the factors affecting individual aphid performance and the reliability of aphid growth rate, development rate and intrinsic rate of increase as predictors of the performance of aphid populations in the field are outlined, and some of the most common factors affecting observed differences between measures of aphid growth and developmental rates and the performance of natural aphid populations are discussed.

Genotype effects

Genetic variability may contribute to the variability inherent in natural populations. In many laboratory and greenhouse studies, the aphids are derived from parthenogenetic lineages, produced by a single parthenogenetic female. Natural populations are rarely as uniform (except in the case of pests of greenhouse crops, which may have very low levels of genetic diversity; Rochat *et al*., 1999). When apterous *S. avenae* were reared on oats, pink individuals developed more quickly than green individuals, highlighting the need to use multiple aphid genotypes in controlled experiments (Araya *et al*., 1996). Similarly, many aphid species such as *M. persicae*, *Aphis craccivora* (cowpea aphid) (Edwards, 2001), *Aphis glycines* (soybean aphid) (Kobayashi *et al*., 2013), *Sitobion miscanthi* and *Sitobion* near *fragariae* (Sunnucks *et al*., 1998), *A. pisum* (pea aphid) (Sandström, 1994), *R. padi* (Khan and Port, (2008) and *Phorodon humuli* (damson–hop aphid) (Lorriman and Llewellyn, 1983) show genetic variation in their growth and developmental rates, even when reared on hosts of similar quality.

Host-plant effects

Aphids used in laboratory-based studies are frequently confined to a specific part of the host plant (e.g. in clip cages) and reared at very low densities in the absence of other pests and diseases. Many aphid species perform better on specific host-plant parts (Watt, 1979; Leather and Dixon, 1981; Cibils-Stewart *et al*., 2015), and experiments that cage aphids on the 'wrong' part of a plant do not give an accurate representation of the performance of natural aphid populations. Hopkins *et al*. (1998) showed that even though *M. persicae* preferred senescing leaves at the base of its host plants (three *Brassica* cultivars, differing in their glucosinolate content) while *Brevicoryne brassicae* (cabbage aphid) preferred young leaves, regardless of the cultivar of the host plant, aphid performance was unaffected by plant defensive chemistry. Similarly, Williams (1995) investigated the impacts of host plants of different ages, with and without *Beet yellows virus* infection, on *M. persicae* and showed that performance was better on younger leaves than on old leaves, and that virus infection improved aphid performance. Table 5.1 shows the fecundity and development time of *S. avenae* when reared on different parts of oat and wheat plants (Watt, 1979).

Difference between nymphs destined to be apterous and alate

Measurements of aphid growth and developmental rates should also take into account differences between nymphs destined to be apterous adults and nymphs destined to be alate adults. Although alate aphids have a longer development time than apterae (Tsumuki *et al*., 1990; Araya *et al*., 1996), in some species (e.g. *R. padi*) alatae have greater longevity than apterae (Foster *et al*., 1988), and may therefore make a greater contribution to population growth rates. However, nymphs that develop into alate adults allocate a smaller proportion of their resources to reproduction (Newton and

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Table 5.1. Effects of rearing on different host plant parts of winter wheat (cv. 'Maris Huntsman') on the fecundity and development of *Sitobion avenae*.

	7-day fecundity	Time to adult moult (days)
Ears	41.7	8.5
Young leaves	26.5	8.4
Lower leaves	13.3	10.4
Flag leaves	17.6	9.8
Senescent leaves	14.5	9.0

Dixon, 1990b), since they must produce wings and the flight muscles needed to power them (Dixon, 1998). As a result, alate aphids typically have lower fecundity than apterae (Elliott *et al*., 1988; Newton and Dixon, 1990b; Collins and Leather, 2001). Alate aphids may also have a lower ovariole number (Dixon and Dharma, 1980; Leather, 1987) than apterae, differ in their amino acid and carbohydrate metabolism (Tsumuki *et al*., 1990) and have greater lipid reserves (Febvay *et al*., 1992). These differences may therefore mean that alatae and apterae respond differently to experimental treatments such as starvation or environmental factors; for example, Garsed *et al*. (1987) showed that the fecundity of alate *Aphis fabae* (black bean aphid) reared on broad bean increased as light levels increased, while that of apterae did not.

Alate production is stimulated by crowding (Watt and Dixon, 1981; Bergeson and Messina, 1997; Dixon, 1998; Muller *et al*., 2001; Hardie, Chapter 4, this volume), although the proportion of the population developing into alatae may vary among populations of the same aphid species on different host plant species (Bommarco and Ekbom, 1996). Alata production may also be stimulated on virus-infected host plants (Blua and Perring, 1992), and may either be stimulated (Liu and Wu, 1994) or suppressed (Parish and Bale, 1990) by low temperatures, depending on the species of aphid involved. As the apterous progeny of alatae may also have lower ovariole numbers than the progeny of apterae (Leather, 1987), the effects of experimental treatments on population growth rates may persist for more than one generation.

Effects of temperature

Aphid responses to temperature are similar to those of other insects. Most aphid species show a strong linear relationship between temperature and growth or development within the range of approximately 7 and 25°C (Campbell *et al*., 1974; Frazer and Gill, 1981), followed by a decline as temperatures increase. The exact shape and range of the curve depends on both the aphid species and the geographic origin of genotypes within the species (Auclair and Aroga, 1987; Lamb and Mackay, 1988; Akey and Butler, 1989), and may also be genotype-specific within a population (Lamb *et al*., 1987). Aphids reared at high temperature may also grow into small adults containing fewer embryos (Leather and Dixon, 1982; Collins and Leather, 2001), or have a poor ability to maintain embryo maturation after the adult moult (Carroll and Hoyt, 1986). High temperatures may also affect the slope of the relationship between adult weight and embryo number, making predictions of fecundity from adult size unreliable (Carroll and Hoyt, 1986).

Plant quality may also modify the impact of temperature on aphid growth and development (Leather and Dixon, 1982; Acreman and Dixon, 1989), as may abiotic factors such as wind (Walters and Dixon, 1984). Other authors (Liu and Perng, 1987; Kieckhefer *et al*., 1989; Xia *et al*., 1999) have also demonstrated that aphid performance decreases when aphids are reared at fluctuating temperatures rather than at the equivalent constant temperature. In contrast, Zhang *et al*. (1991) showed that the population growth rate of *R. padi* was greater at fluctuating temperatures than at constant temperatures.

Population-scale effects

Although a detailed discussion of population-scale effects on aphid performance is beyond the scope of this chapter, population density also has significant effects on aphid performance. At high population densities, aphids frequently produce alatae and leave the host plant (e.g. Watt and Dixon, 1981; Muller *et al*., 2001). Crowding (and intraspecific competition) may also reduce the per capita rate of reproduction as host-plant resources become limiting, the population growth rate decreases (e.g. Farid *et al*., 1998; Hodgson and Godfray, 1999; Awmack and Harrington, 2000; Bosque and Schtozko, 2000; Awmack *et al*., 2004), although in some cases aphid density has no effect on population growth rates (e.g. Messina, 1993). Some plant species may also exhibit a hypersensitive response, which is only apparent above threshold aphid densities (Lyth, 1985; Belefant-Miller *et al*., 1994). In contrast, many aphid species show enhanced

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performance when they are reared in groups, rather than singularly (Way and Cammell, 1970; Dixon and Wratten, 1971), because they are able to divert nutrients from other plant tissues more effectively (Sandström *et al*., 2000). Interspecific competition between aphid species exploiting the same host plant may reduce population growth rates (Fisher, 1987; Moran and Whitham, 1990; Thirakhupt and Araya, 1992; Gianoli, 2000), as may the presence of other herbivores, either directly (Masters, 1995) or via apparent competition involving shared natural enemies (Muller and Godfray, 1997), plant diseases (Coleman and Jones, 1988; Blua and Perring, 1992; Castle and Berger, 1993) or plant defence responses (Zhao *et al*., 2015). Due to the importance of population-scale factors, in some cases it becomes necessary to observe experimental treatment effects on aphid population development rather than using relative measures of performance. This is particularly relevant in field-scale studies, when multiple factors can interact and affect aphid success, including time of infestation, climatic conditions, natural enemies, soil nutrients and agricultural practices; in these cases, caged populations of aphids are often studied (Meihls *et al*., 2010; Thies *et al*., 2011; McCarville and O'Neal, 2013).

Conclusions

To use the growth and development of individual aphids as an indicator of aphid performance can be accurate and has practical and technical advantages, but due to the experimental way in which it is measured, it may not always reflect true aphid performance in the field and so must be used with caution. r_m incorporates aphid development and fecundity and can correlate well with aphid population growth (Wyatt and White, 1977), and so is perhaps a more reliable measure of aphid performance than the growth rate or development rate alone. Given the effects of genotype, feeding location, instar and temperature on aphid performance and the relationship between relative measures of aphid performance, it is vitally important these biotic and abiotic factors are considered and controlled when studying experimental treatment effects on aphid performance. When, however, multiple factors at the population level including competition, crowding, plant resistance and nutrient sink effects are considered, it is more accurate to measure aphid performance in populations rather than in individuals.

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6 Nutrition and Symbiosis

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Introduction

A single question dominates the study of aphid nutrition: how does plant phloem sap, a nutritionally unbalanced diet of high C:N content, support the remarkably high growth and reproductive rates characteristic of many aphid species? The 'short answer' to this question has two elements. First, phloem sap offers a near-continuous supply of small organic compounds, principally sugars and amino acids, which require the minimum of digestive processing; consequently, the assimilation efficiency of aphids is exceptionally high. Second, the key nutritional inadequacy of phloem sap, the low essential amino acid content, is met by symbiotic bacteria in the aphid.

The 'long answer' to this opening question requires a mechanistic understanding of aphid nutrition and its interaction with the functions of the symbiotic microorganisms, and this is the topic of this chapter. Research on aphid nutrition has been dominated by carbon and nitrogen nutrition, and these topics are addressed in the third and fourth sections, respectively. The fifth section summarizes our current understanding of the mineral and micronutrient requirements of aphids. First, however, the key features of microbial symbiosis in aphids are reviewed.

Two technical advances have been vital in the development of research on aphid nutrition and symbiosis: first, chemically defined diets of a composition that is known precisely and can be manipulated readily; and second, aphids can be experimentally deprived of their symbiotic bacteria. Diet studies, often involving bacteria-free aphids, are now used routinely to investigate various aspects of aphid nutrition; for example, the identification of dietary requirements and analysis of nutrient utilization patterns. The value and limitations of such diet-based studies to explore aphid nutrition are assessed in the concluding section of this chapter.

Microbial Symbiosis in Aphids

Diversity of microorganisms

Aphids generally bear very few types of microorganisms, usually less than ten taxa. Nearly all aphids of the family Aphididae possess bacteria, known in the traditional literature as 'primary symbionts' and assigned by molecular criteria to a novel genus and species, *Buchnera aphidicola*, in the γ3-proteobacteria (*Escherichia coli* is also a member of this group) (Munson *et al*., 1991). Many aphids additionally bear one to several other bacteria, known as 'secondary symbionts', usually at a ten-fold lower density than *Buchnera*. The secondary symbionts in various aphid species have been studied, and include γ3-proteobacteria, *Serratia symbiotica*, *Candidatus* Hamiltonella defensa and *Candidatus* Regiella insecticola, a α-proteobacterium *Rickettsia* sp. and *Spiroplasma* (Fukatsu *et al*., 2001; Moran *et al*., 2005; Sakurai *et al*., 2005; Russell *et al*., 2013b). *Buchnera* is coccoid and usually 2–4 μm in diameter, but 'giant' forms exceeding 10 μm occur occasionally. The accessory bacteria are small cocci (<2 μm in diameter) or rods of variable length (<2–20 μm).

Aphids known to lack *Buchnera* are: some members of the subfamily Cerataphidini, which have pyrenomycete yeasts (Suh *et al*., 2001); the Adelgidae, with both β- and γ-proteobacteria (Toenshoff *et al*., 2012a,b); and the Phylloxeridae, which apparently have no symbiotic microorganisms (Buchner, 1966).

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Location of symbiotic microorganisms

The *Buchnera* are restricted to insect cells called bacteriocytes (Fig. 6.1a), which are specialized to house and maintain these bacteria, and are located in the haemocoel of the insect. The bacteriocytes are large (up to 100 μm in diameter), glistening silver or coloured with green, red, or brown pigment, varying between species, and often aggregated together as a coherent organ known as the bacteriome, lying dorsal to the gut. The *Buchnera* cells are restricted to the cytoplasm (Fig. 6.1b) and occupy *c*. 60% of the cytoplasmic volume (Whitehead and Douglas, 1993). The tissue distribution of secondary symbionts is generally wider than that of *Buchnera*. Secondary symbionts (Fig. 6.1c) are very commonly located in 'sheath cells' surrounding bacteriocytes, free in the haemolymph and also within bacteriocytes (although apparently never in the same bacteriocyte as *Buchnera* cells; Fukatsu *et al*., 2000). The incidence of microorganisms in the gut lumen of aphids is variable. The alimentary tract of some aphid individuals is microbially sterile, others have taxa ingested with food and passing directly through the gut, and some bear a more or less resident microbial community, which may include species of the genera *Enterobacter*, *Erwinia* and *Staphylococcus* (Grenier *et al*., 1994; Leroy *et al*., 2011; Sabri *et al*., 2013; Jing *et al*., 2014).

Acquisition of symbiotic microorganisms

Aphids acquire their complement of *Buchnera* exclusively from their mother. In other words, transmission of *Buchnera* is obligately vertical. The bacterial cells are released from bacteriocytes abutting the germarium of the aphid ovaries and are transferred directly to the early embryo (blastoderm stage) in parthenogenetic morphs or the cytoplasm of the unfertilized egg of oviparae (Fig. 6.1d) (Hinde, 1971; Koga *et al*., 2012). *Buchnera* probably have

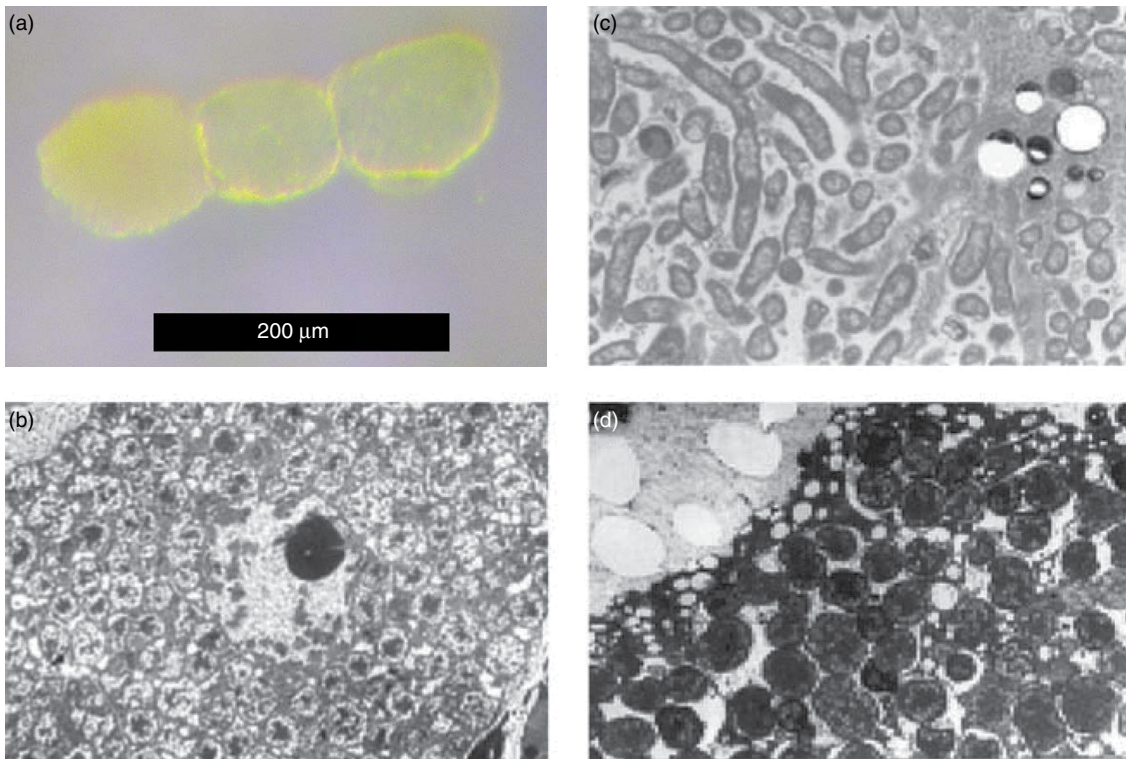

Fig. 6.1. The symbiotic bacteria associated with aphids. (a) The aphid bacteriocyte. Light micrograph of bacteriocyte isolated from 7-day-old larval pea aphid *Acyrthosiphon pisum* (b) *Buchnera* are coccoid cells in cytoplasm of bacteriocytes; (c) rod-shaped accessory bacteria in aphid tissues; (d) *Buchnera* cells are transmitted to the cytoplasm of unfertilized eggs in the ovaries of oviparae. (Previously unpublished micrographs of Jia Hsin Huang and Angela E Douglas.)

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been transmitted faithfully from mother to offspring for more than 100 million years, and possibly since the origin of the Aphididae, as indicated by the remarkable congruence between the phylogeny of aphids and *Buchnera* and the magnitude of sequence differences between rRNA genes of *Buchnera* in different aphid taxa (Moran *et al*., 1993).

The phylogenies of aphids and their secondary symbionts are not congruent (Russell *et al*., 2003, 2013b; Henry *et al*., 2013). Aphids acquire secondary symbionts from multiple sources: vertically from their mother during sexual reproduction (from male to female), and by feeding. Vertical transmission of most secondary symbionts is regular, with an efficiency of >98% (Darby and Douglas, 2003), although lower frequencies have been recorded, for example for *S. symbiotica* (Peccoud *et al*., 2014); sexual transmission rates are low and variable (Moran and Dunbar, 2006; Peccoud *et al*., 2014), and acquisition by feeding is reliable under experimental conditions but of uncertain prevalence in the field (Fukatsu *et al*., 2000; Darby and Douglas, 2003; Chandler *et al*., 2008).

Significance of symbiotic microorganisms to aphids

Experiments using antibiotics at a dose that eliminates the bacteria but has no apparent direct effect on aphid metabolism or behaviour have revealed the crucial importance of *Buchnera* to aphids (Wilkinson, 1998). These bacteria-free individuals are called 'aposymbiotic' aphids. When adult aphids are treated, reproductive output ceases within 1–2 days, reflecting the vital importance of *Buchnera* for embryo growth (Koga *et al*., 2007). Aphids treated at birth display normal development (although the final-larval stadium may be prolonged) but grow slowly and, on reaching adulthood, are very small and produce no offspring, or a few offspring that are stillborn or die without growing or developing (Table 6.1). Aposymbiotic aphids display no known specific abnormalities, for example in feeding or embryogenesis (Wilkinson, 1998), and the role of *Buchnera* is predominantly, and probably exclusively, nutritional.

The variable incidence of secondary symbionts in aphids indicates that the insect does not require these taxa. Two approaches have been adopted to investigate their significance to aphids: comparisons of the performance of: first, multiple clonal lines naturally bearing different complements of bacteria; and second, single aphid clones with their complement of secondary symbionts manipulated experimentally. The results indicate that the fitness consequences of these bacteria vary with aphid and bacterial genotype, the presence of other bacteria and rearing plant and other conditions, especially temperature (Montllor *et al*., 2002; Oliver *et al*., 2006; Koga *et al*., 2007; Chandler *et al*., 2008). In the pea aphid, *Acyrthosiphon pisum*, the secondary symbionts make no evident contribution to nutrition (Douglas *et al*., 2006a), but genomic data have implicated *S. symbiotica* in the nutrition of *Cinara cedri* (Lachninae) (Perez-Brocal *et al*., 2006; Lamelas *et al*., 2011). The role of the secondary symbionts in other aspects of the biology of aphids, especially defence, is considered in Chapter 11, this volume.

Table 6.1. Impact of antibiotics on the performance of apterous *Acyrthosiphon pisum*. Values of mean ± s.e. are shown (26 replicates for untreated aphids, 20 replicates for aphids treated with the antibiotic chlortetracycline). (From Douglas, 1992.)

Aphid	Larval development time (days)	Teneral weight (mg)	Number of offspring
Untreated	8.2 ± 0.12	3.06 ± 0.064	59 ± 3.1
Antibiotic treated	10.0 ± 0.26	0.49 ± 0.017	0–5

Carbon Nutrition

Sugars

Phloem-mobile sugars are the principal source of carbon for aphid respiration and growth. Virtually all research has been conducted on aphid utilization of ingested sucrose, a disaccharide of glucose and fructose and the sole sugar in the phloem sap of many plants. Aphid utilization of galactose-based oligosaccharides (raffinose, stachyose and higher homologues) that occur in the phloem sap of many Cucurbitaceae and Lamiaceae and of sugar alcohols (e.g. sorbitol, dulcitol, mannitol) in the sap of Celastraceae, Prunoideae and Rosaceae has not been studied.

Phloem sucrose poses two physiological 'problems' for aphids. First, sucrose is not assimilated directly across animal guts, and its nutritional value depends on hydrolysis to its constituent monosaccharides, glucose and fructose. Second, the sucrose concentration in phloem sap is very high, usually between 0.5 and >1.0 M, and its osmotic pressure

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is considerably higher than that of aphid body fluids (Downing, 1978; Wilkinson *et al*., 1997). The resultant osmotic gradient would be expected to cause uncontrolled flux of water from the aphid tissues to the gut lumen, and desiccation of the aphid.

Gut enzymes are central to the resolution of both these physiological problems. The aphid midgut has high activity of: (i) sucrase, α-glucosidase that hydrolyses sucrose to glucose and fructose; and (ii) transglycosidase, which synthesizes glucose-based oligosaccharides (3–>15 hexose units), so reducing the osmotic pressure per hexose unit in the gut lumen (Cristofoletti *et al*., 2003; Price *et al*., 2007). The monosaccharides are assimilated across the gut wall into the haemolymph via sugar transporters that have been identified (Price *et al*., 2010), and the oligosaccharides are voided via the honeydew (Wilkinson *et al*., 1997). It is very likely that a single enzyme may mediate both sucrose hydrolysis and oligosaccharide synthesis by inserting a molecule of water and glucose, respectively, at the glucosidic bond (Ashford *et al*., 2000; Price *et al*., 2007). The enzyme activity is of aphid (and not microbial) origin, as the activity is unaffected by experimental elimination of microorganisms with antibiotics (Wilkinson *et al*., 1997). Dietary sugars are important, not only as the principal source of carbon but also because they are the single, most important nutritional determinant of aphid feeding rate. The rate at which aphids ingest food varies inversely with the dietary concentration of sucrose (Mittler and Meikle, 1991; Douglas *et al*., 2006b) (Fig. 6.2). This response generally is interpreted as a compensatory feeding response; that is, that aphids can compensate behaviourally, at least partially, for low dietary sucrose by feeding at higher rates. Overlaying this feeding response, sucrose acts as a phagostimulant; that is, sustained feeding by aphids depends on the presence of dietary sucrose. As a result, aphids feed at a progressively increasing rate with declining sucrose concentration to a minimal concentration of 0.05–0.2 M (varying with species and conditions), below which sustained feeding is not exhibited (Pescod *et al*., 2007).

Research on the behavioural regulation of carbon acquisition by aphids has been conducted almost exclusively with aphids on chemically defined diets. The extent to which these data are relevant to aphids feeding on plants is far from clear. The key issues are:

- The sucrose concentration in plant phloem sap varies both with instantaneous irradiance and over the diurnal cycle (Geigenberger and Stitt, 2000), but the aphid behavioural and physiological responses to fluctuating sucrose concentrations are not fully understood (Cull and van Emden, 1977; Taylor *et al*., 2012).
- Phloem sucrose concentrations can often exceed 1.0 M (Pescod *et al*., 2007), considerably higher than the concentrations usually used in diet studies.
- Phloem sap is under positive hydrostatic pressure, and aphids may not be able to regulate the feeding rate from sieve elements as precisely as from diets at atmospheric pressure (Turgeon, 2010).

Lipids

Two lines of evidence indicate that aphid lipids are of endogenous origin: the natural diet of phloem sap contains very little lipid, and the chemically

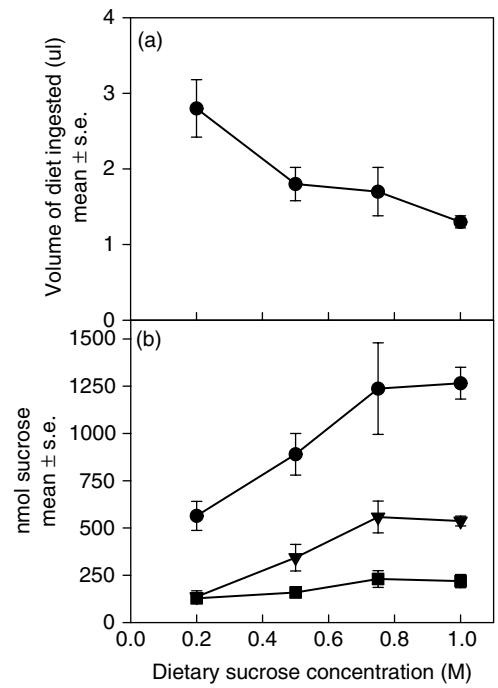

Fig. 6.2. Feeding response of *Acyrthosiphon pisum* to variation in concentration of dietary sucrose. Eight replicate final-instar apterous larvae were caged individually for 48 h on diets containing 0.2–1.0 M sucrose. (a) Volume of diet ingested. (b) Amount of sucrose ingested (circle) and recovered from aphid tissues (square) and honeydew (triangle). (Previously unpublished data of W.A. Smith and A.E. Douglas; methodology as in Ashford *et al*., 2000.)

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defined diets routinely used for maintaining aphids through multiple generations are lipid free.

The composition of aphid lipids is most unusual for animals. The dominant lipids are triglycerides with acyl moieties of short chain length. For example, in *A. pisum* myristic acid (C14) and hexanoic acid (C6) make up 90% of the triglyceride fatty acids, and the most abundant triglyceride is 1,3-dimyristoyl-2-hexanoyl glycerol (Rahbe *et al*., 1994). The triglyceride content and composition of both *A. pisum* and *Macrosiphum euphorbiae* (potato aphid) are not significantly modified by treatment with the antibiotic rifampicin (Rahbe *et al*., 1994; Walters *et al*., 1994; Fig. 6.3a), indicating that these compounds are synthesized by the aphid and not the symbiotic microorganisms. The principal function of aphid triglycerides is as an energy source when aphids are not feeding (and so do not have access to sugars). The key periods of extended non-feeding are during moulting, flight and, for some species, the adult gynopara and male morphs. It has also been suggested that triglycerides are a crucial energy source for embryos but, to our knowledge, the relative importance of sugars and lipids for energy metabolism of maternal tissues and embryos in virginoparae has not been investigated systematically (Walters *et al*., 1994). The significance of the unusual fatty acid composition of aphid triglycerides is uncertain. The short acyl chain length ensures that the triglycerides are above their melting point, and this may be linked to one function of the haemolymph triglycerides as precursors of secretions from the siphunculi. When aphids are agitated, droplets rich in triglycerides of composition similar (but not identical) to the haemolymph triglycerides (Fig. 6.3b) are exuded from the siphuncles and, on release, these siphuncle secretions change into a sticky solid that deters potential predators. The triglycerides containing sorbic acid (C6:2) have also been implicated in defence against microbial antagonists (Brown, 1975), because sorbic acid is a potent fungistatic agent, but this suggestion has not been tested systematically (Brown, 1975).

The principal phospholipids in aphids are phosphatidylethanolamines and phosphatidylcholines; the levels of phosphatidylinositols are very low (Febvay *et al*., 1992). The fatty acids in aphid phospholipids are generally of longer chain length than in the triglycerides. For example, in the phospholipids of *A. pisum*, the dominant fatty acid is linoleic acid (C18:2). Radiotracer studies have confirmed that, as with the triglyceride fatty acids, the phospholipid fatty acids are synthesized endogenously by the aphid (de Renobles *et al*., 1986).

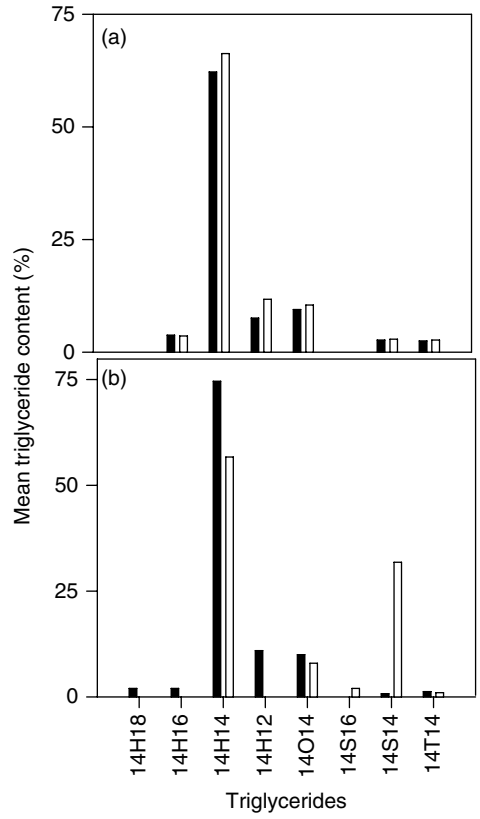

Fig. 6.3. Fatty acid composition of triglycerides in *Acyrthosiphon pisum*. (a) Aphids treated with rifampicin to eliminate the symbiotic bacteria (open bars) and untreated aphids (closed bars) reared on chemically defined diets. (b) Cornicle secretion (open bars) and fat body (closed bars) of plant-reared aphids. 14H18: 1-myristoyl-2-hexanoyl-3-stearoyl glycerol; 14H16: 1-myristoyl-2-hexanoyl-3-palmitoyl glycerol; 14H14: 1,3-dimyristoyl-2-hexanoyl glycerol; 14H12: 1-myristoyl-2-hexanoyl-3-lauroyl glycerol; 14O14: 1,3-dimyristoyl-2-octanoyl glycerol; 14S16: 1-myristoyl-2-sorboyl-3-palmitoyl glycerol; 14S14: 1,3-dimyristoyl-2-sorboyl glycerol; 14T14: 1,3-dimyristoyl-2-octatrienoyl glycerol. (Redrawn from Rahbe *et al*., 1994.)

Aphids require preformed sterols because, like other insects, they cannot synthesize these compounds *de novo*. The significance of the dietary supply of sterols for aphids is indicated by the improved reproductive output of both *A. pisum* and *Myzus persicae* (peach–potato aphid) when chemically defined diets are supplemented with cholesterol or

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certain phytosterols; that is, sterols of plant origin bearing an alkyl side chain (Bouvaine *et al*., 2012, 2014). Analyses of the composition of aphid sterols and the performance of aphids on diets with different sterol supplements suggest that aphids may have limited capacity to dealkylate phytosterols (Behmer *et al*., 2011), although this may vary both across different phytosterols and among aphid species.

Nitrogen Nutrition

Amino acids and their sources

The chief nitrogenous compounds utilized by aphids are free amino acids derived from two sources: the phloem sap and the symbiotic bacteria in the aphids.

Amino acids are the dominant nitrogenous compounds in the phloem sap of most plant taxa, and aphids assimilate them very efficiently. Additionally, aphids derive a supplementary supply of essential amino acids from the symbiotic bacteria in their tissues. The three core lines of evidence are that:

- Aphids do not have a dietary requirement for many essential amino acids (e.g. Douglas *et al*., 2001; Macdonald *et al*., 2011).
- The isolated bacteria are capable of essential amino acid synthesis (Sasaki and Ishikawa, 1995; Russell *et al*., 2013a).
- Amino acids synthesized by the bacteria in aphid tissues are translocated to the aphid partner (Douglas, 1988; Russell *et al*., 2013a).
- *Buchnera* genome contains genes coding enzymes in the essential amino acid biosynthesis (Shigenobu *et al*., 2000).

The fate of amino acids in aphids

Aphids mediate considerable amino acid interconversions by transamination and other reactions (Wilson *et al*., 2010, 2011), and protein synthesis is quantitatively a major fate for amino acids. More than 95% of the amino acid content of aphids is in the protein fraction, and protein accounts for 10–25% of aphid fresh weight.

Some amino acids have important functions other than in protein synthesis. Several amino acids are, or are precursors of, neurotransmitters and neurohormones, for example glutamic acid, dopamine (derived from tyrosine) and serotonin (derived from tryptophan). Tyrosine is also a major precursor of cuticle synthesis. One consequence of the link between certain amino acids and cell-signalling interactions is that the biological ramifications of a shortfall in the supply of these compounds might be expected to extend beyond negative effects on protein synthesis to aphid growth and reproductive rate. This issue has not been studied in detail but, as a possible example, 5-hydroxytryptamine (a derivative of dietary tryptophan) has been reported to inhibit the production of alatiform *M. persicae* (Harrewijn, 1978).

Amino acids are also a vital constituent of the haemolymph of aphids. All 20 protein-amino acids are readily detectable in the haemolymph and, as in other insects, the haemolymph amino acids represent both a metabolic store of nitrogen and an osmoprotectant. Haemolymph amino acids play a crucial role in nitrogen nutrition, because the haemolymph is the first destination of both dietary amino acids assimilated across the gut wall and *Buchnera*-derived amino acids released from the bacteriocytes. Research on the molecular identity, specificity and kinetic properties of the amino acid transporters on the gut and bacteriocyte membranes mediating the flux of amino acids has been initiated. Candidate transporters have been identified from proteomic and transcriptomic analysis of bacteriocytes (Hansen and Moran, 2011; Poliakov *et al*., 2011; Macdonald *et al*., 2012). One transporter, ApGLNT1, has been localized to the bacteriocyte membrane and has been shown to mediate the uptake of glutamine (Price *et al*., 2014). The haemolymph amino acid pool has very high turnover. In addition to supporting protein synthesis and other functions (see above), haemolymph amino acids are consumed at a high rate in respiration. For example, in plant-reared *Aphis fabae* (black bean aphid), haemolymph glutamic acid is metabolized to carbon dioxide at a rate of 1.2 nmol carbon/mg aphid weight/h (Wilkinson *et al*., 2001), and in diet-reared *A. pisum*, respiration accounts for 60% of the total glutamic acid assimilated (Febvay *et al*., 1992). Perhaps amino acids are important to the energy metabolism of particular cell types, even though, in comparison with sucrose, they are minor respiratory substrates for aphids at the level of the whole organism (Wilkinson *et al*., 2001).

Ammonia is the principal nitrogenous product of amino acid catabolism. Aphid honeydew contains appreciable concentrations of ammonia, but not the alternative nitrogenous waste compounds, urea or uric acid (Wilkinson and Douglas, 1995). It has been suggested that the symbiotic bacteria contribute to the overall nitrogen nutrition of aphids by recycling

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nitrogen; that is, the bacteria assimilate aphid waste ammonia into essential amino acids, which are released back to the aphid. However, genome-scale metabolic modelling of *Buchnera* reveals that this bacterium is a net producer of ammonia (Thomas *et al*., 2009), and that the principal fate of ammonia in the bacteriocyte is as a substrate for transamination reactions mediating the terminal step in the synthesis of four essential amino acids, isoleucine, leucine, phenylalanine and valine (Macdonald *et al*., 2012; Russell *et al*., 2013a).

Other dietary sources of nitrogen

Although research on the nitrogen nutrition of aphids has concentrated on the utilization of dietary amino acids, plant phloem sap does contain other nitrogenous compounds, including proteins and polyamines (Kehr, 2006; Sichhart and Drager, 2013). In general, these compounds are at lower concentrations than are the free amino acids, but they may be biologically significant in certain plants or in relation to certain amino acids. The phloem sap of cucurbits has been reported to contain high concentrations of protein (>1 mg/ml), but the 'phloem sap' exudates obtained from cucurbits are now recognized to be grossly contaminated by the contents of multiple cell types, and the high protein content is almost certainly artefactual (Zhang *et al*., 2012).

The fate of peptides and proteins in the aphid gut is poorly understood. Evidence that aphids can utilize small peptides comes from the demonstration of aminopeptidase activity in the gut of pea aphids (Rahbe *et al*., 1995), and the capacity of the dipeptide glycyl-methionine to support the dietary methionine requirements of *A. fabae* (Leckstein and Llewellyn, 1974). The capacity of aphids to utilize dietary proteins is less clear. Multiple cysteine protease genes are expressed in the aphid gut, but it is not established whether they are intracellular or secreted into the gut lumen (Rispe *et al*., 2008). In the study by Rahbe *et al*. (1995) on pea aphids, various proteins added to the diet passed through the gut to the honeydew without chemical modification; but in contrast, experiments by Pyati *et al*. (2011) are indicative of proteolysis in the gut of cereal aphids.

Minerals and Micronutrients

The study of the mineral requirements of aphids has been dominated by the need for a convenient mineral mixture suitable for maintaining aphids on chemically defined diets, and there has been no systematic analysis of aphid requirements for inorganic ions. All the published diet formulations include relatively high concentrations of potassium and phosphate, reflecting their high concentrations in phloem sap, and of magnesium and sulfate: at micromolar concentrations, iron, copper, manganese and zinc are included. It is recognized that aphid requirements for other metals may go undetected because these elements are present in the diet as impurities of other dietary constituents. In all probability, the inorganic requirements of aphids are comparable to those of other phytophagous insects.

Early studies indicated that aphids had a dietary requirement for the seven core B vitamins: thiamine, riboflavin, nicotinic acid/nicotinamide, pyridoxine, pantothenic acid, folic acid and biotin, and these compounds were included routinely in most chemically defined diet formulations (Dadd *et al*., 1967). Some data, however, suggest that symbiotic bacteria may meet, partially or completely, the riboflavin requirements of aphids. In particular, the *Buchnera* genome includes the genetic capability for riboflavin synthesis (Shigenobu *et al*., 2000), and the pea aphid is reportedly independent of dietary riboflavin (Nakabachi and Ishikawa, 1999).

The only other vitamin provided in published aphid diet formulations is ascorbic acid (vitamin C). This reflects its role as both an essential dietary component and a chelator of dietary metal ions, especially Fe^{3+} (citric acid is also included in diets for the latter purpose) (Mittler, 1976). The lipophilic vitamins A, D and E are not usually included in diets (see below), suggesting that they are not dietary requirements for aphids.

Artificial Diet

History of artificial diets for aphids

A major contribution to the considerable variation in the growth and reproductive performance of individual aphids, even within the progeny of the same mother, is assumed to be variable nutrition. Such variation occurs between apparently identical plants, and even between locations on the same leaf. Variance of the mean relative growth rate (MRGR) of *M. persicae* was significantly higher on replicate plants than on an artificial diet (Wojciechowicz-Zykto and van Emden, 1995). The possibility of rearing aphids on a nutritionally uniform substrate has been explored ever since Hamilton (1930) showed

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that aphids would feed on fluids through a natural membrane (onion epidermis). The real breakthrough came 30 years later, when Mittler and Dadd (1962) published a fully defined artificial diet for *M. persicae*, closely followed by Auclair and Cartier (1963) with a diet for *A. pisum*. Both pairs of workers used stretched Parafilm 'M'™ as the membrane. The diet published by Dadd and Mittler (1966) has proved the most successful and widely used for several species of aphids, yet for many years the diet failed to sustain any species permanently, even for the originators. However, in February 1976, a culture of *M. persicae* was started on the diet at the University of Reading, and this culture persisted without contact with plants before it eventually died out in December 2008. Another successful use has been to introduce antibiotics into aphids to produce aposymbiotic individuals (Douglas, 1988; Prosser and Douglas, 1991).

By comparison, fully defined diets have been used for many other aphid species, but usually for experiments involving only the few days survival required for testing toxins or behaviour-modifying chemicals (e.g. Corcuera *et al*., 1985; Hansen, 2006; Fitches *et al*., 2008; OingNiang *et al*., 2009; Sprawka *et al*., 2013). However, such short-term experiments usually can be conducted just as well with adult aphids and simple sucrose solutions in the sachets.

Wille and Hartman (2008) tested five diets from different sources with soybean aphid, *Aphis glycines*. The most successful diet was developed from the amino acid profile of young potato plants and sustained the aphid for about 12 days. More host-restricted aphids may need host-related secondary compounds added to the diet to improve phagostimulation (e.g. the addition of lupanine with a lupin-feeding population of *M. persicae*; Cardoza *et al*., 2006). Pike (2010) has claimed that *Pemphigus spyrothecae* should be a good candidate for developing an artificial diet based on the *A. pisum* one. This claim is based on the similarity in amino acid profiles of carcass hydrolysates of the two species, but does not appear to have been tested.

Recipe for the diet and practical procedures

The recipes for the two diets referred to above (for *M. persicae* and *A. pisum*) are given in modified form in Table 6.2. The two have substantial differences in ingredients and their quantities. The glass still with glass-covered elements used at Reading until 2004 appears to have contributed to the success there; nanopure water does not seem as suitable (too pure?) and switching to it may have contributed to the eventual demise of the Reading *M. persicae* culture. It is important that the ingredients are added in exactly the order given in the table, and that each ingredient is fully dissolved before the next is added. In practice, this involves setting up a magnetic stirrer for much of a day and alternating diet preparation with other work. It appears increasingly difficult to find sources of a pure form of the chelated metals used in the *M. persicae* culture. One alternative could be to use 'dirty' chelate mixtures. This may not actually be a bad thing in terms of providing trace elements, but has yet to be tested. A commercial salt mix as in the *A. pisum* recipe may provide another solution.

The diet is not sterilized at this stage, but is divided into convenient 25–30 ml aliquots in tubes (Fig. 6.4b), which can be deep-frozen for up to 6 months until needed. The aliquots are thawed when needed, to make large numbers of diet sachets, which similarly can be stored deep-frozen. It is during the preparation of these sachets that sterile procedures are required, and the tubes, the thawed diet and 50 × 35 mm squares of unstretched Parafilm 'M'™ are placed in a laminar flow unit under a UV lamp for 35 min to sterilize the top surface of the Parafilm squares. Parafilm will deteriorate if exposed to more than 40 min of UV light.

When the UV is switched off, a square of Parafilm is stretched two ways from the underside (Fig. 6.4c), to keep the area that covers the opening of the tube sterile, and placed over one end of a diet tube. This forms one surface of the eventual 'sachet' of diet. Diet is poured into a syringe fitted with a disposable millipore (0.22 μm) bacterial filter unit and the diet is pipetted into a sterile tube. An automatic pipette set to 0.6 ml dispenses that volume of diet on to the sterile surface of the Parafilm. The liquid is then covered with another stretched sheet of Parafilm, inverted so that the liquid is sandwiched between two sterile surfaces, and the projecting flaps of Parafilm pulled down on to the side of the tube. These flaps can be used to hold two diet tubes together at their open ends (Fig. 6.4d), and this is critical in the way sachets are replaced. The diet deteriorates quickly, especially since aphid stylets are not sterile, and the aphids have to be provided with new sachets every 2–3 days (2 whenever possible).

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Table 6.2. Composition of artificial diets as mg of chemical dissolved in 100 ml nanopure water. It is important that the chemicals are dissolved completely in the order shown in the left-hand column (recipe for *Myzus persicae* is modified from Dadd and Mittler, 1966; that for *Acyrthosiphon pisum* is adapted from Auclair, 1965).

	For *Myzus persicae*	For *Acyrthosiphon pisum*
Sucrose	15,000.0 (15 g)	35,000.0 (35 g)
Di-potassium hydrogen orthophosphate	750.0	See salt mixture
Magnesium sulfate	123.0	See salt mixture
Magnesium chloride	0.0	200.0
L-tyrosine	40.0	20.0
L-asparagine hydrate	550.0	300.0
L-aspartic acid	140.0	100.0
L-tryptophan	80.0	100.0
L-alanine	100.0	100.0
Gamma-amino butyric acid	0.0	20.0
L-arginine monohydrochloride	270.0	400.0
L-cysteine hydrochloride, hydrate	40.0	6.0
L-glutamic acid	140.0	200.0
L-glutamine	150.0	600.0
L-glycine	80.0	20.0
L-histidine	80.0	200.0
DL-homoserine	0.0	800.0
L-isoleucine (allo free)	80.0	200.0
L-leucine	80.0	200.0
L-lysine monohydrochloride	120.0	200.0
L-methionine	40.0	100.0
L-phenylalanine	40.0	100.0
L-proline	80.0	100.0
L-serine	80.0	100.0
L-threonine	140.0	200.0
L-tyrosine	0.0	20.0
L-valine	80.0	200.0
Ascorbic acid (vitamin C)	100.0	10.0
Thiamine HCl (vitamin B_1)	2.5	2.5
Riboflavin	0.5	6.0
Nicotinic acid	10.0	10.0
p-aminobenzoic acid	0.0	10.0
Folic acid	0.5	1.0
Calcium pantothenate (vitamin B_5)	5.0	6.0
Inositol (meso) active	50.0	50.0
Choline chloride	50.0	50.0
EDTA Fe(III)-Na chelate pure	1.5	0.0
EDTA Zn-Na_2 chelate pure	0.8	0.0
EDTA Mn-Na_2 chelate pure	0.8	0.0
EDTA Cu-Na_2 chelate pure	0.4	0.0
Pyridoxine hydrochloride (vitamin B_6)	2.5	2.5
D-biotin, crystalline	0.1	0.1
Sodium acetate	320.0	0.0
Salt mixture[a]	0.0	6.0

Notes: [a]Salt mixture USP XIII (Nutritional Biochemical Corporation, Cleveland, Ohio) used by Auclair (1965) had the following per cent composition:

Calcium lactate	32.70
Di-potassium hydrogen orthophosphate	23.98
Ferric citrate	2.97
Magnesium sulfate	13.70
Monosodium phosphate	8.72
Sodium chloride	4.35
Superphosphate	13.58

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Fig. 6.4. The artificial diet technique. (a) *Myzus persicae* feeding on the diet; (b) equipment for dispensing the diet; (c) stretching the Parafilm so as to keep one surface sterile; (d) new diet tube with free edges of Parafilm, which are used to hold two tubes together, as in (e).

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This replacement involves using the Parafilm flaps to fix the open end of a new diet tube to the open end of the tube where the aphids are feeding (Fig. 6.4e). The upper Parafilm of the sachet with the aphids is then gently slit open with the end of a needle and inverted on to filter paper so that the old diet runs out and is absorbed. The aphids then climb the tubes rapidly to transfer to the new sachet, with no handling of the insects being necessary.

Relation between the diet and plant phloem sap

Dadd and Mittler's (1966) diet was based on Mittler's (1953, 1958) analysis of willow (*Salix acutifolia*) phloem sap obtained from the cut ends of the inserted stylets of *Tuberolachnus salignus* (giant willow aphid). However, developing a successful diet from this basis involved many changes; Dadd and Mittler tested and re-tested different concentrations of individual components against many different backgrounds of a balance of the other constituents. Their 1966 *M. persicae* diet is the diet used at Reading, with slight modifications.

The diet is composed of 15% sucrose and 2.4% amino acids. Mittler (1958) reported percentages in willow phloem sap of around 8.3% sucrose and total nitrogen of between 0.03% and 0.13%. Zimmermann and Ziegler's (1975) compilation of the sucrose concentration in the phloem of 532 plant species in 102 families shows that 49% of the species recorded sucrose in the 10–20% range. An amino acid analysis (H.F. van Emden and M.A. Bashford, unpublished results) is also available for the phloem sap of glasshouse-grown castor oil plant (*Ricinus communis*), a shrub or small tree that is a host for *M. persicae*. The sap was obtained by the EDTA method (King and Zeevaart, 1974). Figure 6.5 plots the concentration in the artificial diet against the concentration in the castor bean plant phloem sap of those amino acid compounds for which data from both liquids were available. Both Figure 6.5 and Mittler's (1958) analyses point to the need for higher concentrations of both sucrose and most amino acids in the diet than in plant phloem sap; however, there is no consistent quantitative change in the ratio (contrast especially arginine and glutamic acid in Figure 6.5).

That concentrations of most ingredients need to be higher in the diet than in phloem sap is not surprising, since uptake from the diet is much reduced compared with that from the phloem. Uptake from diet sachets by both *M. persicae* (Mittler, 1970) and *A. pisum* (Auclair, 1965) is 0.3–0.4 µl per aphid per day, only about one-eighth of that of *A. pisum* from pea (*Pisum sativum*) (Auclair and Maltais, 1961). Phloem sap is under considerable pressure (Mittler, 1958), but pressurizing a 10% sucrose solution to 2 kg/cm^2 only extended the longevity of adult *A. fabae* by 20% (van Emden, 1967). One reason limiting the reduced uptake from diet is probably

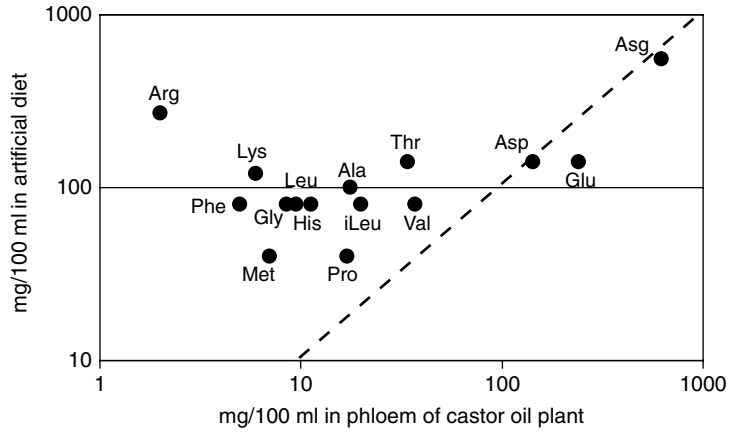

Fig. 6.5. Relationship between the concentration of individual amino acids in artificial diet and phloem sap of the castor oil plant (*Ricinus communis*); the dotted line is the line of equality in both substrates.
Notes: Ala = alanine; Arg = arginine; Asg = asparagine; Asp = aspartic acid; Glu = glutamine; Gly = glycine; His = histidine; iLeu = isoleucine; Leu = leucine; Lys = lysine; Met = methionine; Phe = phenylalanine; Pro = praline; Thr = threonine; Val = Valine.

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the high osmolality of the aphid haemolymph resulting from the constant high sugar concentration (see earlier under 'carbon nutrition'; also Cull and van Emden, 1977), whereas sugar concentrations in the phloem fluctuate with ambient radiation, with a strong reduction at night. There may also be an element of gustatory 'habituation' to an unchanging food source. T.E. Mittler and H.F. van Emden (unpublished results) found that neonate *A. fabae* attained a mean weight of 147 mg if fed on a cycle of 17 h full diet: 7 h water for 3 days, but only 127 mg if the full diet was replaced with further full diet for the 7 h period. Moreover, also with *A. fabae*, the same workers found that a steady excretion rate of around 0.5 honeydew drops per aphid per hour rose to over 8 drops per hour (Figure 6.6) for a few hours on full-strength diet after the aphids had been on half-strength diet for just 15 min (van Emden, 1996). Low uptake from diet therefore may well have a largely behavioural component.

Aphid performance on the diet

Even after nearly 30 years on the diet at Reading, *M. persicae* still performed badly compared with the same original genotype when plant reared (van Emden, 1988; van Emden and Andrews, 1997). Adult weight was lower, generation times extended and fecundity reduced (Fig. 6.7). The main contributor to extended generation time on diet was an adult pre-reproductive period of several days. Even after 20 years, fecundity was only about a half of that on plants. Nutritionally, or through phagostimulation, the diet was clearly suboptimal. Aphids returned to plants as neonates hardly improved their performance in the first generation (van Emden and Andrews, 1997; Fig. 6.7), but the MRGR of their offspring then rose to match that of individuals maintained on plants throughout. van Emden *et al.* (2014b) used the diet recipe given by Douglas and van Emden (2007) to impose stress on the aphids to demonstrate large variability between *M. persicae* genotypes in their ability to survive on the diet. With six genotypes of *A. pisum*, Vogel and Moran (2011) found that only one required dietary arginine in the diet, and this could be related to a mutation in a *Buchnera* gene involved in amino acid biosynthesis.

Soon after the Reading culture had died out in 2008, we had occasion to measure the titre of alarm pheromone in *M. persicae* on diets with and without a small amount of sodium acetate, added as possibly providing an initial step in the biosynthesis of the pheromone. This proved unnecessary for pheromone production, but unexpectedly gave diet-reared aphids as large as those reared on plants (van Emden *et al.*, 2014a); hence, the addition of sodium acetate to our diet recipe (Table 6.1).

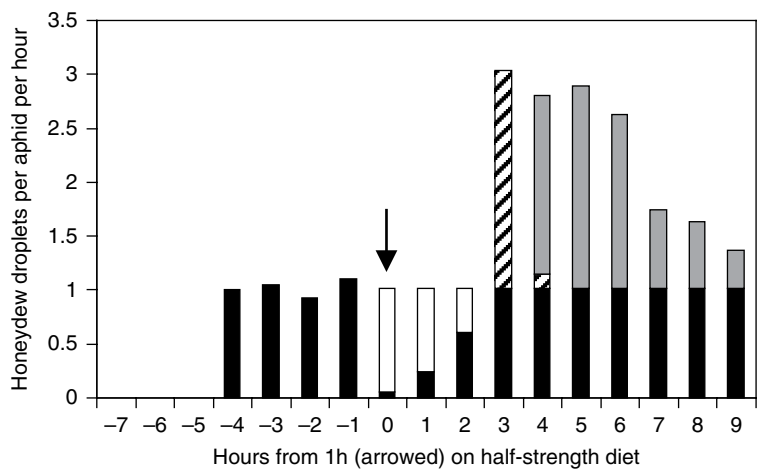

Fig. 6.6. Mean number of honeydew droplets excreted per hour by *Aphis fabae* on artificial diet before and after a 15-min period (arrowed) on half-strength diet.
Notes: Black = baseline droplet excretion rate; white = reduction in rate following 1 h on half-strength diet; striped = amount of extra excretion to bring average back to baseline rate; grey = droplet excretion above average baseline rate.

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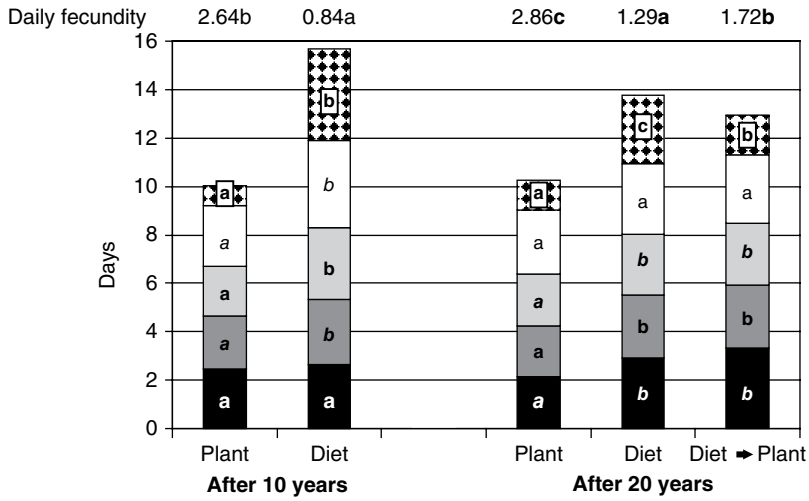

Fig. 6.7. Development of *Myzus persicae* on plants and artificial diet after 10 years on the diet (left) and after 20 years (right), together with development of aphids born to mothers moved from diet to plants. The divisions of the columns (from bottom to top) are durations (days) of: first instar (black); second instar (dark grey); third instar (light grey); fourth instar (white); and the adult pre-reproductive period (chequered).

How useful is the diet for studies on aphid nutrition?

What would seem an obvious use of diet – to test the cause and effect for apparent correlations between aphid performance and the concentration of nutrients, particularly amino acids, in plants – can in practice prove rather unsatisfactory. There seem to be three main reasons for this:

- It is not possible to increase the concentration of one nutrient without reducing another or changing the balance between compounds. The balances between ingredients seem to be as critical to success as the concentration of individual compounds.
- The diet is not strictly a mimic of plant sap (as shown in Figure 6.5). Beneficial interactions between, for example, amino acids and metal availability that may occur in the homogeneous diet, may not occur in the plant (Mittler, 1972).
- Dadd and Mittler (1966) developed their diet to maximize the growth and reproduction of *M. persicae*. That any variation in the recipe will lower the performance of the aphid is therefore only to be expected, and has indeed proved to be the case (van Emden, 1996), with one exception. For the phagostimulant and essential amino acid methionine alone, doubling the concentration did increase the growth rate of *M. persicae* significantly, and halving it reduced it.

However, the diet has contributed substantially to studies on nitrogen metabolism in aphids (see earlier in connection with aposymbiotic aphids).

Conclusions and Future Prospects

The single, most perplexing issue in aphid nutrition is the high rate at which the unbalanced diet of phloem sap is transformed into new aphid biomass (see Introduction). As this chapter summarizes, key factors are the speed and efficiency with which aphids assimilate, or otherwise dispose of, ingested nutrients. For example, aphids on many plants ingest a surfeit of sucrose. The sucrose is hydrolysed to completion in the gut lumen and, within 15–20 min of ingestion, the hydrolysis products are assimilated across the gut wall to the haemolymph, or transformed to oligosaccharides that pose no obvious osmotic hazard to the aphid, and voided via honeydew. In a comparable fashion, ingested amino acids are assimilated rapidly or voided. This efficiency is compatible with the aphid's absolute nutritional requirement for essential amino acids only because the symbiotic bacteria *Buchnera* provide the aphid with supplementary essential amino acids. The bacteria can be described as 'upgrading'

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the quality of the diet by converting non-essential amino acids (i.e. amino acids that the aphid can synthesize *de novo*) to essential amino acids (which the aphid cannot synthesize *de novo* and require absolutely). The bacteria may additionally recycle ammonia, the chief nitrogenous waste product of aphid metabolism, but, contrary to some early reports, *Buchnera* has no capacity to promote aphid nitrogen nutrition by fixing atmospheric nitrogen (Shigenobu *et al*., 2000).

Many issues relating to aphid nutrition and symbiosis remain to be resolved. In particular, we have no physiological information on aphid utilization of phloem sugars other than sucrose, even though many aphid species feed exclusively on plants with galactose-based oligosaccharides as the dominant phloem sugars. Similarly, the significance to aphid nutrition of phloem nitrogenous compounds other than free amino acids is obscure. Compounding these areas of ignorance is the dearth of information on the significance of accessory bacteria to aphids. There are indications in the recent literature that these bacteria may influence aphid host-plant range, thermal tolerance and propensity to develop into alatiform (dispersal) morphs (Chen *et al*., 2000; Wilkinson *et al*., 2001; Montllor *et al*., 2002; Oliver *et al*., 2003), but the physiological processes underlying these effects are, at present, unknown.

Finally, the main achievements in our understanding of aphid nutrition have come primarily through experiments conducted with aphids on chemically defined diets. However, we have only the most cursory understanding of the nutrition of plant-reared aphids, largely because of the technical difficulties with quantifying or manipulating phloem-mobile nutrients. With the advent of methodologies for routine sampling and analysis of single plant cells (e.g. Tomos and Sharrock, 2001), we are now well placed to address the nutrition of aphids on plants. There is every expectation that aphids display a suite of behavioural and physiological adaptations that optimize nutrient extraction from phloem sap, a diet of far greater biochemical complexity and variability than chemically defined diets.

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7 Aphids and Stress

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Introduction

Aphids are a hugely successful insect group, feeding on a broad range of plant species over a wide range of climates. Many host-plant species are important crops, and the impact of aphids on crops through resource removal, facilitation of pathogens (Chapter 11, this volume) and virus transmission (Chapter 15, this volume) in temperate climates is predicted to increase as climate change alters the environment in their favour (Harrington *et al*., 1995, 2001, 2004). Aphids feed from the phloem sap of plants; locating and exploiting this non-ideal food source requires a suite of adaptations (Chapter 9, this volume), including symbiosis with bacteria, the significance of which is only just becoming fully appreciated (Chapter 6, this volume). Their specialist feeding within a single cell type gives aphids a particularly intimate association with their host plant. This association makes it is impossible to consider the effects of abiotic stress on aphids in the absence of the plant. We argue that the two most important stressors on aphids and plants are temperature and drought, the latter having a particularly well-studied and fundamental effect on plants. In this chapter, we consider the effect of drought and temperature stress directly on the aphid and the plant, and the indirect consequences of stress on the host plant on this important insect herbivore group.

Temperature Effects on Aphids

Aphids are ectothermic and temperature can be a serious constraint on their rate of growth and survival. As a general rule, as temperature increases from around 3°C to 25°C, aphid development and reproduction also increase (Dean, 1974; Collins and Leather, 2001; Kuo *et al*., 2006). Once temperatures exceed about 25°C, there is a decline in aphid growth rate (Dixon, 1998). Exact developmental responses to temperature can differ between species, and even clones, illustrated in Table 7.1. For example, *Schizaphis graminum* (greenbug) requires 90 day-degrees to complete a generation, whereas *Drepanosiphum platanoidis* (sycamore aphid) requires 250 (Harrington *et al*., 1995).

Low temperature can be detrimental to aphids in a variety of ways; for example, ice crystal formation within the aphid can cause mortality, while low temperature slows down development and prevents movement. Studies on *Sitobion avenae* (English grain aphid) and *Rhopalosiphum padi* (bird cherry–oat aphid) exposed to temperatures of –5 to –10°C have shown that exposure for as little as 6 h can have negative effects on aphid performance, from increasing development time, to reducing fecundity and longevity (Parish and Bale, 1993; Hutchinson and Bale, 1994). The negative effect of cold stress on aphid performance is magnified as temperatures decrease and exposure times increase. Exposure to sub-zero temperatures not only affects the exposed aphids negatively but also can have an effect on aphid progeny, and thus affect subsequent population dynamics (Harrison and Barlow, 1972; Carter and Nichols, 1989).

Low temperature can also affect other aspects of aphid biology, such as dispersal and migration. Studies have shown that despite anholocyclic clones of *R. padi*, *S. avenae* and *Myzus persicae* (peach–potato aphid) having supercooling points (SCP) around –20°C, it is higher temperatures of just below –5°C that cause most winter mortality. The timing of spring migration is therefore linked to winter survivorship, and consequently winter temperature (Walters and Dewar, 1986; Bale *et al*., 1988).

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Table 7.1. Comparison of the mean supercooling points (SCP) and lower lethal temperatures in two aphid species, *Myzus persicae* and *Sitobion avenae*. (From Bale, 1991, with permission.)

Species and stage	Mean SCP (°C)	LT_{50} (°C)
Myzus persicae		
Adult	–26.0 ± 0.2	–6.9 ± 0.9
Nymph	–27.4 ± 0.2	–8.1 ± 1.0
Sitobion avenae		
Adult	–25.5 ± 0.2	–7.0 ± 0.4
Nymph	–26.9 ± 0.2	–10.8 ± 1.2

Low temperatures can also suppress aphid wing development; first-instar, anholocyclic *S. avenae* clones exposed to –5°C for 6 h showed a reduction in wing development by 20% (Parish and Bale, 1990).

While lower developmental thresholds of aphids can vary between species (Campbell *et al*., 1974; Zhou *et al*., 1989), so can temperature tolerance, even between closely related species. For example, the lower lethal temperature varied from –6.6°C for *Myzus ornatus* (violet aphid) to –12.7°C and –13.9°C for *M. persicae* and *Myzus polaris*, respectively, when reared at 15°C (Hazell *et al*., 2010a). However, it has been suggested that the measurement of non-lethal thermal thresholds is more important for determining aphid thermal biology than measuring lethal temperatures, as survival at temperature extremes is of little importance if an insect is rendered inactive (Bale, 1987). For all clones mentioned above, the temperature threshold for chill coma and activity increased with rearing temperature (from 10 to 25°C), indicating that aphid chill coma temperatures were plastic and could decrease following acclimation (Hazell *et al*., 2010a).

Following on from this work, Alford *et al*. (2012a) demonstrated that thermal tolerance varied with clone in *M. persicae*, and Powell and Bale (2008) showed that cold tolerance could be inherited and increase over successive generations in *S. avenae*, indicating that the clonal make-up of a population could be the predominant cause of observed regional thermal adaptation.

Temperature can affect aphid flight and walking behaviour (Chapter 10, this volume). Aphids have temperature thresholds for flight, which can vary both inter- and intraspecifically. In *R. padi*, the lower temperature threshold for flight ranges from 16 to 17°C in spring, to 9 to 10°C in autumn (Wiktelius, 1981); this seasonal difference has been suggested to be due to the different morph functions. While there are seasonal differences in thresholds for flight, there are also temperature thresholds for different phases of flight. In *Aphis fabae* (black bean aphid), the threshold temperature needed for take-off is 17°C, while for horizontal flight it is 13°C, and for wing beating only 6.5°C (Johnson and Taylor, 1957; Cockbain, 1961). Similar to flight, Alford *et al*. (2012b) showed that walking speeds of *M. persicae* declined with declining temperature; *M. persicae* acclimated at higher temperatures (10°C, 20°C and 25°C) demonstrated higher walking threshold temperatures (0°C, 7.5°C and 12.5°C, respectively).

Locomotion temperature thresholds are important for aphid survival; heat/cold avoidance through movement in the canopy (Hazell *et al*., 2010a), or burrowing in the soil (Wiktelius, 1987), could be the difference between life and death for an aphid.

Adaptation to Cold Stress

Low temperature is a lethal stressor for all insects, and the level of cold stress that can be tolerated varies greatly between species. Bale (1996) suggested that all insects could generally be divided into distinct groups according to the nature of their cold tolerance; freeze avoiding, freeze tolerant, chill tolerant, chill susceptible and opportunistic survivors.

Aphids are a typical example of insects in the chill-susceptible group, with 'pre-freeze mortality' being the dominant cause of death at low temperatures (Bale *et al*., 1988). In chill-susceptible insects, winter mortality is unrelated to the SCP, with death occurring even after brief exposures (hours) to temperature below –5°C. However, aphid eggs are considerably more cold hardy than active morphs, and are able to survive prolonged periods at much lower temperatures. Aside from overwintering eggs, aphids have some other mechanisms that allow them to adapt to cold stress. These are increasing cold tolerance in specialist morphs, and acclimation.

Overwintering specialist morphs

The egg stage for most aphid species has a greater cold hardiness than the winter environment usually requires. Aphid eggs can survive temperatures as low as –30°C for over a month without significant mortality (Strathdee *et al*., 1995). However, not all aphids overwinter as an egg, with many species having a proportion of the population overwintering in the mobile stage on the same host-plant species as they

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feed on in summer. Aphids overwintering in the mobile stage can benefit from continued development and reproduction if temperatures are high enough, whereas diapausing eggs cannot. During harsh winters, the mobile stages have low survival, and populations can persist as the more cold hardy egg.

While overwintering mobile stages are not as cold hardy as eggs, they are physiologically distinct from summer forms. *Pemphigus bursarius* (poplar–lettuce root aphid) overwinters as a hiemalis morph, which is more cold hardy (Phillips *et al*., 2000) than its summer counterpart. The increased cold hardiness of the hiemalis morph is associated with higher levels of triglycerides, an ability to accumulate energy reserves and to survive in a starved condition.

Acclimation

In Britain, the population of *M. persicae* is predominantly made up of anholocyclic clones. Clough *et al*. (1990) found that when first-instar *M. persicae* were reared for a generation at 20, 15, 10 and 5°C, their $LTemp_{50}$ (the temperature at which 50% of the population was killed) decreased from –8.1 to –16.4°C; likewise, when adults were reared at those temperatures, their $LTemp_{50}$ decreased from –6.9 to –11.4°C. Alford *et al*. (2012a) found that acclimation at 10°C for one generation in *M. persicae* could depress the movement threshold from 8.8 to 2.5°C. The process of acclimation enables aphid clones to be more cold hardy, presumably through temperature-induced mechanisms such as the synthesis of cryoprotectants. Aphids that acclimate during maturation later have progeny that have enhanced cold tolerance; however, once these offspring are subjected to higher temperatures, this cold hardiness can be lost quickly (Clough *et al*., 1990). Acclimation is an important mechanism for aphid adaptation to seasonal temperature change.

Lee *et al*. (1987) discovered a phenomenon in aphid acclimation known as rapid cold hardening (RCH). This is the ability of aphids to survive a few hours of exposure at a discriminating temperature (where at least 80% mortality occurs after direct transfer from rearing temperature) or brief exposure at 3–4°C below the discriminating temperature. Powell and Bale (2005) showed that exposure of aphids to an RCH regime could lower the chill coma (activity) threshold. RCH could be an important mechanism that allows aphids to respond to diurnal fluctuations in temperature.

Effects of High Temperature

Generally, aphid fecundity and longevity increase with increasing temperature; however, once the upper thermal limit is reached, aphid performance is reduced rapidly (Dean, 1974; Asín and Pons, 2001; Kuo *et al*., 2006). McCornack *et al*. (2004) showed that *Aphis glycines* (soybean aphid) suffered a net reduction in fecundity, generation time and life expectancy as temperature increased from 20 to 35°C; aphids had fewer progeny and spent less time reproducing between 30 and 35°C, with nymphs reared at 35°C unable to complete development. Kuo *et al*. (2006) found that when reared at 35°C, only a few *R. padi* nymphs survived to complete development. In *Metopolophium dirhodum* (rose–grain aphid), temperature, length of exposure and aphid life stage all affected survival at higher temperatures. Adult aphids had a lower tolerance of high temperatures than nymphs, while survival decreased as temperature and exposure time increased (Ma *et al*., 2004).

The upper thermal limit and optimal developmental and reproductive temperatures vary both between and within species. For example, in *Acyrthosiphon pisum* (pea aphid), the upper thermal limit can vary between 20 and 30°C (Hullé *et al*., 2010), while *R. padi* originating from the Mediterranean can tolerate higher temperatures than those with a UK origin (Asín and Pons, 2001). Aphids can acclimate to both high and low temperatures, but this effect is less pronounced at high temperatures (Hazell *et al*., 2010a; Alford *et al*., 2012a).

Behavioural adaptations to high temperature

Hazell *et al*. (2010b) suggested that behavioural, as well as genetic, adaptation was key to adaptive potential to heat in insects. At higher temperatures, aphids can become more active (Nguyen *et al*., 2009), and even display behaviours such as burying into the soil to avoid increasing temperatures (Wiktelius, 1987). *Metopolophium dirhodum* and the *Aphis gossypii* (cotton aphid or melon aphid) move down the host plant under heat stress (Liu *et al*., 2000), while *S. avenae* drops off the plant, presumably as a high-temperature avoidance response (Ma and Ma, 2012a,b). Ma *et al*. (2004) defined the point at which an aphid walks back down a temperature gradient as the heat-escape temperature (HET), illustrated in Fig. 7.1. HET decreased as acclimation temperature and time increased.

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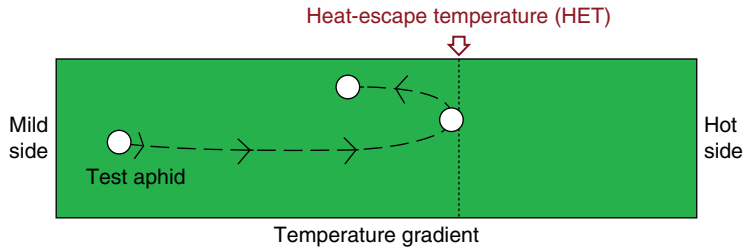

Fig. 7.1. Schematic diagram detailing the experimental set-up for determining the heat-escape temperature (HET) in aphids. HET is a measure of the temperature at which the aphid walks back down a temperature gradient. (From Ma and Ma, 2012b, with permission.)

Other indices include the percentage of aphids displaying avoidance behaviour (Ma and Ma, 2007) and the drop-off temperature (DOT), which is the temperature at which aphids drop off the plant but still have control of their muscles (Ma and Ma, 2012b). Similarly to HET, DOT decreased as acclimation temperature and exposure time increased.

Emerging technologies to study aphids and stress

The pea aphid and, recently, the peach–potato aphid genome have been sequenced (Tagu *et al*., 2008; AphidBase, 2015; Chapter 2, this volume). While the DNA sequence describes a full set of information, not all of it is read at any one time. Organisms switch on different genes in relation to development or to react to changes in the environment. The transcriptome, which represents the RNA being expressed, indicates which genes are currently switched on. Studies have exploited transcriptomics to examine aphid interactions with their environment (Couldridge *et al*., 2007; Shelden and Roessner, 2013). RNA is translated into proteins; the proteome describes the proteins that have been produced by the transcriptome. While some studies have measured aphid proteins (e.g. Nguyen *et al*., 2009), in particular focusing on the salivary proteome (Carrillo *et al*., 2014), none has so far taken a systematic analysis of the aphid proteome and how it is altered by stress. Proteins regulate metabolism and produce the metabolome, the totality of the small molecule complement of an organism at a moment in time. As with the proteome, with some exceptions (Burke *et al*., 2010a), there have been very few systematic studies of the response of the aphid metabolome to stress.

These 'omics' technologies can produce huge amounts of data and require robust and consistent bioinformatics analysis. While these approaches can be costly and require specialist expertise, there are potentially huge advances to be made in the study of aphid responses to stress. Systematic examination of these different levels of 'omics' of multiple aphid genotypes (both intra- and interspecies) and their reaction to environmental change may crystallize some general features of response to stress.

Physiological adaptations to high temperature

Aside from behavioural adaptations, aphids have an array of physiological mechanisms to ameliorate the effects of high temperature. Exposure to high temperatures can be associated with changes in the proteome. For example, a reduction in metabolic enzymes and an increase in an exoskeleton-related protein were observed in *Macrosiphum euphorbiae* (potato aphid) (Nguyen *et al*., 2009). Heat treatment can trigger increases in sugar alcohols such as mannitol in *A. gossypii* and sorbitol in *A. pisum* (Burke *et al*., 2010a), which are known to be protective against temperature stress. Other metabolite changes include increases in β-alanine production in *A. pisum* and decreases in polyamine precursors, suggesting polyamine biosynthesis occurs in response to heat stress (Burke *et al*., 2010a). β-Alanine production and polyamine production are both responses that occur in other organisms (Kaplan *et al*., 2004; Malmendal *et al*., 2006), with β-alanine thought to have a role as a chemical chaperone preserving enzyme function (Mehta and Seidler, 2005).

Similar to other insects, aphid heat shock proteins (HSPs) have been implicated in the response to heat stress. HSPs chaperone protein–protein interactions at elevated temperatures (Bowler and Terblanche, 2008). Following heat shock, HSPs increase in aphids (Wilson *et al*., 2006). It is interesting to note

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that following heat shock, an increase in HSPs has also been found to occur in the obligate primary aphid symbiont, *Buchnera aphidicola* (Wilson *et al*., 2006). Adaptation to temperature stress could be facilitated by the faster mutation rate of bacterial symbionts. Dunbar *et al*. (2007) demonstrated that a single point mutation in the bacterial symbiotic *Buchnera* severely reduced expression of a small HSP concomitant with a reduction in aphid fitness. The reduction in aphid fitness was suggested to be due to secondary nutrient stress as a consequence of the reduced *Buchnera* load.

It is not only primary symbionts that are implicated in heat shock responses in aphids; secondary symbionts such as *Serratia symbiotica* may also have a protective effect on both aphid and *Buchnera* against heat shock (Burke *et al*., 2010b). *Serratia symbiotica* appears to ameliorate heat stress effects on *Buchnera* cell density and bacteriocyte numbers (Montllor *et al*., 2002; Russell and Moran, 2006). The lysis of *S. symbiotica* and subsequent release of metabolites to *Buchnera* is a potential mechanism for the positive effect of the symbiont under heat stress (Burke *et al*., 2010b). While the secondary symbiont, *S. symbiotica*, improves aphid fitness under high temperatures (Chen *et al*., 2000; Montllor *et al*., 2002), the current evidence does not support a similar effect for other facultative secondary symbionts; for example, *Candidatus* Hamiltonella defensa and *Candidatus* Regiella insecticola appeared to provide little heat protection (Russell and Moran, 2006) and showed no effect on performance at low temperatures in *S. avenae* (Lukasik *et al*., 2011). Aside from the effects on aphid symbionts, high temperatures have also been found to compromise resistance to parasitoids in some aphid species (Stacey and Fellowes, 2002).

Temperature Effects on Diet

The response of aphids to temperature stress cannot be fully understood in isolation from how extremes of temperature affect the host plant. Metabolomic studies have shown that both cold and heat shock can trigger changes in the plant *Arabidopsis thaliana*, leading to alteration in protein degradation and thus changes in amino acid availability to herbivores (Caldana *et al*., 2011). Temperature extremes can be accompanied by host-plant accumulation of sugars and alcohols in whole tissue, as well as altering the concentration of potential defence compounds such as resin acids and phenols (Holopainen and Kainulainen, 2004; Maruyama *et al*., 2009; Odabas *et al*., 2010).

Despite the importance of diet in determining aphid performance (Chapter 6, this volume), little is known of the changes the phloem undergoes when the plant is exposed to high or low temperature, information that would be central to understanding the response of herbivores whose diet is dominated by phloem sap. Physical factors could affect aphid feeding; under low temperatures, sieve element sap viscosity could increase to a point where it became energetically unfavourable, or indeed impossible, for aphids to take up sap. Wardlaw and Bagnall (1981) demonstrated that under low temperatures, sorghum had reduced phloem-carrying capacity, which could reduce nutrient delivery to a feeding aphid. Winter survival of parthenogenetic forms may be influenced by the secondary effects of low temperature on the host plant; for example, *R. padi* showed greater survival post-freezing when cooled while on the host plant, barley, than when cooled in isolation (Butts *et al*., 1997).

Knowledge of the temperature effects on phloem composition is central to predicting the effects on aphids; however, difficulty in sampling this important compartment means that data are currently limited. Cucurbit phloem sap can be collected relatively easily, providing some data on the temperature effects on phloem composition for these species. In muskmelon, *Cucumis melo*, exposure to chilling temperatures increased sugar and amino acid levels in both leaf and phloem sap (Mitchell and Madore, 1992). In melon plants exposed to high temperatures, there was an increase in phloem sucrose (Gil *et al*., 2012); such a change would increase phloem C:N ratio and potentially make the sap a poorer diet for aphids. Such increases in C:N ratios are likely to represent a general response of host plants, but the consequent effects on aphids are not consistent; increases in phloem C:N ratio when host plants were grown under elevated CO_2 had diverse effects on the performance of five aphid species, with one showing an increase in performance and one a decrease, while others were unaffected (Hughes and Bazzaz, 2001).

Aside from direct effects on diet via changes in phloem sap composition, temperature-induced changes to host-plant tissues may affect the aphid's ability to locate the sieve element (Chapter 9, this volume). *Arabidopsis* plants lacking the AKT2/2 K^+ transporter had lowered phloem sucrose (Deeken *et al*., 2002), correlating with an increase in the

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time taken by *M. persicae* to commence phloem feeding (J. Pritchard, unpublished). Supporting this is the observation that, in choice tests, aphids preferred sucrose over other carbohydrates (Hewer *et al.*, 2010). In contrast, changes in sieve element amino acids *in vivo* did not affect phloem location by *M. pers*icae (Hunt *et al.*, 2010). These data are consistent with a role for sieve element directed gradients in apoplastic sucrose as a cue for phloem location; thus, any environmentally induced changes in phloem C:N ratio could affect the ability of aphids to locate their food source, and therefore affect subsequent performance. Under drought conditions, the overall solute concentration of sieve element sap increases (Tully and Hanson, 1979; Girousse *et al.*, 1996; Isaacs *et al.*, 1998; Ponder *et al.*, 2000). The concentration of phloem sap may be beneficial for the aphid if essential amino acids become more available, or may be detrimental as aphids face difficulty in feeding as turgor pressure is decreased, and sap viscosity and osmolarity are increased, making the diet increasingly hyperosmotic to haemolymph. So far, there is no consensus on whether water loss and subsequent drought of host plants is beneficial or detrimental to aphids (Pritchard *et al.*, 2007). This uncertainty may be due to the variability of the host plant/aphid species/stress levels used, or may represent real adaptive biological variation.

Drought and Aphids

Drought is a major stressor of plants, inducing both adaptive and stress-induced changes that affect their physical and chemical composition. Such changes affect aphid performance, although, despite the apparent similarity of the biology of aphid species, it has proved difficult to identify a general response of aphids to environmental changes (Hughes and Bazzaz, 2001; Pritchard *et al.*, 2007).

Pure water has a water potential of zero, while the water potential of the atmosphere can vary from zero in water-saturated air to well below –15 MPa at a relative humidity of around 40%. Like many organisms, aphids face water loss to the atmosphere through a number of routes. Water can be lost by evaporation through the cuticle, from the spiracles and through excretion.

In plants, changes in the external water potential, which become more negative under drought, are compensated for by use of a large vacuole, allowing significant changes in solute composition through changes in hydrostatic pressure. Invertebrates can respond to changes in external water potential either by tolerance of water loss or by avoidance through tight homeostasis of haemolymph composition.

Some invertebrates are able to tolerate significant water loss. For example, Antarctic collembola accumulate significant sugars and polyols, which act to stabilize membranes as water is lost and haemolymph osmotic pressure increases (Elnitsky *et al.*, 2008). Similarly, mites can survive up to 35% water loss and show a range of adaptations to dry environments, including thicker cuticles, to conserve water and absorption of water vapour to rehydrate (Benoit *et al.*, 2008). Aphids are exposed to similar dehydrating environments, but have a qualitatively different strategy; that is, to maintain a constant internal hydric environment. Since the aphid cuticle is not a significant barrier to water loss (Lamb, 1963), the mechanism of aphid osmoregulation lies elsewhere.

In addition to low external water potential, aphids have the problem of a fluctuating and often hyperosmotic diet. Phloem sap generally has a high osmotic pressure that varies with plant species, plant nutrition and plant water status. Phloem osmotic pressure was found to be around 1.0 MPa in the rubber tree (*Hevea brasiliensis*) (An *et al.*, 2014). In barley, sieve element sap from leaves was 1.24 MPa (Pritchard, 1996). In roots of barley, the osmotic pressure of phloem sap was variable, increasing from 1.42 MPa to 1.62 MPa when plants were supplied with additional potassium (Gould *et al.*, 2004). The imposition of drought on the host plant can increase phloem sap osmotic pressure significantly; for example, in a study of native British grasses, phloem sap osmotic pressure increased from 1.2 MPa in well-watered plants to over 2.5 MPa following drought (Hale *et al.*, 2003).

Partly because of the specialist nature of their feeding and partly because comparison between experiments is difficult due to the use of different treatments and species, there is currently no clear consensus on the effect of host-plant drought on aphids. Drought increased sieve element sucrose and some amino acids, which was associated with an increased rate of population growth of *M. persicae* but had no effect on *Brevicoryne brassicae* (cabbage aphid) (Mewis *et al.*, 2012). It is interesting that in this study, a different set of plant transcripts was induced by the feeding of the different aphid species, emphasizing the subtlety of the interaction

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between plant and herbivore. The difficulty of predicting whether the effects of drought of the host plant will increase or decrease aphid performance is supported by the contradictory conclusions of two studies: a meta analysis that concluded that sap feeders would generally be affected negatively by drought (Huberty and Denno, 2004) and the findings of Rivelli *et al*. (2013), who concluded that water stress had both positive and negative effects on aphid species.

Haemolymph osmotic homeostasis

The maintenance of a constant internal osmotic pressure provides an alternative to the strategy shown by invertebrates that are able to tolerate desiccation. Aphids are able to maintain a constant haemolymph osmotic pressure in a fluctuating environment. The haemolymph of *A. pisum* was unchanged at 1.07 MPa for aphids feeding on both hypo- and hyperosmotic diets of 0.5 or 1.88 MPa, and there was no effect on the survival of the aphids over the range of diet osmotic pressures tested (Karley *et al*., 2005). The osmotic pressure of pea aphid haemolymph was constant when feeding on an artificial diet ranging from 0.38 to 2.5 MPa osmotic pressure (Wilkinson *et al*., 1997). Similarly, *Tuberolachnus salignus* (giant willow aphid) has a haemolymph osmotic pressure of 1.13 MPa, despite feeding on willow phloem sap with an osmotic pressure of 2.4 MPa (J. Pritchard, unpublished). There is a balance between the cost of osmoregulation and the need for water in the diet; aphid survival was greatest on a sucrose solution of 1.39 MPa but was reduced at higher (2.77 MPa) or lower (0.78 MPa) dietary osmotic pressure (Mittler and Dadd, 1963). It may be significant that the dietary osmotic pressure associated with optimal performance is often observed to be similar to the phloem osmotic pressure of well-watered plants, and close to the haemolymph osmotic pressure.

How do aphids osmoregulate?

Aphids are clearly successful osmoregulators, maintaining constant and equivalent haemolymph and honeydew osmotic pressures in the face of a widely varying ingested diet (Wilkinson *et al*., 1997). Several suggestions have been made as to how aphids are able to osmoregulate in the face of large changes in their diet (Douglas, 2006). When fed on a hyper-osmotic diet of 1.9 MPa sucrose, aphid honeydew contained significant amounts of oligosaccharides arising from the polymerization of dietary sucrose. In contrast, honeydew contained mainly glucose and fructose when fed on a hypo-osmotic diet of 0.9 MPa (Rhodes *et al*., 1996). It was hypothesized that the osmotic pressure of incoming phloem sap was modulated by the regulation of sugar polymerization in the aphid gut, illustrated in Fig. 7.2. Consistent with this, when the inhibitor acarbose was used to lower gut sucrase activity, the proportion of oligosaccharides in honeydew was lowered (Karley *et al*., 2005). Additionally, the removal of the putative osmoregulatory mechanism affected the ability of aphids to osmoregulate, since haemolymph osmotic pressure was unchanged when dietary osmotic pressure was increased from 0.5 to 1.9 MPa in the controls, but was raised to over 1.7 MPa when fed the inhibitor. Thus, sucrose-modulated changes in the osmotic pressure of the gut have a central role in aphid osmoregulation and adaptation to drought.

Water movement during osmotic adjustment is a consequence of both the driving force of water potential differences (or osmotic pressure in the absence of any significant hydrostatic pressure difference) and the resistance of the pathway. Membrane resistance (permeability) to water can be altered by the presence of aquaporin water channels. Changes in membrane permeability regulated by aquaporins may have a role in aphid osmoregulation since inhibition of an aquaporin in the aphid gut increased haemolymph osmotic pressure on both hyper- and hypo-osmotic diets (Shakesby *et al*., 2009), demonstrating a reduced ability to osmoregulate. Interestingly, removal of the bacterial symbiont *Buchnera* elevated the haemolymph osmotic pressure by 0.3 MPa, while still maintaining constant haemolymph osmotic pressure across a dietary osmotic pressure range of 0.38–2.5 MPa (Wilkinson *et al*., 1997), a result that could be explained by the change in availability of amino acids in the absence of the symbiont.

Aphids are also able to maintain a constant haemolymph osmotic pressure by rehydrating from the xylem. Xylem vessels normally have a significantly lower osmotic pressure than sieve element sap. The time aphids spent feeding on a sucrose-rich artificial diet was correlated positively with subsequent feeding time in the xylem, consistent with this behaviour as an osmoregulatory strategy (Pompon *et al*., 2011). *Myzus persicae* and *B. brassicae*

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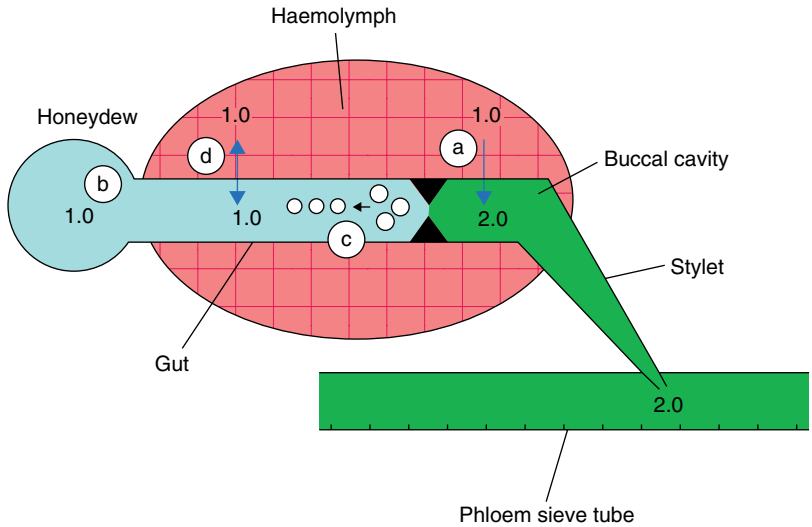

Fig. 7.2. Schematic diagram of the aphid–sieve tube continuum: numbers refer to solution osmotic pressures (MPa). Sieve element sap is frequently hyperosmotic to aphid haemolymph and so exerts osmotic stress on aphids. In this example, phloem sap with an osmotic pressure of 2 MPa enters the buccal cavity, where the osmotic gradient indicates an influx of water from the haemolymph into the buccal cavity (a). Since exiting honeydew is iso-osmotic with haemolymph (b; Wilkinson *et al*., 1997), the ingested sap has had its osmotic pressure reduced to prevent dehydration. This could have been achieved by the polymerization of gut sugars into oligosaccharides by sucrases (c; Karley *et al*., 2005) and the dilution of gut contents by incoming water, in which case the recycling of water from the gut to haemolymph may be facilitated by appropriately located aquaporins (d; Shakesby *et al*., 2009).

fed longer from the xylem when feeding on drought-stressed *Brassica nigra* in comparison to the unstressed control plants (Vickers, 2011). Interestingly, aphids deprived of their symbiotic bacterium *Buchnera* fed for longer from the xylem than those with *Buchnera* present, also supporting a role for the symbiont in osmoregulation. This observation is consistent with the elevation in haemolymph osmotic pressure in asymbiotic aphids, consistent with increased drought, noted by Wilkinson *et al*. (1997). Reduced xylem feeding (induced by the xylem mobile insecticide, thiomethoxam) decreased aphid water content, with a subsequent reduction in growth and reproduction (Daniels *et al*., 2009), again indicating a central role for xylem in osmoregulation by aphids. Since the xylem operates at negative pressures when plants are transpiring, any consideration of the value of xylem feeding in rehydrating aphids must be offset by a consideration of the costs of extracting xylem fluid at negative pressure. Such analysis has not been done for aphids, but information is available in the xylem-feeding leaf hoppers (Malone *et al*., 1999).

Secondary effects of drought on aphids – nutrition

Aphids can clearly osmoregulate in the face of drought stresses presented by their diet. However, drought stress may induce other changes in the host plant that can affect aphid performance detrimentally. These include altering plant nutritional value (Chapter 6, this volume) and affecting plant defences (Chapter 22, this volume). Aphids, like most herbivores, are limited by nitrogen. Changes in dietary nitrogen, in particular the sieve element amino acids, can be induced by drought. In the grasses *Dactylis glomerata*, *Arrhenatherum elatius* and *Holcus lanatus* subjected to drought, sieve element amino acids increased along with sap osmotic pressure; however, the aphid *R. padi* did not perform better, presumably as the cost of osmoregulation outweighed the benefit of higher nitrogen (Hale *et al*., 2003). A similar negative correlation between plant nitrogen status and aphid performance was seen in field experiments where drought increased the leaf nitrogen content of barley, shepherd's purse (*Capsella bursa-pastoris*) and common groundsel

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(*Senecio vulgaris*), but aphid (*R. padi*) abundance was reduced (Johnson *et al*., 2011). More subtle interactions were seen in a study of barley under drought that had reduced leaf nitrogen, but there was no effect on overall aphid numbers; however, the population structure was affected, resulting in a higher proportion of nymphs (Aslam *et al*., 2013). It is difficult to draw general conclusions when the level of drought imposed is often not measured, since different levels of drought can have qualitatively different effects on aphid performance. For example, on spring wheat aphid (*R. padi*) numbers increased at moderate drought but decreased at higher levels, with a positive correlation with leaf carbohydrate and protein levels but a negative one with tannins (Xing *et al*., 2003). Similarly, over a range of drought stresses applied to cabbage (*Brassica oleracea* var. *capitata*), the two aphid species *M. persicae* and *B. brassicae* had higher intrinsic rates of increase and fecundity and did best at moderate drought, an observation that did not correlate with the increased leaf nitrogen at higher levels of stress (Tariq *et al*., 2013a).

Secondary effects of host-plant drought on aphids – allocation to defence

While some studies have noted an increase in aphid performance following drought and attributed this to improved nutrition (Mewis *et al*., 2012), host-plant drought is often accompanied by reduced aphid performance; for example, on poplar (Ramirez *et al*., 2009), wheat (Pons and Tatchell, 1995) and *B. oleracea* (Simpson *et al*., 2012). These observations counter the plant stress hypothesis where plant response to stress is hypothesized to divert resources to defence, thus predicting that aphids will perform better on stressed plants. However, some studies have reported that drought stress can increase putative defence compounds; for example, the alkaloid gramine increased in drought-stressed barley (Larsson *et al*., 2011) and an increase in tannins was observed in drought-stressed wheat (Xing *et al*., 2003). In contrast, glutathione synthase, which has a detoxification role for plant xenobiotics, was induced by aphid feeding on watered, but not droughted, plants, consistent with a reduction in allocation to defence by the stressed plant (Khan *et al*., 2011).

Plant defence can take many forms, including recruitment of parasitoids. In this regard, it was interesting that volatile organic compound (VOC) production was reduced on droughted *B. oleracea*, accompanied by reduced parasitism of the aphids feeding on the stressed plants (Tariq *et al*., 2013b). A reduced number of adult aphids on droughted plants was associated with a reduction in attack by parasitoids (Aslam *et al*., 2013), although in this case it was not clear if this was due to the reduction in VOC emission by the plants or to the smaller numbers of suitable prey for the parasitoids. The adaptation of aphids to temperature stress can also be complicated by their relationship with parasitoids. *Acyrthosiphon pisum* became more susceptible to parasitoids at 25°C compared to 20°C, which correlated with a loss of the secondary symbiont *Ca*. H. defensa at the higher temperature, whereas aphids without symbionts were susceptible to the parasitoid at all temperatures (Bensadia *et al*., 2006).

Reactive oxygen species (ROS) as stress and defence

An underlying theme of this chapter is that aphid response to stress can only be fully understood if the effect of the stress on the host plant is also known. The specific effects of temperature and drought on plants have been considered in the previous sections. However, a common feature of the effects of abiotic stress on plants, including drought and low temperature, are changes in ROS and the redox state, which are thought to be important in coordinating and maintaining normal plant function during stress, and as such may be involved in detection, signalling and coordination of defence responses (Suzuki *et al*., 2012). If stress becomes more acute, the accumulation of ROS can itself become an oxidative stress, resulting in negative effects on both the plant and associated insect herbivores (Choudhury *et al*., 2013). Plants subjected to drought accumulate ROS (Cruz de Carvalho, 2008) and have associated detoxification mechanisms, including ascorbate and superoxide dismutase (SOD). However, as the level of drought increases, these detoxification mechanisms may become inadequate and the oxidative stress affects plant performance negatively (Lee *et al*., 2012). Oxidative bursts induced in host plants by stress can also have a negative impact on invertebrate herbivores and subsequently reduce their performance; following feeding by the corn earworm, *Helicoverpa zea*, on soybean, the subsequent increase in ROS was accompanied by damage to the midgut of the

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herbivore (Bi and Felton, 1995). The specialized nature of aphid feeding in the sieve tubes of the phloem does not allow circumvention of any damage by stress-induced oxidative burst, since the sieve element contains a full complement of antioxidant defences (Walz *et al*., 2002), and these can be induced by stress (Divol *et al*., 2005); however, evidence is not yet available that these phloem-located ROS directly reduce aphid performance.

Similar to the observations on chewing insect herbivores (Bi and Felton, 1995), aphid feeding can itself be a stress, inducing an oxidative burst in a plant; to counter this, aphids have a suite of antioxidant defences of their own (Łukasik and Goławska, 2013). It is not always clear whether oxidative bursts induced by aphid feeding are a stress, a regulatory response or a defence against the herbivory. The elevation of superoxide radicals induced by *A. pisum* on pea plants was followed by an increase in plant antioxidants consistent with a causal herbivory-induced stress (Mai *et al*., 2013). Higher levels of hydrogen peroxide have been noted in aphid-resistant varieties of wheat, implying a role in defence against aphid herbivory (Moloi and van der Westhuizen, 2006, 2008). Conversely, potato varieties with higher levels of the antioxidant ascorbate supported higher rates of growth of *M. persicae* (Kerchev *et al*., 2012). Phloem specificity for an oxidative defence is implicated in wheat by a decreased amount of phloem ingestion recorded on the resistant varieties of wheat using electronic penetration graphs (EPG) (Łukasik and Goławska, 2013). Aphid antioxidant detoxification mechanisms vary according to host-plant species, presumably reflecting the level of oxidative stress imposed by different plant species. The situation could be clarified with more data documenting the performance of aphid species on host plants with elevated ROS.

Molecular Clues to Aphid Stress Responses

Recent advances in the emerging 'omics' techniques have been applied successfully to examine the response of host plants to both aphid feeding (Couldridge *et al*., 2007) and the effects of abiotic stress (Shelden and Roessner, 2013). In these approaches, plant response to stress can be followed by looking at the suite of genes or proteins that are up- or downregulated and by examination of the annotations of the significantly affected genes making inferences about whether the response is adaptive or the result of 'damage'. The hypotheses generated by these candidate gene lists can then be tested by functional analysis using further molecular approaches to alter regulation or localize target genes. Despite the power of these approaches, most of the emerging molecular studies of aphids have focused on the interaction between aphids and their bacterial symbionts (Burke and Moran, 2011) and aphid saliva (Bos *et al*., 2010), and there is little information at present in the literature directly addressing the responses of aphids at the molecular level to stresses such as temperature and drought.

Whatever stress aphids are exposed to, they are clearly successful and able to adapt, both at the population and the individual level. A genome approach is being facilitated by the recently sequenced pea aphid genome (Tagu *et al*., 2008; International Aphid Genomics Consortium, 2010). Analysis of the aphid genome did not identify any striking suite of stress-related genes; however, in relation to aphid feeding and osmoregulation, it is interesting that Na^+-sugar transporters, which are required to transport sugar against a concentration gradient, are absent from the *A. pisum* genome. In contrast, the uptake of sugars via transport down the favourable sugar concentration gradient from gut to haemolymph could be facilitated by an expanded family of sugar uniporters when compared to similar genes in the common fruit fly, *Drosophila melanogaster* (International Aphid Genomics Consortium, 2010; Price *et al*., 2010). Further study of an aphid aquaporin identified in the *A. pisum* genome sequence suggested that it may have a role in response to drought, as it was noted to transport polyols which, in addition to water, could be involved in osmoregulation and/or membrane stabilization (Wallace *et al*., 2012); since aphids are unable to tolerate significant water loss, a role in osmoregulation is likely. In other invertebrates, transcriptome sequencing has implicated the upregulation of aquaporins during rehydration of the dehydration-tolerant tardigrade *Milnesium tardigradum* (Grohme *et al*., 2011). Late embryogenesis abundance (LEA) proteins have been implicated in ahydrobiotic species (Hand *et al*., 2011), but these have not been noted in aphids, consistent with their strategy of drought avoidance rather than tolerance.

Nguyen *et al*. (2009) demonstrated an alteration in the aphid proteome when feeding on droughted plants, but while protein spot identities implicated changes in aphid energy metabolism or behaviour, the lack of quantification of the drought effect on the plant and the aphid remain too preliminary to

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make causal connections. *Myzus persicae* feeding on drought-stressed *B. nigra* had elevated transcripts of amylases, aquaporins, cytochrome p450 and some HSPs (Vickers, 2011). Li *et al.* (2013) performed transcriptomics on the cotton aphid in spring and summer and identified 58 HSPs and 48 cytochrome p450s. The study also identified differential expression patterns between spring and summer morphs consistent with adaptation to the changing abiotic stress, with summer being arguably less stressful based on the seasonal changes in plant physiology and biochemistry. Adaptive explanations can be sought in reduced resource availability and/or imbalanced phloem composition in spring compared to summer. It is not obvious how such a change in nutritional value would affect the more specific adaptations of HSPs and cytochrome p450s, normally implicated in the detoxification of toxic compounds.

Conclusions

The importance of aphids as pests cannot be overstated, and is likely to increase with climate change. As herbivores, the impact of climate change, particularly abiotic stresses, is often ameliorated or buffered by the effect on the host plant, so direct stress effects are not always clear or predictable. We have argued that the two main stresses affecting aphids are temperature and drought; the former can affect the aphid directly, or through secondary effects on the host plant, whereas drought almost exclusively affects the aphid indirectly. It is striking that studies of stress effects on aphids have focused largely on temperature, in particular examining and categorizing the responses of aphids, with less focus on the underlying physiological and molecular causes. In contrast, there has been less examination of the effects of drought on aphids. It is often the case that secondary effects such as changes in nutrition induced by temperature or drought are the focus, rather than the underling primary physiological effects of the stress. Thus, studies of aphids do not parallel the more physiological approach taken in the study of the responses of their host plants to the same stresses.

While there is an increasing number of studies on the physiological effect of stress on aphids, the emergence of a general prediction of responses is confounded by the difference in host plant, application of the stress and the study species used; indeed, the extensive use of clonal aphid material may mask important adaptive information that can sometimes be seen in latitudinal studies. Further progress is likely when focused laboratory experiments combine more with ecophysiological and evolutionary information; however, it is the current view of the authors that there may be no single paradigm to be uncovered, and that the diversity of host-plant responses to environmental stress has driven a diversity of adaptive strategies by aphids.

The burgeoning molecular toolkit that is now available is a new opportunity to uncover the mechanisms by which aphids adapt to, or are damaged by, stress; these approaches are facilitated by the availability of the aphid genome sequence, and it is to be hoped that further research effort in these areas will qualitatively move forward our understanding of aphids' response to stress.

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8 Chemical Ecology

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Introduction

The ecology of aphids is, like that of most insects, highly dependent upon signals. Signals from host and non-host plants convey information that is vital for selecting feeding, larviposition and mating sites. Signals from aphids themselves are important in attracting a mate, aggregating with conspecifics, avoiding competition and sensing or giving warning of threats. Chemical signals (semiochemicals) are relatively efficient to biosynthesize, specific, easy to disperse into the environment and, not least, easy to detect. Aphid life cycles are characterized by complex interactions, and those species that alternate between hosts and have a sexual phase are faced with considerable challenges, such as locating the correct winter (primary) host, finding mates, leaving the winter host in the spring and successfully colonizing the summer (secondary) host. Therefore, it is no surprise that aphids make extensive use of semiochemicals, both in gathering information from their environment and in signalling to each other. Parasitoids and predators have also evolved responses to some of these semiochemicals. It has been 25 years as of 2017 since the last major review of aphid chemical ecology (Pickett *et al*., 1992). In this time, significant advances have been made in studies on the systemic production of aphid-induced volatiles by plants, volatiles that sometimes have a composition specific to an aphid species. There have also been advances in respect of the role of aphid sex pheromone-related chemistry beyond parasitoid chemical ecology and into predator behaviour, as well as increased realization of the role played by blends of volatiles in host-plant recognition by aphids.

There are around 4000 species of aphid (Aphididae). However, for two reasons, this review will necessarily focus on a very small number, principally in the subfamily Aphidinae. First, the great majority of information that exists on aphids has been obtained through the study of species from the temperate regions of the northern hemisphere (Dixon, 1998), and second, studies have naturally tended to focus, not exclusively but in large measure, on those species that are agricultural pests. Arguably, the aphids most studied in terms of their chemical ecology have been *Aphis fabae* (black bean aphid) and *Rhopalosiphum padi* (bird cherry–oat aphid), both from the Aphidinae and both host-alternating species that regularly manifest themselves as pests in the northern hemisphere. In the case of *R. padi*, the importance of chemical signals in the complex life cycle of a host-alternating aphid is readily apparent, and is summarized in Fig. 8.1. We now also see the first application of molecular biological techniques to aphid chemical ecology and, in particular, in the study of olfactory mechanisms and alarm pheromone biosynthesis (Field *et al*., 2000). Already, the first aphid gene involved in processing secondary plant metabolites (Jones *et al*., 2001; Pontoppidan *et al*., 2001) has been identified (Jones *et al*., 2002). Now that the first aphid, the pea aphid (*Acyrthosiphon pisum*), genome is available, it is being mined for genes involved in olfaction (Zhou *et al*., 2010). The molecular biology of aphid olfaction would be a chapter in itself and is beyond the scope of this chapter.

In this review, we examine the many varied interactions in aphid ecology in which semiochemicals

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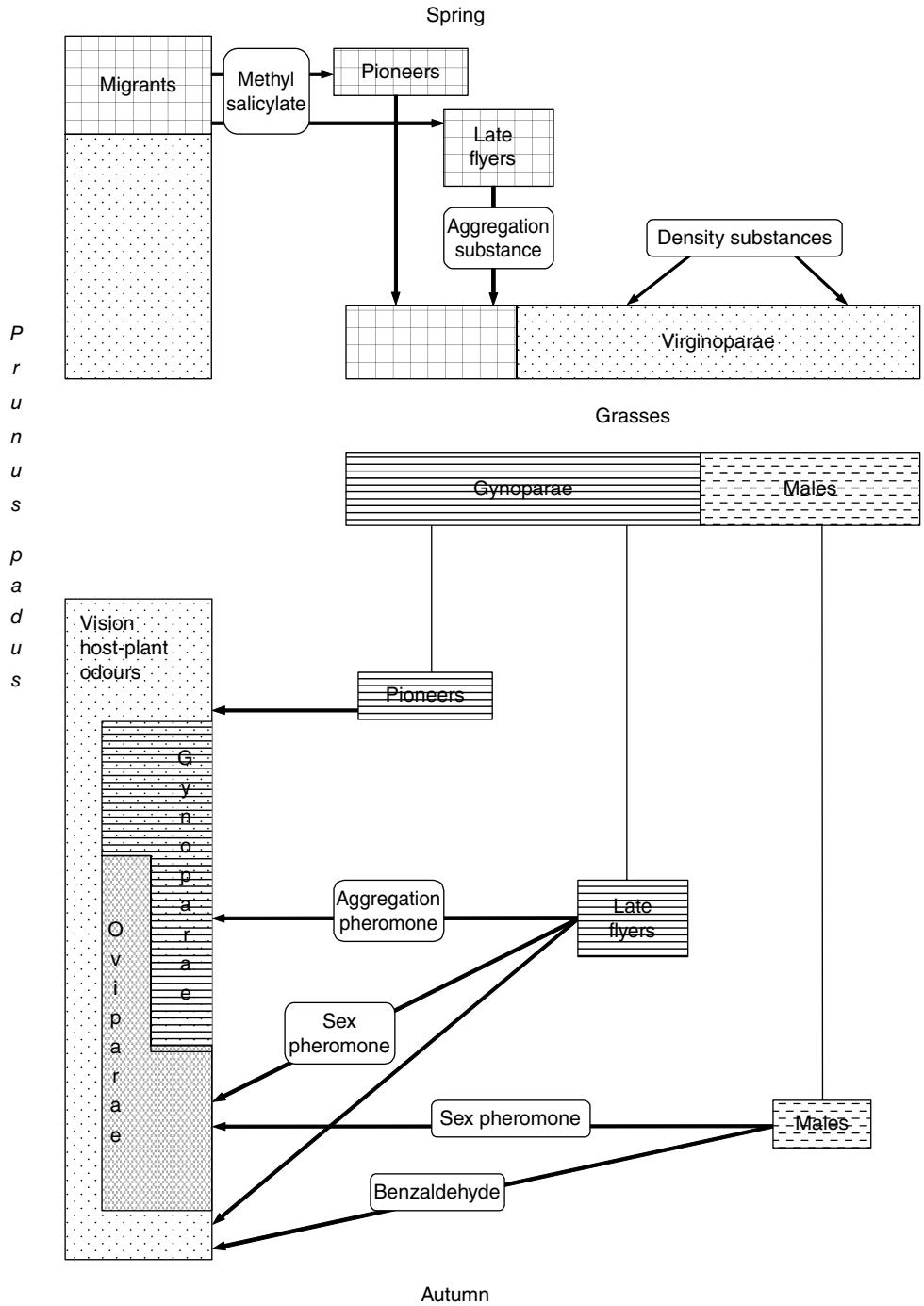

Fig. 8.1. Chemical ecology of host alternation in *Rhopalosiphum padi* (bird cherry–oat aphid). The diagram summarizes the interactions in which chemical signals are important for the aphid as it migrates from its winter host bird cherry, *Prunus padus*, to grasses and cereals, and back to *P. padus* in the autumn to undergo the sexual phase. (Based on Pettersson, 1994; Pettersson *et al*., 1994, 1995; Hardie *et al*., 1996; Glinwood and Pettersson, 2000a; Park *et al*., 2000.)

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play important roles. Taking a trophic level approach, we present examples of chemically mediated interactions between aphids, between aphids and plants and between aphids and their natural enemies.

Methods

Since this is a review of aphid chemical ecology, the 'Methods' section will be brief, but may be useful in highlighting some recent developments that have played an important generic role in the advances described in subsequent sections. It may also be of value to those workers contemplating new studies on aphid chemical ecology.

Bioassay techniques have continued to employ the Pettersson olfactometer (Pettersson, 1970a) and the linear track olfactometer with or without the modification (Hardie *et al*., 1994b), allowing the continuous release of test compounds. Approaches to obtaining volatile samples involve entrainment of air above the natural system by absorption on to porous polymers. The use of the solid-phase microextraction (SPME) technique has become widespread, and is extremely convenient. However, SPME does not provide a single consistent sample for multiple analysis, suffers from some other disadvantages and has been the subject of comparative quantitative investigation, which confirms the value of entrainment systems that give samples as solutions (Agelopoulos and Pickett, 1998).

When studying semiochemical release from intact plants, or plants colonized by particular herbivores such as individual aphid species, any cutting of petioles or damage to roots can alter the volatile profile. Entraining from semi-open vessels placed over the plant material can solve this problem. To avoid pressure or other damage at hermetic seals, a loose seal is established in the enclosing vessel and air is sampled from the positive pressure that can be created within (Dicke *et al*., 1990; Turlings *et al*., 1991; Röse *et al*., 1996; Agelopoulos *et al*., 1999).

Electrophysiological recordings coupled to capillary gas chromatography (GC) are important approaches for the initial identification of volatile semiochemicals, and can comprise an electroantennogram (EAG) (Birkett *et al*., 2000) as well as single cell (neuron) recordings (SCR) (Pickett *et al*., 1992). However, tentative identification by GC-coupled mass spectrometry (MS) can remain problematic, as the threshold detection level for MS, or at least the level for obtaining useful spectra, can be higher than for GC-SCR, or even the less sensitive technique of GC-EAG. Where GC is coupled directly to behavioural measurement, for example, of wing fanning by aphid parasitoids (Nazzi *et al*., 1996), the response threshold can be even lower than for GC-SCR. Increased sample size can cause loss of GC resolution due to the width of peaks increasing, but sometimes biological solutions to the problem can be found; for example, if a plant compound is involved, related cultivars or species that may contain more of the active compound can be investigated (L.J. Wadhams, unpublished).

Non-volatile semiochemicals can also mediate important aspects of chemical ecology (Powell and Hardie, 2001; Powell *et al*., 2006; Chapter 9, this volume). Techniques for studying these materials have advanced with liquid chromatography (LC)-coupled MS using reverse-phase columns and electrospray ionization in both positive and negative ion modes (Takemura *et al*., 2002, 2006). High-performance LC can also be used to produce fractions and pure samples of the putative non-volatile semiochemicals for analysis by nuclear magnetic resonance spectroscopy using a 500 MHz Fourier Transform instrument (Takemura *et al*., 2002).

Interactions between Aphids

Sex pheromones

Aphid sex pheromones were demonstrated unequivocally by Pettersson (1970b), and the first was chemically characterized in 1987 (Dawson *et al*., 1987a). The subject has been reviewed by Hardie *et al*. (1999) and Dewhirst *et al*. (2010). The sex pheromones, released by the sexual females, excite males and increase mating success (Fig. 8.2). The pheromones are produced in glandular epidermal cells lying beneath scent plaques on the tibiae of the hind legs of the sexual females and released through porous cuticles above the plaques. During pheromone release, the female engages in typical 'calling' behaviour, with the hind legs raised (Fig. 8.3). The olfactory receptors for sex pheromones are placoid sensilla, in the secondary rhinaria on the antennae of male aphids. The secondary rhinaria are mainly on the third, fourth and sometimes fifth antennal segments, and are highly sensitive to sex pheromone components (Chapter 9, this volume). There are separate receptor cells for individual pheromone components, which usually have different response amplitudes, both cells having to be activated to trigger a behavioural response.

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Sex pheromones have been chemically characterized from a number of species, all of which are in the subfamily Aphidinae. GC-SCR has played a major role in these studies, followed by GC-MS and confirmation of structures by synthesis and spectroscopy (Hardie *et al*., 1999; Boo *et al*., 2000). The pheromones usually comprise (4a*S*,7*S*,7a*R*)-nepetalactone (**1**, Fig. 8.4) and (1*R*,4a*S*,7*S*,7a*R*)-nepetalactol (**2**, Fig. 8.4), monoterpenoids in the cyclopentanoid or iridoid series. However, *Phorodon humuli* (damson–hop aphid) employs neither compound **1** nor **2**, but a mixture of the two diastereoisomeric (1*S*)- and (1*R*,4a*R*,7*S*,7a*S*)-nepetalactols (**3** and **4**, Fig. 8.4) (Campbell *et al*., 2003), although EAG responses to **1** have been recorded in males of this species (Pope *et al*., 2004). A further compound, (1*S*,2*R*,3*S*)-dolichodial (**5**, Fig. 8.4), has been identified from oviparae of *Dysaphis plantaginea* (rosy apple aphid) and found

Fig. 8.2. Mating in the aphid *Megoura viciae*. The darker, slightly thinner male (top) is attracted by sex pheromone released by the ovipara, the sexual female aphid. (Colour photograph courtesy of Rothamsted Research, UK.)

Fig. 8.3. The typical 'calling' position of a sexual female (ovipara) of *Megoura viciae*, with the hind legs raised. Sex pheromone components are produced in glandular epidermal cells lying beneath scent plaques on the tibiae of the hind legs. (Colour photograph courtesy of Rothamsted Research, UK).

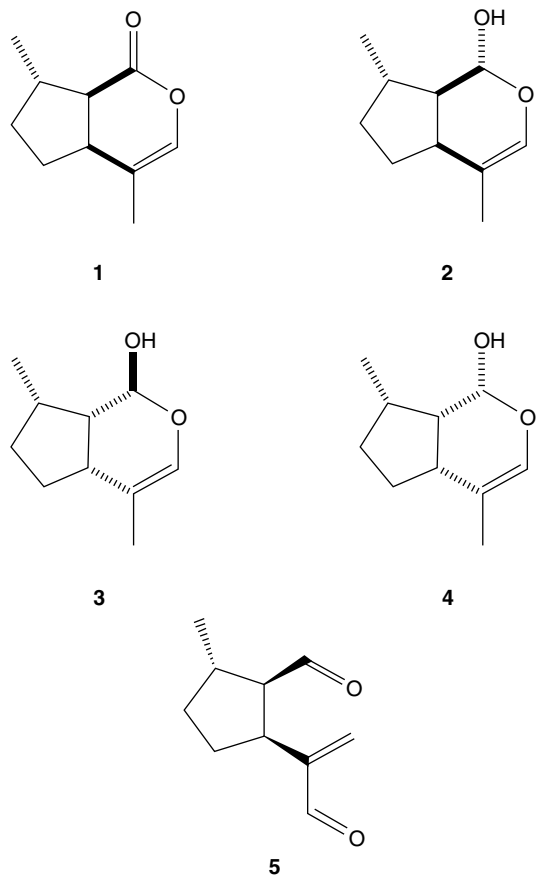

Fig. 8.4. Chemical structures for aphid sex pheromone components (4a*S*,7*S*,7a*R*)-nepetalactone (**1**), (1*R*,4a*S*,7*S*,7a*R*)-nepetalactol (**2**), (1*S*,4a*R*,7*S*,7a*S*)-nepetalactol (**3**), (1*R*,4a*R*,7*S*,7a*S*)-nepetalactol (**4**) and (1*S*,2*R*,3*S*)-dolichodial (**5**).

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to elicit electrophysiological and behavioural responses from males (Dewhirst *et al*., 2008). This species produces a blend of **1** and **2** (Stewart-Jones *et al*., 2007), and it remains to be shown whether **5** represents a further sex pheromone component. This dolichodial occurs also in many other aphids, often as a trace, but here the function is entirely unknown (J.A. Pickett, unpublished; Dewhirst *et al*., 2008).

The nepetalactone **1** is familiar as a compound from the catmint plant *Nepeta cataria* in the Lamiaceae, and can be chemically reduced selectively to the nepetalactol **2**. This provides a commercial (Botanix Ltd, Paddock Wood, UK) route to these compounds in which specific cultivars of *N. cataria* are grown as arable crops, harvested wet and then directly subjected to steam distillation to yield the essential oil with a very high proportion of **1**. Further conversion by hydride reduction to the nepetalactol **2** can also be achieved on a commercial scale. Formulation (AgriSense-BCS Ltd, Rhondda Cynon Taff, UK) is as a polymeric rope, where the length determines the overall release rate or field dose. The nepetalactone giving the nepetalactols **3** and **4** is also found in the related *Nepeta racemosa* (Birkett and Pickett, 2003).

The biosynthesis of nepetalactones in plants has received considerable attention (Kries *et al*., 2015) and may be achieved by a similar route in aphids. The isoprenoid precursor is geraniol and/or the (*Z*)-isomer nerol, or possibly citronellol, and a detailed analytical study of the aphid sex pheromone from various species has revealed that citronellol (with undetermined stereochemistry) is a common, but minor, component of volatiles associated with sex pheromone release. It has shown no electrophysiological or behavioural activity, at least in connection with mate location, and may therefore be the precursor for the cyclopentanoid biosynthesis of aphid sex pheromones (Dawson *et al*., 1996).

Most aphids examined so far employ a limited range of pheromone components, but there are differences in relative and absolute compositions. Only *P. humuli* produces **3** and **4**, while the other aphid species studied produce blends of **1** and **2** or the individual components (Hardie *et al*., 1999; Boo *et al*., 2000; Goldansaz *et al*., 2004; Symmes *et al*., 2012). However, there does not seem to be sufficient variability to allow species specificity, even merely within the Aphidinae. Indeed, a number of species use the same single-component **1** alone – for example, *Sitobion avenae* (English grain aphid), *Sitobion fragariae* (blackberry–cereal aphid) and *Brevicoryne brassicae* (cabbage aphid) (Hardie *et al*., 1999). Laboratory males are more responsive to the pheromone blend closest to that released by the conspecific sexual females than to other blends. The addition of **2** inhibited the olfactometric responses of males of *S. avenae* (Lilley *et al*., 1995) and *S. fragariae* (Lilley and Hardie, 1996) to their sex pheromone component **1**. Field trap-catch data show a remarkable specificity. Water traps releasing only **1** recorded males of 21 aphid species, including mainly *S. fragariae* (Hardie *et al*., 1992). Even the addition of minimal quantities of **1** reduced catches of *R. padi*, which employs only **2** (Hardie *et al*., 1997), to levels similar to unbaited traps. In traps releasing **1**, **2**, or a 1:1 blend of **1** and **2**, 66% of male *Aphis* spp. and 85% of male *Dysaphis* spp., including *D. plantaginea*, were captured by the blend, while 88% of *Rhopalomyzus lonicerae* were found in traps releasing **1**. *Myzus cerasi* (cherry blackfly) was also captured in traps releasing only **1** (Hardie *et al*., 1994c).

Trap catches appear to be associated with pheromonally mediated anemotaxis, although this was considered, before the availability of synthetic pheromone, to be an unlikely possibility. Indeed, it has been shown that *P. humuli* can fly towards a source of its pheromone against wind speeds of up to 0.7 m/sec, and can detect pheromone 3–4 m downwind (Hardie *et al*., 1996). The sex pheromones have potential for use in population monitoring and control of pest aphids, though the main agricultural use under development is in the attraction of parasitoids (see 'Interaction with plants' below). Asexual morphs of *Myzus persicae* (peach–potato aphid) have shown electrophysiological responses and behavioural repellency to **1**, albeit at relatively high concentrations (Fernandez-Grandon *et al*., 2013).

There is now clear evidence of an interaction between sex pheromone and host-plant volatiles in some aphid species (Hardie *et al*., 1999; Pope *et al*., 2007; van Tol *et al*., 2009). More *P. humuli* males were caught in traps releasing **3/4** together with the winter host plant (*Prunus* spp.), volatiles benzaldehyde or methyl salicylate than with **3/4** alone (Pope *et al*., 2007). Similar results were found with *R. padi* when combining either volatile with **2**. However, the release of both volatiles together with the appropriate sex pheromone increased catches of male *R. padi* but reduced those of male *P. humuli*, suggesting a role for host-plant volatiles in species discrimination. It should be mentioned that sex

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pheromones can interact with visual cues, the latter also affecting the behaviour of male aphids. For example, surface colour is crucial and catches of males of three species in water traps were affected dramatically by trap colour (Hardie *et al*., 1996).

Alarm pheromones

The asexual forms, and most often the wingless females, of many aphids release an alarm pheromone when disturbed. Nearby aphids exhibit a variety of behaviours, ranging from the removal of mouthparts from the plant and moving away, to running, dropping off the plant and even attacking the predator. This aspect of aphid chemical ecology has been reviewed in depth (Hardie *et al*., 1999; Vandermoten *et al*., 2012).

Variation in response to alarm pheromones is seen both intra- and interspecifically, and relates to the relative risks of predation and costs of escape. Aphids that have dropped from a plant may either recolonize it or search for another host plant, but in both cases face a greatly increased risk of predation (Griffiths *et al*., 1985; Sunderland *et al*., 1986) or starvation. Fallen aphids exposed to alarm pheromone often appear behaviourally reluctant to regain their host plant (Klingauf, 1976). A lack of response from the early instars may arise from the risk of predation to these larvae being lower than the risk involved in ceasing to feed. Winged adults are more responsive to alarm pheromone, perhaps because they move more readily off the natal host. However, with *Ceratovacuna lanigera* (sugar cane woolly aphid), it is the first-instar nymphs that show attack behaviour in response to alarm pheromone, while older nymphs and adults merely disperse (Arakaki, 1989). In this species, however, the first-instar nymphs have long frontal horns and are able to mount an effective defence against predators.

Considerable variation exists among aphid species in their sensitivity to alarm pheromones in both the speed and the form of the response, variation that often can be related to the ecology of the species. For example, some aphids, particularly those tended by ants, respond by walking or 'waggling' their abdomens rather than falling off the plant (H.F. van Emden, unpublished). Response to alarm pheromone is affected by many additional factors, and in some cases may be dependent on physical cues, or other semiochemicals, as discussed below (Hardie *et al*., 1999). Insecticide-resistant *M. persicae* responded to alarm pheromone more slowly and in lower numbers than insecticide-susceptible forms (Dawson *et al*., 1983; Foster *et al*., 1999, 2005; Chapter 19, this volume). This may be due to the pleiotropic physiological effects associated with resistance affecting mobility, or to the impairment of nerve function (Foster *et al*., 1999). Production can also vary, as aphids reared in isolation have been found to produce less (*E*)-β-farnesene (Verheggen *et al*., 2009). However, there is no contagious release of alarm pheromone (Hatano *et al*., 2008; Verheggen *et al*., 2008a).

Exposure to alarm pheromone can lead to an increase in the production of winged morphs in an aphid colony (Kunert *et al*., 2005, 2007; Hatano *et al*., 2010). Since this effect was seen when groups of aphids, but not isolated individuals, were exposed to the pheromone, it seems likely that the exposure causes a 'pseudo crowding' effect, with increased physical contacts triggering the shift in morph production. A higher proportion of winged morphs has been found in the offspring of aphids exposed either to the alarm pheromone itself (Kunert *et al*., 2007) or attacked by a predatory lacewing larva (Schwartzberg *et al*., 2008). An increase in the proportion of winged morphs even occurs when aphids are exposed to (*E*)-β-farnesene under field conditions (Hatano *et al*., 2010).

Droplets secreted from the siphunculi, on attack or mechanical interference, contain the minor, rapidly vaporizing fraction that is the alarm pheromone. A waxy fraction, consisting mainly of triglycerides, that crystallizes on contact with foreign particles outside the aphid's body, is also produced. The waxy component appears to function as a sticky irritant to predators and parasitoids.

The main component of the alarm pheromone of many aphids is the sesquiterpene hydrocarbon (*E*)-β-farnesene (**6**, Fig. 8.5) (Bowers *et al*., 1972; Edwards *et al*., 1973; Wientjens *et al*., 1973; Pickett and Griffiths, 1980). Other components may also be present. For example, the alarm pheromone of *Megoura viciae* (vetch aphid) contains the monoterpenes α-pinene, β-pinene, (*Z*,*E*)-α-farnesene and (*E*,*E*)-α-farnesene, in addition to **6**, and these can synergize the activity of **6**. There is a high degree of cross-activity of both natural alarm pheromone and **6** among species within the Aphidinae and Chaitophorinae, typical of insect alarm pheromones in general. The main component of the alarm pheromone of *Therioaphis trifolii maculata* (spotted alfalfa aphid) and *Therioaphis riehmi* (sweet clover aphid) (Calaphidinae), however, is the cyclic

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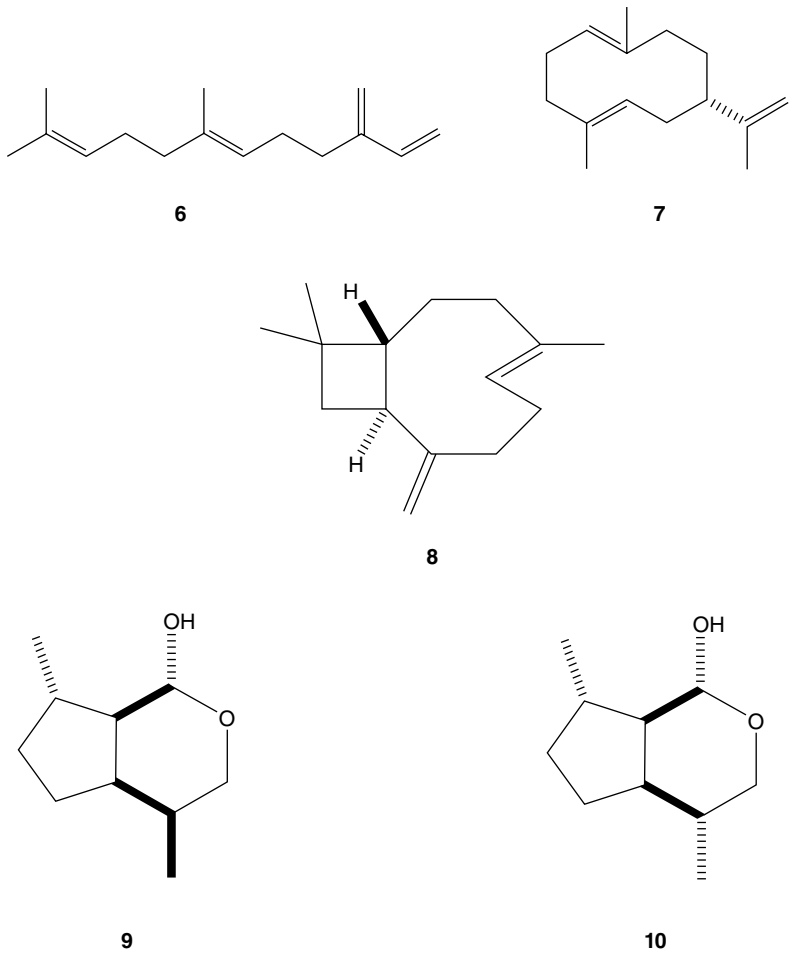

Fig. 8.5. Chemical structures for other aphid-related semiochemicals: (*E*)-β-farnesene (**6**), (*S*)-germacrene-A (**7**), (*E*)-caryophyllene (**8**), (1*R*,4*S*,4a*R*,7*S*,7a*R*)-dihydronepetalactol (**9**) and (1*R*,4*R*,4a*R*,7*S*,7a*R*)-dihydronepetalactol (**10**).

sesquiterpene (10*S*)-germacrene-A (**7**, Fig. 8.5). Both **6** and **7** are volatile, highly labile compounds and produce a short-lived, though for some species dramatic, alarm signal. The alarm pheromone is detected by the primary rhinaria on the fifth and sixth antennal segments, which can be seen from recordings from single olfactory cells, for example with *M. persicae* (Dawson *et al*., 1987b).

Sesquiterpene hydrocarbons, including (*E*)-β-farnesene itself **6**, are commonly produced by plants. A gene for an enzyme from peppermint (*Mentha* × *piperita*) that effects conversion of farnesyl pyrophosphate to this sesquiterpene has been cloned and functionally expressed in *Escherichia coli* (Crock *et al*., 1997). However, many other sesquiterpenes are also produced that could cause inhibition of the alarm response (see below). Nevertheless, the compound **6** in the volatiles produced by leaf hairs of the aphid-resistant wild potato, *Solanum berthaultii*, caused alarm behaviour in wingless adult *M. persicae* (Gibson and Pickett, 1983). Aphids disturb these hairs or trichomes so that they release a burst of pure (*E*)-β-farnesene **6**. However, the sesquiterpene (*E*)-caryophyllene (**8**, Fig. 8.5), together with other sesquiterpenes commonly accompanying **6** in plants, was found to inhibit alarm activity (Dawson *et al*., 1984). This enables the aphid to distinguish whether **6** emanates from alarm pheromone or from a plant source. Olfactory cells in aphids have been found that are sensitive to either **6** or **8**, but not to both,

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and the two cell types are located in rhinaria on different antennal segments (Campbell *et al*., 1993). For *Lipaphis pseudobrassicae* (mustard aphid), there is synergy between **6** and the generally toxic defence compounds such as organic isothiocyanates, which are produced from glucosinolates apparently sequestered from host plants in the Brassicaceae (Dawson *et al*., 1986).

The use of (*E*)-β-farnesene in aphid control strategies has been hindered by its instability. However, there is renewed interest in exploiting plant essential oils rich in the substance, such as that of *Syncolostemon petiolatus* (Lamiaceae), which contains >70% (*E*)-β-farnesene. Although laboratory studies suggest that the presence of the minor components (+)-bicyclogermacrene and germacrene D may inhibit the alarm response of certain aphid species, a slow-release formulation reduced *A. pisum* (pea aphid) numbers in the field, giving a promising route for the deployment of (*E*)-β-farnesene in the management of pest aphids (Bruce *et al*., 2005). More recently, studies have been undertaken with transgenic plants transformed with (*E*)-β-farnesene synthase enzymes to release the aphid alarm pheromone. In the laboratory, **6**-emitting *Arabidopsis* elicited alarm and repellent responses with the aphid *M. persicae* and an arrestant response with its parasitoid, *Diaeretiella rapae* (Beale *et al*., 2006). However, continuous exposure to the alarm pheromone in aphid colonies raised on these plants that produce **6** leads to habituation within three generations, and habituated aphids show no avoidance response (de Vos *et al*., 2010). This, however, carries a fitness cost because (*E*)-β-farnesene-responsive aphids have a higher survival rate in the presence of a coccinellid predator (*Hippodamia convergens*), and thus outperform habituated aphids that do not show an avoidance response (de Vos *et al*., 2010). Wheat engineered to release **6** did not have lower aphid infestation (Bruce *et al*., 2015). Continuous emission when there is a constitutive promoter on the (*E*)-β-farnesene synthase gene is not ideal because aphids naturally release **6** in a pulse when attacked by predators (Kunert *et al*., 2010; Bruce *et al*., 2015).

Natural enemies of aphids use (*E*)-β-farnesene **6** as a foraging cue (Beale *et al*., 2006; Almohamad *et al*., 2008), and thus it could be used to attract these beneficial insects in agricultural situations. Overexpression of (*E*)-β-farnesene synthase in transgenic tobacco plants resulted in the emission of **6**, and transformed lines were significantly more attractive to lacewings (Yu *et al*., 2012). Cui *et al*. (2012) used **6** extracted from chamomile (*Chamaemelum nobile*) to attract natural enemies to reduce cabbage aphid numbers in Chinese cabbage (*Brassica rapa* subsp. *pekinensis*) fields. An example of natural occurrence of this is orchid flowers that mimic aphid alarm pheromones to attract hover flies for pollination (Stokl *et al*., 2011). Furthermore, ants use aphid alarm pheromones as a cue indicating the presence of aphid colonies (Verheggen *et al*., 2012).

Social interactions: aggregation, density regulation and avoidance

Aphids live in colonies that often reach a high density of individuals. Several selective forces may maintain this habit, and the capacity for rapid reproduction combined with low mobility can be seen as either a reason for, or an adaptation to, colonial living. One benefit of aggregation is increased protection from natural enemies (Turchin and Kareiva, 1989), although forming heterospecific aggregations could satisfy this. Therefore, it is possible that conspecific aggregation improves the food quality of the host plant (Chapter 6, this volume). Aphid colonies can grow to such a size that their sustainability on the plant is threatened, so there should be a point at which the advantage switches from the recruitment of further individuals to the plant to their deterrence from it. Therefore, control over social interactions both within and between species is important for aphid survival, and it is no surprise that semiochemicals play a role in maintaining such interactions. Current knowledge is biased towards aphid species that are considered to be economically important; furthermore, aggregation and avoidance interactions may be especially important in host-alternating species.

Aggregation

Gynoparae of *R. padi* show an aggregated distribution after settling on the winter host *Prunus padus* that cannot be explained by differences in microclimate or leaf quality (Pettersson, 1993). Gynoparae are attracted to the odour of other gynoparae (Pettersson, 1993, 1994), and to the odour of *P. padus* leaves, but there is no increased response to leaves infested with gynoparae. Thus, the aggregation of colonizing aphids on the winter host is mediated by an aggregation pheromone. Although it is unclear whether gynoparae of *R. padi* feed on

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the winter host, it is likely that one benefit of aggregation is the subsequent aggregated distribution of oviparae, which should maximize the attraction of males to the sex pheromone.

The aggregation of *R. padi* gynoparae is further enhanced by the attraction of late flyers to the sex pheromone nepetalactol (**2**, Fig. 8.4), produced by oviparae already on the winter host (Fig. 8.1). Nepetalactol-baited traps captured gynoparae in the field (Hardie *et al.*, 1996), but since the traps caught only a relatively small proportion of the aerial population, it was suggested that the response of gynoparae to nepetalactol was weaker than that of males. This was later confirmed by EAG and behavioural studies (Park *et al.*, 2000). Since gynoparae of *S. fragariae* and *P. humuli* are also attracted to sex pheromones, this aggregation mechanism may be common among host-alternating species (Hardie *et al.*, 1996; Lösel *et al.*, 1996).

Semiochemicals are also involved in aggregation on summer host plants. In olfactometer tests, spring migrants of *P. humuli* were more attracted by spring migrants feeding on a leaf of their summer host, hop (*Humulus lupulus*), than to an uninfested leaf (Campbell *et al.*, 1993). The entrainment of hops, followed by GC-MS, identified three compounds released by the plant on feeding: (*E*)-2-hexenal, (*E*)-caryophyllene and methyl salicylate, all of which were shown by GC-SCR to elicit responses from separate olfactory receptors on the aphid antenna. Interestingly, the addition of methyl salicylate caused the other two compounds to lose attractiveness in the olfactometer, and it was suggested that methyl salicylate might be produced by the plant in response to high densities of feeding aphids, effectively preventing the recruitment of further migrants to the plant. Analogous to the above results for *P. humuli*, *R. padi* spring migrants are more attracted to odour produced by spring migrants feeding on oat leaves than to uninfested leaves (Pettersson, 1994), again suggesting the presence of an aggregation substance for the migrating morph. In this case, the origin of the substance or substances has not been identified.

Aggregation pheromones in non-migratory morphs have also been reported. Alatae of two brassica-feeding aphids, *B. brassicae* and *L. pseudobrassicae*, emit an odour that attracts conspecific alatae, but not conspecific apterae (Pettersson and Stephansson, 1991). Apterae of *Aphis craccivora* (cowpea aphid) were attracted to the odours emitted by both apterae and alatae in small groups (≤10 individuals), and alatae were also attracted to small groups of apterae (Pettersson *et al.*, 1998). In both these studies, it appears that the aggregation signals are also involved in density regulation and avoidance interactions (see the following section). Arrestment of alatae by odour from settled alatae was shown in *A. fabae* (Kay, 1976). In the examples reviewed here, early colonizers can be considered as pioneers that act as 'beacons' for later arriving individuals (Pettersson, 1994).

Density regulation and avoidance

Based on observations of the increase in walking activity of *R. padi* apterae when colony density passes a critical threshold, Pettersson *et al.* (1995) investigated the presence of a semiochemical-based, density-regulating mechanism. In olfactometer tests, colonies of *R. padi* apterae on oat leaves became repellent to other apterae when the density threshold was exceeded. Air entrainment, followed by GC-MS, identified three compounds associated with high, but not lower, densities of *R. padi* apterae feeding on wheat; 6-methyl-5-hepten-2-one, 6-methyl-5-hepten-2-ol and 2-tridecanone, with the enantiomeric composition of 6-methyl-5-hepten-2-ol determined as a 1:3 ratio of (+) and (-) (Quiroz *et al.*, 1997). In olfactometer tests, all the compounds were repellent, the strongest repellence being obtained with the ratio of compounds present in air-entrainment samples. However, when the enantiomers of 6-methyl-5-hepten-2-ol were presented either individually or in the incorrect ratio, they were behaviourally inactive (Quiroz and Niemeyer, 1998). Chemicals that influence aphid behaviour, especially those that are repellent, are of great interest as potential components of integrated pest management strategies. The *R. padi* density-related substances applied to cereal crops in the form of slow-release wax pellets suppressed aphid populations, especially in combination with methyl salicylate (Ninkovic *et al.*, 2003).

A similar density-regulating mechanism to that of *R. padi* may operate in *A. craccivora*. Odours from groups of apterae repelled both apterae and alatae in an olfactometer when a critical group size of 20 or more individuals was surpassed (Pettersson *et al.*, 1998). The aggregation pheromones emitted by alatae of the brassica-feeding aphids *B. brassicae* and *L. pseudobrassicae*, described earlier, also appeared to facilitate interspecies avoidance, with alatae of both species

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repelled by the odour of alatae of the other species (Pettersson and Stephansson, 1991).

Although, in some cases, semiochemicals that influence aphid social interactions are pheromonal, in other cases their origins are unclear. In functional terms, it makes little difference whether the aphid or the plant produces the substance; the message is the same. Indeed, the induction of plant chemicals by aphids and their ability to detect them has certain advantages, such as avoidance of the costs of pheromone production and the conveyance of additional information about the condition of the plant. It is interesting that species that share a common host plant have the ability to detect each other using odour alone (Pettersson and Stephansson, 1991; Johansson *et al*., 1997).

Interaction with Plants

Host-plant semiochemicals

Where host-plant semiochemicals have been identified, their perception has been found generally to be associated with highly specific cells, usually in the primary rhinaria of the fifth and sixth antennal segments. Recent reviews have discussed the role of host volatiles in plant–aphid interactions (de Vos and Jander, 2010; Webster, 2012).

Semiochemicals of the primary host of host-alternating aphids

The use of chemicals by return migrants searching for their primary hosts in the autumn has been reviewed (Powell and Hardie, 2001), providing evidence of semiochemical use by *A. fabae*, *P. humuli*, *R. padi* and *S. fragariae*, among others.

In the autumn, the orientation of *R. padi* to its primary host *P. padus* is largely dependent on aphid-produced signals, although the role of the host chemical benzaldehyde has also been demonstrated (Pettersson, 1970a). In the spring, the challenge facing the migrating morphs is to leave *P. padus* and, rather than recolonizing it, to locate a suitable summer host successfully. In the search for substances that could be used for the control of summer generations, Pettersson *et al*. (1994) identified methyl salicylate as a volatile chemical occurring in the primary, but not the summer, host. The substance was repellent to *R. padi* spring migrants in olfactometer tests, and also switched off the response to their aggregation cue (the odour of migrant-infested cereals). Pettersson *et al*. (1994) hypothesized that methyl salicylate could be used by aphids as a host discrimination cue, and also pointed out the potential role of the substance in plant defence signalling and as a promoter for induced resistance (Shulaev *et al*., 1997). Methyl salicylate may also function as a host-leaving stimulus. Glinwood and Pettersson (2000a) showed that volatiles from foliage infested with developing spring populations of *R. padi* were repellent to spring migrants in olfactometer tests, whereas volatiles from uninfested foliage were behaviourally neutral. The subsequent collection and identification of volatiles from intact uninfested and infested foliage on *P. padus* saplings revealed that methyl salicylate was released in response to aphid infestation (Fig. 8.6). Thus, it appears that methyl salicylate is a damage-induced plant signal that is used as a behavioural cue by the aphid species that induces its production. Methyl salicylate has been deployed successfully in the integrated control of cereal aphids (Pettersson *et al*., 1994; Ninkovic *et al*., 2003), including *Diuraphis noxia* (Russian wheat aphid) in South Africa (Prinsloo *et al*., 2007). However, there is evidence that the response of *R. padi* to this substance varies with the physiological age of the aphid (Glinwood and Pettersson, 2000b) and may be disrupted if the aphid is infected by a virus (Ban *et al*., 2008).

Aphis fabae on spindle does not seem to parallel the *R. padi–P. padus* system in terms of the importance of chemical signals. Evidence of the attraction of gynoparae to spindle volatiles is contradictory (Powell and Hardie, 2001), and there is no evidence of the induction of volatiles by feeding spring generations analogous to the induction of methyl salicylate in the *R. padi–P. padus* system (R. Glinwood, unpublished). Volatiles collected from blackcurrant, the winter host of the currant–lettuce aphid, *Nasonovia ribisnigri*, were significantly repellent to the summer form in olfactometer experiments (T.J.A. Bruce, unpublished).

Semiochemicals of the secondary host of host-alternating aphids

A substantial part of the existing knowledge in this area has been reviewed extensively by Pickett *et al*. (1992), and more recently by de Vos and Jander (2010) and Webster (2012), and therefore will not be dealt with here. It is, however, worth noting that

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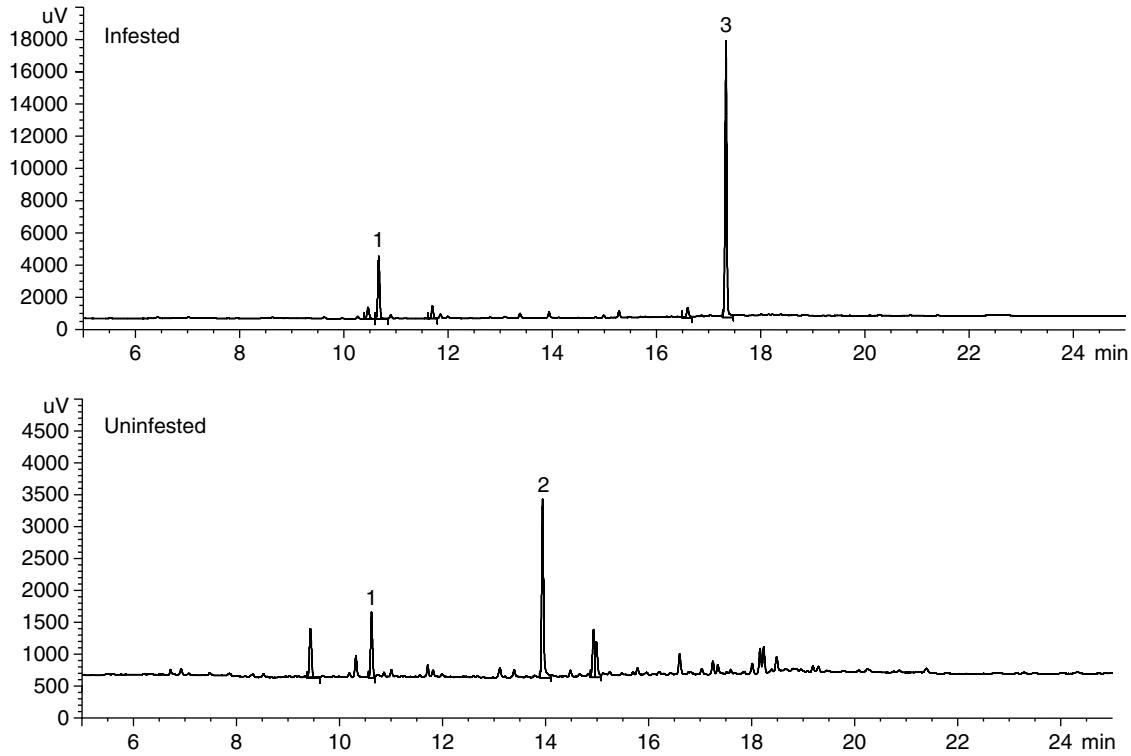

Fig. 8.6. GC of volatiles collected from *Prunus padus* that was either infested or uninfested with spring generations of *Rhopalosiphum padi* (bird cherry–oat aphid). Major peaks identified by GC-MS as: (1) (*Z*)-3-hexenyl-acetate, (2) benzaldehyde and (3) methyl salicylate.

the significance of volatile blend composition is becoming apparent for phytophagous insects in general (Bruce and Pickett, 2011), and a striking example is found in *A. fabae*. A range of compounds that were repellent alone in an olfactometer became attractive to alate virginoparae when combined in a blend (Webster *et al*., 2010). Further, this aphid species has shown evidence of the type of experience-based learning of host-plant volatile blends found in many other insect herbivores (Webster *et al*., 2013).

While the ability of aphids to perceive chemical cues, and the importance of these cues in host finding is undoubted, eventual host acceptance is expected to depend on the interaction of chemical, visual and nutritional cues (Powell *et al*., 2006; Chapter 9, this volume). It should be noted that volatiles from host plants can also have negative effects on aphids; for example, by directly reducing fecundity (Hildebrand *et al*., 1993) or by inducing responses in neighbouring plants (Glinwood *et al*., 2011).

Non-host-plant semiochemicals

The study of semiochemicals used by aphids to avoid unsuitable hosts has provided important new discoveries since the review by Pickett *et al*. (1992). In 1994, there was evidence that, besides taxonomically unsuitable hosts being avoided by aphid migrants (Nottingham and Hardie, 1993; Hardie *et al*., 1994b), the primary host became a non-host in the spring (Pettersson *et al*., 1994), and that the associated repellency was perceived by specific olfactory cells, again in the primary rhinaria, that responded to non-host semiochemicals. Two of these, (1*R*,5*S*)-myrtenal from gymnosperms, which are non-hosts for *A. fabae*, and methyl salicylate from *P. padus*, the primary host for *R. padi*, not only caused repellency but, at lower levels, also interfered with the attraction to host plants (Hardie *et al*., 1994a; Pettersson *et al*., 1994). Fieldwork with methyl salicylate showed that the compound reduced the populations of several species of cereal aphids in addition to *R. padi*, including *S. avenae*

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(Pettersson *et al*., 1994; Ninkovic *et al*., 2003). The effect on aphid species other than *R. padi* can be interpreted as this substance acting as a promoter for plant-induced resistance. Plants under stress from herbivory also produced methyl salicylate. The compound presumably is derived from salicylate, which is considered a product of the inducible phenylalanine ammonia lyase pathway, although an alternative involvement of isochorismate synthase has been suggested (Wildermuth *et al*., 2001).

Halbert *et al*. (2009) screened repellents for the corn aphid, *Rhopalosiphum maidis*, and found some activity with β-citronellol, farnesol, geraniol, linalool and oils distilled from several species of *Artemisia* and *Achillea millefolium*. Repellent activity of *Nepeta grandiflora* and *Nepeta clarkei* (Lamiaceae) oils against the cereal aphid, *Sitobion avenae* has been shown (Birkett *et al*., 2010). It is also important to note that aphids can perceive host compounds as non-host ones when they are presented alone and outside the context of the host volatile blend. Webster *et al*. (2010) discovered that volatiles functioning as host cues in a blend became non-host cues when presented alone to *A. fabae*. Although in some ways unexpected, this makes ecological sense because the aphid is very unlikely to encounter the compounds on its own in a natural situation with a host plant.

During studies on the semiochemical basis for host alternation by *N. ribisnigri*, a number of compounds from the primary host *Ribes nigrum* were identified that interfered with the attractancy of the secondary host lettuce (*Lactuca sativa*). One, *cis*-jasmone, was found to repel other aphids and also to attract *Coccinella septempunctata* (7-spot ladybird) and the parasitoid *Aphidius ervi* (Birkett *et al*., 2000). This positive effect on the higher trophic level was also observed for methyl salicylate. Since methyl salicylate had, furthermore, been shown directly to induce defence against pathogens by intact plants (Shulaev *et al*., 1997), the possible role of *cis*-jasmone as a plant signal was investigated. *cis*-Jasmone, although commonly induced during herbivory, was widely considered and originally expected by ourselves to be semiochemically inactive, except when released from flowers as a pollination attractant. However, surprisingly, when released into air above intact broad bean plants, *cis*-jasmone caused the induction of a defence response, resulting in the attraction of parasitoids, an effect that persisted long after the *cis*-jasmone could no longer be detected (Birkett *et al*., 2000). Although *cis*-jasmone is considered to be a biosynthetic product from jasmonic acid (Koch *et al*., 1997), jasmonic acid and its volatile methyl ester do not give a similarly persistent effect in comparative studies also using *V. faba* (Birkett *et al*., 2000). Since then, an effect of *cis*-jasmone on cereals, which causes repellency of aphids, has been exploited in the field (Bruce *et al*., 2003). Furthermore, *cis*-jasmone-induced accumulation of defence compounds was shown in wheat (Moraes *et al*., 2008). Because of the availability of microarrays for investigating gene expression, the study system was changed to *Arabidopsis thaliana*, and genes possibly associated with aphid defence were identified that are specifically induced by *cis*-jasmone (Matthes *et al*., 2003, 2010; Bruce *et al*., 2008). Plant–plant communication was shown in an experiment where a *cis*-jasmone responsive gene tagged with luciferase was switched on in *Arabidopsis* exposed to volatiles from *Magnolia grandiflora* (Matthes *et al*., 2011). For crop protection, the persistence of the *cis*-jasmone induction effect, with the initial success in the field and the prospects of exploiting the developing molecular mechanism by which *cis*-jasmone acts, is promising for the future (Birkett *et al*., 2001; Chamberlain *et al*., 2001).

Germacrene D, mentioned above as a plant-derived compound in connection with the aphid alarm pheromone as the *S* isomer, can act as a repellent to aphids by being a non-host cue, and could potentially be used in pest management. However, it is highly unstable to aerial oxidation, but could potentially be released from genetically modified plants (Bruce *et al*., 2005), as has been achieved with (*E*)-β-farnesene (Bruce *et al*., 2015). For unstable compounds as leads for the development of conventional insecticides, the general approach to development would be to synthesize stable analogues and use these in crop protection. However, the rational production of analogues of pheromones and other semiochemicals has not proved possible, as we still lack sufficient information on the associated olfactory processes in the organisms involved, and not least for insects. An alternative approach has been demonstrated successfully for producing active analogues of (*S*)-germacrene D. This involves feeding unnatural substrates to the (*S*)-germacrene D synthase enzyme initially testing the hypothesis that, if the false substrate is accepted and converted by the enzyme, then the product will have a chemical space similar enough to the natural product to be active. Thus, analogues of (*S*)-germacrene D have

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been produced that are indeed active (Touchet *et al*., 2015). An unexpected outcome of this work is that with some molecular perturbation of the (*S*)-germacrene D products e.g. (*S*)-14, 15-dimethyl-germacrene D has a reversal of activity and acts in the laboratory as an aphid attractant (Touchet *et al*., 2015). This approach is now being developed for practical control of aphids and for application to other sucking insects.

Aphid effects on the plant

Although aphids are considered to be 'stealthy' feeders in comparison to biting/chewing herbivores, their feeding induces the production of chemical cues by the host plant (reviewed by Dewhirst and Pickett, 2010). Aphid-induced volatiles have been identified from broad bean (Du *et al*., 1998) and cotton (Hegde *et al*., 2011), for example. Induced cues can also originate from the rhizosphere. Broad bean infested with *A. pisum* produces root exudates that can induce volatile emissions in neighbouring plants (Chamberlain *et al*., 2001). Fascinatingly, this type of plant–plant communication can be signalled via mycorrhizal mycelia associated with the plant roots (Babikova *et al*., 2013). Finally, aphids may suppress the emission of plant volatiles as well as inducing them. *Acyrthosiphon pisum* reduced emissions of volatiles from bean plants induced by larvae of the beet armyworm (*Spodoptera exigua*) (Schwartzberg *et al*., 2011), and *Lipaphis erysimi* suppressed floral volatile production on its host plant white mustard (*Sinapis alba*) (Pareja *et al*., 2012). It has recently been shown that *S. avenae* can make wheat more suitable for *Fusarium graminearum* head blight disease infection (Drakulic *et al*., 2015). Plants exposed to both aphids and *F. graminearum* inoculum showed accelerated disease progression, with a two-fold increase in disease severity and fivefold increase in mycotoxin accumulation compared with plants treated only with *F. graminearum*. However, aphid survival and fecundity was reduced on diseased plants. Disease-induced plant volatiles were repellent to aphids, and 2-pentadecanone was the key semiochemical underpinning the repellent effect.

Interaction with Natural Enemies

A disadvantage for an insect employing semiochemicals in intraspecific communication is that these can betray the often-sophisticated crypsis that the insect has attained. Insects also leave other clues from which searching predators and parasitoids can elicit information, such as waste products and other excretions. Given the importance of chemical signals to aphids, it is no surprise that their natural enemies have evolved to exploit them in host location. In an interesting reversal of this interaction, aphids have been shown to use chemicals in the walking trails of a predator, the aphidophagous ladybird *C. septempunctata*, to assess predation risk (Ninkovic *et al*., 2013). In the following section, natural enemy use of damage-induced chemicals produced by aphid-attacked plants and chemicals of direct aphid origin will be discussed separately.

Responses of natural enemies to aphid-produced chemicals

Parasitoids

Initial studies on the use of kairomones as host location cues by aphid parasitoids focussed on aphid honeydew. Parasitoids respond to it with intensified searching behaviours (Cloutier and Bauduin, 1990) and by increasing their residence time in honeydew-contaminated patches (Budenberg *et al*., 1992). These experimental studies suggest that honeydew is detected on contact by the parasitoid, although attraction to honeydew odour has been reported (Wickremasinghe and van Emden, 1992).

The first evidence that parasitoids were attracted to aphid sex pheromones came during field experiments designed to observe the response of field-flying male aphids to synthetic sex pheromone (Hardie *et al*., 1991). Besides capturing male aphids, large numbers of parasitoids of the genus *Praon* were recovered from water traps baited with nepetalactone (**1**, Fig. 8.4). All the wasps were female, and 98.5% were found in pheromone-baited traps as opposed to unbaited controls. Since clear traps and synthetic pheromone were used, all other visual and olfactory cues were ruled out, clearly demonstrating that parasitoids were attracted by the pheromone.

When the experiments were repeated during the following autumn in winter cereal fields, attraction to nepetalactone was again demonstrated (Powell *et al*., 1993; Hardie *et al*., 1994a). This time, 89% of the captured wasps were *Praon volucre*, with over 99% occurring in the pheromone-baited traps. The trials were replicated at sites in south-western,

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central and northern England, and in northern Germany, and the response to sex pheromone was apparent at all sites that had parasitoid populations. The nepetalactol-baited traps were included in several of the trials, but caught significantly fewer parasitoids than those baited with nepetalactone.

Attraction to aphid sex pheromones in laboratory assays has been demonstrated for *P. volucre* (Lilley *et al*., 1994), *Aphidius eadyi* and *A. ervi* (Glinwood *et al*., 1999a), *Aphidius matricariae* (Isaacs, 1994), *Aphidius rhopalosiphi* and *Ephedrus plagiator* (Glinwood, 1998) and *Aphidius colemani* (Ameixa and Kindlmann, 2012). *Diaeretiella rapae* was attracted to traps baited with nepetalactone in the field (Gabrys *et al*., 1997). Electroantennogram responses have been shown in *Lysiphlebia japonica* (Hou and Yan, 1995).

There are opportunities for applied use of aphid sex pheromones in integrated management of aphid pests, because aphid parasitoids are important members of the aphid natural enemy complex, yet their impact is often diminished by poor synchrony between their arrival in crops and aphid population development (Carter *et al*., 1980). Aphid sex pheromone deployed in field margins in the autumn (Powell *et al*., 1993) or in the crop in the spring (Glinwood, 1998) might reduce this asynchrony. Attempts to increase parasitization in aphid colonies in the field using sex pheromones have been successful. When potted cereal plants were artificially infested with *S. avenae* and exposed in the field, the presence of nepetalactone significantly increased parasitism of *S. avenae* by *Praon* spp. (Lilley *et al*., 1994; Glinwood *et al*., 1998) and *A. rhopalosiphi* (Glinwood *et al*., 1998). In a field trial (Glinwood, 1998), the deployment of nepetalactone lures in spring wheat significantly increased the numbers of parasitized aphids in treated plots (Fig. 8.7). Although the impact of parasitization was not sufficient to control the aphid population, levels of parasitization in pheromone plots were clearly shifted to earlier in aphid population development, indicating that this strategy might indeed enhance the synchrony discussed previously.

Initially, it was concluded that the parasitoid response to aphid sex pheromones was either induced by environmental stimuli (i.e. the changes in temperature and photoperiod that occur in the autumn) or developed in response to parasitoids learning to associate suitable hosts with the presence of pheromone by attacking sexual aphids when they appeared in the autumn (Hardie *et al*., 1994a). However, the parasitoid response to aphid sex pheromones is now believed to be innate.

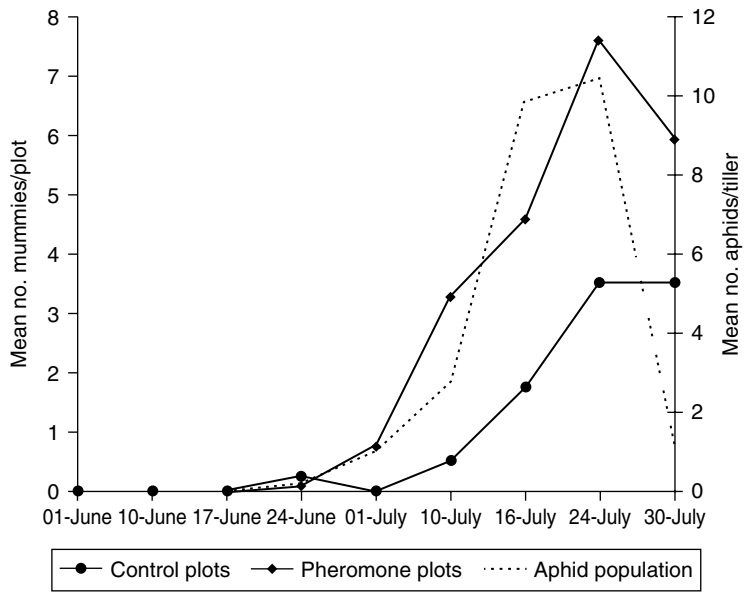

Fig. 8.7. Effect of aphid sex pheromone on parasitization levels of cereal aphids in plots of spring wheat. Parasitization increased earlier in plots treated with pheromone, and in greater synchrony with the increase in the aphid population. (From Glinwood, 1998.)

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Both *P. volucre* and *A. ervi* were attracted equally by plant-extracted and fully synthetic (4a*S*,7*S*,7a*R*)-nepetalactone (**1**, Fig. 8.4) in wind tunnel bioassays (Glinwood *et al*., 1999b). However, in field tests with baited aphid-infested plants, the synthetic 7*R* isomer was unattractive, and even rendered the 7*S* isomer unattractive when combined in a 50% blend (Glinwood *et al*., 1999b). This indicates that enantiomeric purity of the pheromone is more important for parasitoid response than is the presence of plant-derived contaminants. This is in contrast to the response of male aphids (Hardie *et al*., 1997), which raises interesting questions about the evolution of the response of the two different sexes to this signal.

The parasitoid *Aphidius uzbekistanicus* was attracted to the aphid alarm pheromone (*E*)-β-farnesene (**6**, Fig. 8.5) in a simple Y-tube olfactometer bioassay (Micha and Wyss, 1996). Detailed measurements of the foraging response of the parasitoid *D. rapae* to **6** showed increased movement and tighter turning angles, behaviours likely to increase the probability of host encounters (Foster *et al*., 2005).

The searching behaviour of aphid parasitoids seems to be influenced by cues present in the aphid mummy that are experienced by the adult wasp on emergence. Several reports have shown that this experience can prime parasitoids to search preferentially for and oviposit in a particular aphid species (van Emden *et al*., 2008). This underlines the subtlety of chemical interactions between parasitoids and their aphid hosts.

Predators

Predators have been considered as less sophisticated users of host-location kairomones than parasitoids. One reason may be that a parasitoid's reproductive success is more critically dependent on finding suitable hosts for oviposition than is that of a predator whose search is usually directed towards a food resource. However, in the case of predators such as coccinellids, syrphids and chrysopids, the location of aphid colonies by adults is also critical for the survival of their offspring. Thus, they may be considered as similar to parasitoids in this respect.

The responses of several ladybird species to aphid siphunculus secretions and alarm pheromone ((*E*)-β-farnesene, **6**, Fig. 8.5) have been investigated, and there appears to be some variation in response between species and between larval and adult stages. In olfactometer tests, *Adalia bipunctata* (2-spot ladybird) larvae were attracted to the odour of aphids under attack by conspecific larvae, whereas there was no response to larvae or aphids alone (Hemptinne *et al*., 2000). The hypothesis was that the larval response was adaptive, since it allowed the larvae to share the aphid prey of other larvae that had hunted successfully. Adults of *A. bipunctata* have also been shown to respond to **6** in an olfactometer (Francis *et al*., 2004). Adults of *Harmonia axyridis* (harlequin ladybird) responded electrophysiologically and also showed attraction to **6** (Verheggen *et al*., 2007). Electroantennograms in response to **6** have been recorded from *Coleomegilla maculata* (12-spot ladybird) (Zhu *et al*., 1999). Behavioural studies were not reported, but the authors claimed to have obtained behavioural responses from *Hippodamia convergens* and *Harmonia axyridis* in preliminary studies, subsequently confirmed to involve **6** for attraction of *H. convergens* (Acar *et al*., 2001).

The most comprehensive study of ladybird response to **6** (Al Abassi *et al*., 2000) demonstrates both electrophysiological and behavioural responses in *C. septempunctata* (7-spot ladybird). Not only was attraction to **6** demonstrated, but it was also shown that increasing concentrations of the plant-derived alarm pheromone inhibitor (*E*)-caryophyllene (**7**, Fig. 8.5) inhibited ladybird response, analogous to the system that controls inhibition of response in aphids (Dawson *et al*., 1984). The receptor cells for **6** and **8** in *C. septempunctata* are paired and are frequently found in close proximity, with larger amplitude consistently recorded for the cell specifically responding to **6**. The co-location of these cells may provide the mechanism by which different behavioural responses are exhibited when the inhibitor is present together with the attractant (Al Abassi *et al*., 2000). A laboratory study suggested that **6** did not affect short-range foraging behaviour by *C. septempunctata* or the lacewing *Chrysoperla carnea* when searching on the plant (Joachim *et al*., 2015), and artificial release of **6** at natural levels did not increase predator visits to aphid colonies in the field (Joachim and Weisser, 2015).

The behavioural responses of ladybirds to aphid sex pheromones either have not been studied or studies have not been reported due to a negative outcome. Electroantennogram responses to the nepetalactone and nepetalactol sex pheromone

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components have, however, been shown in *C. maculata* (Zhu *et al*., 1999). The same authors also obtained EAG responses to both of these sex pheromone components from *C. carnea*. Another lacewing, *Chrysopa pallens*, showed EAG responses to both nepetalactone and nepetalactol, as well as positive behavioural responses to these compounds in an olfactometer and attraction to pheromone-baited traps in the field (Boo *et al*., 1998). *Chrysopa oculata* showed EAG responses to sex pheromone components, and the (1*R*,4a*S*,7*S*,7a*R*)-nepetalactol attracted adults to field traps (Zhu *et al*., 2005). *Chrysoperla carnea* showed an EAG response to **6** (Zhu *et al*., 1999), whereas *C. pallens* did not (Boo *et al*., 1998). Aphid sex pheromone compounds 1 and 2 attracted males of *Chrysopa formosa* and *C. pallens* to baited traps in the field (Koczor *et al*., 2010).

Earlier literature revealed that the lacewing *C. pallens* was attracted to the vine *Actinidia polygama*, a plant that generated two dihydronepetalactols previously named neomatatabiol and isoneomatatabiol (Hyeon *et al*., 1968). These compounds are structurally related to nepetalactone and nepetalactol but incompletely characterized. The enantiomerically pure diastereoisomers (1*R*,4*S*,4a*R*,7*S*,7a*R*)- (**9**, Fig. 8.5) and (1*R*,4*R*,4a*R*,7*S*,7a*R*)-dihydronepetalactol (**10**, Fig. 8.5) were synthesized (Hooper *et al*., 2002) diastereoselectively from (4a*S*,7*S*,7a*R*)-nepetalactone (**1**). The stereochemistry of the compounds was determined by NMR spectroscopy and X-ray crystallography, and the compounds were shown to be identical to those previously referenced as neomatatabiol and isoneomatatabiol, respectively. (1*R*,4*S*,4a*R*,7*S*,7a*R*)-Dihydronepetalactol (**9**) was found to catch significant numbers of three species of lacewing in the field: in Korea, *C. pallens*, and in the UK, *Nineta vittata* and most notably, *Peyerimhoffina gracilis*. All species caught in significant numbers were found more frequently in traps releasing (1*R*,4*S*,4a*R*,7*S*,7a*R*)- (**9**) rather than (1*R*,4*R*,4a*R*,7*S*,7a*R*)-dihydronepetalactol (**10**), while more *C. pallens*, *C. formosa* and *Chrysopa phyllochroma* were found in traps releasing the nepetalactol (Hooper *et al*., 2002; Boo *et al*., 2003). The capture of *P. gracilis* with (1*R*,4*S*,4a*R*,7*S*,7a*R*)-dihydronepetalactol (**9**) was of particular interest, as this lacewing was discovered for the first time in the UK due to its attraction to the aphid sex pheromone components (Donato *et al*., 2001). Attraction to aphid sex pheromones does not seem to be universal in lacewings; **1** and **2** reduced trap catches of *C. carnea* in traps baited with a floral compound lure (Koczor *et al*., 2015).

There are few published examples of hover fly responses to aphid semiochemicals. Non-volatile kairomones present in extracts of the siphunculus secretion of *A. fabae* influenced the searching behaviour of adult females of *Eupeodes (Metasyrphus) corollae* (Shonouda *et al*., 1998), and **6** has been shown to induce oviposition in *Episyrphus balteatus* (Verheggen *et al*., 2008b). Effects included stimulation of oviposition and arrestment on bean plants treated with the extracts. Interestingly, it has been shown that volatiles from microorganisms in aphid honeydew, rather than from the honeydew itself, attract *E. balteatus* adults (Leroy *et al*., 2011), a further example of the important role of microorganisms in aphid ecology. Olfactory responses to aphid honeydew have been shown in the aphid midge, *Aphidoletes aphidimyza* (Choi *et al*., 2004).

Responses of natural enemies to aphid-induced plant signals

Herbivore-induced chemicals from infested plants provide natural enemies with information that is both easily detectable and a highly reliable indicator of the presence of hosts or prey (Vet and Dicke, 1992). These signals are often considered to be plant SOS signals, i.e. synomones that enhance recruitment of the attacking herbivores' enemies. However, in most cases, the consequences of production of these signals for plant fitness are unknown. Chemically mediated host location by aphid natural enemies in general, and ladybirds in particular, has been reviewed by Hatano *et al*. (2008) and Pettersson *et al*. (2008), respectively.

Parasitoids

In wind tunnel bioassays, *A. ervi* was attracted equally to the plant–host complex (*V. faba*–*A. pisum*) and to aphid-damaged plants from which aphids had been removed (Du *et al*., 1996). The parasitoid was able to discriminate between bean plants previously infested with *A. pisum* and a non-host aphid, *A. fabae*, even after the plants had been washed to remove traces of aphid honeydew and exuviae. Thus, the plant produces aphid species-specific volatile cues that can be used by female parasitoids in host location. The plant response that leads to the production of these volatiles is now known to be systemic, the upper leaves becoming attractive to parasitoids 48–72 h after aphid infestation of the basal leaves (Guerrieri

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et al., 1999). Air entrainment of the bean plants, followed by GC-MS, identified several volatiles that were produced at higher levels by plants infested with *A. pisum*, including 6-methyl-5-hepten-2-one, (*E*)-β-ocimene, (*Z*)-3-hexen-1-ol, (*Z*)-3-hexenyl acetate, (*R*,*S*)-linalool and (*E*)-β-farnesene from the plant (Du *et al*., 1998). All the chemicals were behaviourally active, with 6-methyl-5-hepten-2-one eliciting significantly more upwind flights by *A. ervi* in a wind tunnel than the other substances. *Aphidius ervi* was attracted to volatiles induced by *Macrosiphum euphorbiae* (potato aphid) feeding on tomato (*Solanum lycopersicum*), with (*E*)-caryophyllene, methyl salicylate and (*Z*)-3-hexen-1-ol identified as the active substances (Sasso *et al*., 2009). Using principal component analysis of volatile blends, linked to multivariate analysis of olfactory responses, Pareja *et al*. (2009) showed that *A. ervi* could use relatively minor but consistent aphid-induced volatile compounds while ignoring compounds produced in larger amounts but with high between-plant variability.

Work on the transfer of damage-induced messenger substances between plants has demonstrated that root exudates of *A. pisum*-infested bean plants contain compounds that are systemically translocated and, when taken up by an intact plant, elicit the release of the same volatiles that are induced by aphid feeding (Chamberlain *et al*., 2001; Babikova *et al*., 2013). These volatiles are also attractive to the parasitoid *A. ervi*. Most studies on parasitoid responses to aphid-induced volatiles have focused on species with agricultural importance, and more studies on naturally occurring plant–aphid systems, such as that by Pareja *et al*. (2007), are needed to understand fully these interactions.

Predators

Studies on predator attraction to aphid-induced plant signals are in their infancy compared with those on parasitoids. Adult female ladybirds (*A. bipunctata*) were more attracted to the odour of *V. faba* infested with *A. pisum* than to uninfested *V. faba* (Raymond *et al*., 2000). However, when aphids and aphid products (exuviae and honeydew) were removed from the plant, the attraction was lost. Therefore, the attraction of ladybirds to honeydew and alarm pheromone cannot be ruled out in this study. There is stronger evidence for attraction to aphid-induced signals in *C. septempunctata* (Ninkovic *et al*., 2001). Olfactometer responses to solvent extracts from air entrainments of barley and the aphid *R. padi* showed that attraction to a host-damaged plant from which aphids had been removed was as strong as attraction to the plant–host complex. There was no response to the undamaged plant or to aphids alone. Attraction or arrestment of *C. septempunctata* by aphid-induced volatiles has been shown with *M. persicae* feeding on *Brassica* spp. (Girling and Hassall, 2008). Glinwood *et al*. (2011) showed that adult *C. septempunctata* were attracted to aphid-induced volatiles from barley and could learn to associate aphid presence with the particular volatile blends released by different cultivars.

It is clear from laboratory experiments that a broad range of aphid parasitoids and predators has evolved behavioural responses to both aphid kairomones and aphid-induced plant signals. What is not as clear, however, is the importance of such responses for the success of natural enemies in their natural habitats and, in the case of plant signals, whether there are genuine fitness benefits for the emitting plants.

Conclusions

The intimate relationship between aphids and their host plants has resulted in the evolution of fascinating chemical ecological interactions. The range of molecular structures of the semiochemicals involved is restricted by the limited array of plant secondary metabolites with appropriate physico-chemical characteristics, and has given rise to diverse activities from relatively simple compounds such as methyl salicylate, 6-methyl-5-hepten-2-one and the nepetalactones, which appear in various roles in this review. It appears that blends and ratios of volatiles can change the way in which the aphid perceives them, as evidenced by the stark contrasts in the behavioural responses elicited by different combinations of compounds. The parsimony in the usage of semiochemicals in aphid chemical ecology bodes well for their applied use in pest management through restricting the number of compounds required for registration. However, it should be borne in mind that there are still areas, for example, those involving the chemical ecology and plant signalling related to aphid feeding and aphid parasitoids and predators, where new chemistries will be identified. Furthermore, improving understanding of the influence of ecological context and the way in which semiochemicals are released over time on aphid responses will be interesting areas for future investigations.

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It appears from recent work that the main problem in developing semiochemicals for aphid pest management, which at least for arable crops represents cheap delivery, is now being solved. Thus, the discovery that genes relating to the production of aphid semiochemicals by plants can be 'switched on' by benign chemical signals means that the plants themselves can generate target semiochemicals. Already, volatile signals from damaged plants that have this potential have been identified, but further work is needed, both in this area and on signals active in the rhizosphere. Signalling by undamaged plants is also an area of increasing interest (Chapter 9, this volume). These studies will be enhanced greatly by a deeper understanding of the molecular biology of aphid chemosensory receptors, and of the genetics underpinning plant secondary metabolism, particularly those pathways induced by external signals. Currently, the latter studies rely heavily on *A. thaliana*, but as genomic information from other plants more relevant to pest aphid chemical ecology becomes available, more rapid advances will be made.

Finally, it must be emphasized that we are now entering a post-genomic era in which the genome sequences of aphids and their host plants will provide new opportunities for the exploitation of chemical ecology. Indeed, we anticipate that chemical ecology, which has always been an interdisciplinary subject at the interface between chemistry and biology, will now become very useful in finding which genes or traits are ecologically relevant. An understanding of chemical ecology puts genes that produce metabolites such as volatiles in their biological and ecological context.

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9 Host-plant Selection and Feeding

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Introduction

Prominent traits in aphid ecology are rapid reproduction and advanced adaptation to host-plant ecology and physiology. This includes host-plant and feeding-site discrimination using sensitive chemosensory information that has proved to be an important research topic over the past few decades (Chapter 8, this volume). Cues shown to be important in host-plant selection, phloem finding, phloem acceptance and the sensory aspects are described in the sequence of choices from a distance, to the plant surface, to the internal plant factors, and ultimately to phloem feeding.

Visual cues constitute an initial step in host selection for alate aphids and have an important role for approaching and landing on a plant. Different aspects of spectral patterns have been studied with regard to orientation (Döring and Chittka, 2007).

Olfactory cues cover a broad spectrum of semiochemicals related to both host-plant discrimination and host-plant quality (Chapter 8, this volume). The main receptors for olfactory cues are rhinaria on the antennae. Although there is considerable knowledge on the behavioural importance of olfactory cues for host-plant recognition and the interaction between these and other aspects of aphid movement and settling, it is still a challenging field.

Probing is a complex activity, encompassing stylet penetration of plant tissues, saliva excretion, sap sampling, xylem ingestion and ultimately phloem feeding. Probes may include three distinct behavioural phases: pathway, xylem and phloem waveforms, revealed by the electrical penetration graph (EPG) technique. Rejection of plants may occur at any time during these activities, and even before probing. The stylet track followed during the pathway phase is intercellular, but most cells along the track are briefly punctured (pd waveform) while saliva is injected and sap sampled.

Presently, research is becoming focused on the molecular aspects of compatible and incompatible aphid–plant interactions. Aphids anticipate wound and defence responses by excreting salivary components, which can be based on very specific aphid–host-plant interrelations, some presumably gene-for-gene interactions. Some of these interactions are discussed in this chapter, but more molecular aspects are covered in Chapter 2, this volume.

The predisposition of aphids to certain plant characteristics, which is not only the result of immediately apparent aphid–plant interactions, is discussed briefly. Changes in response can be influenced by plant–plant interactions, above and below ground, as well as by interactions between plants and other pathogens, pests, or commensal/symbiotic organisms.

Orientation and Host-plant Finding

Aphids are poor flyers but can remain airborne for many hours and can be transported over considerable distances by air movements. This contributes to host-plant location on a landscape scale and has an impact on population dynamics and behavioural ecology (Wiktelius *et al*., 1990; Kirchner *et al*., 2013; Parry, 2013) (see also Chapter 10, this volume).

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Visual responses

The ecological impact of visual responses of aphids has been reviewed by Döring and Chittka (2007), who conclude that, in general, aphid visual reactions are related both to species-specific and morph-specific behaviour. For example, the mealy plum aphid (*Hyalopterus pruni*) responded to the specific hue of the host plant, and in the laboratory maximum landing response was shown to unsaturated yellows that reflected some ultraviolet resembling the light reflected from *Phragmites* reed, the summer host. Using monochromatic light and a vertical wind tunnel, it was shown that *Aphis fabae* (black bean aphid) and *Rhopalosiphum padi* (bird cherry–oat aphid) were most responsive to wavelengths in the green region of the spectrum, *c.*550 nm (Hardie, 1989; Nottingham *et al*., 1991a). In studies of aphid colour detection and preferences for different surfaces, it was shown that autumnal red leaf colours could be less attractive than yellow or green leaves (Döring *et al*., 2009). The early post-teneral period of adult alate aphids is usually dominated by flight, when aphids respond to a bright, white light when in an experimental chamber keeping the aphid flying. Autumn migrants (gynoparae) of *A. fabae* and *R. padi* flew for 2–3 h before responding to plant-like visual stimuli (David and Hardie, 1988; Nottingham and Hardie, 1989; Nottingham *et al*., 1991a). Differences in the duration of such migratory behaviour at the start of maiden flight, when insects were unresponsive to plant-like visual stimuli, were found between winged morphs of *A. fabae*, *Phorodon humuli* (damson–hop aphid) and *R. padi* (David and Hardie, 1988; Hardie and Campbell, 1998). The summer virginoparae showed a short or negligible period of migratory behaviour. Readiness to respond to plant colour, i.e. during foraging flight, increased in both winged virginoparae and gynoparae after starvation, and this reduced the duration of the initial migratory period (Hardie and Schlumberger, 1996). Anaesthesia or treatment with juvenile hormone also reduced the period of migration (Hardie *et al*., 1989).

Unfavourable wind conditions can restrict aphid flight. Wind tunnel and field experiments show that flying aphids can reach air speeds of 70–75 cm/s, but aphids cannot make headway in wind speeds greater than this (Hardie *et al*., 1996). As can be inferred from the effectiveness of yellow traps and landing responses to plant material (Åhman *et al*., 1985), aphid landing is a visually guided event controlled by the insect (Chapter 10, this volume). Detailed analysis of the three-dimensional flight tracks of aphids in the laboratory and in the field has shown that aphids can control ground speed and that they land into the wind (Hardie and Young, 1997; Storer *et al*., 1999).

Olfactory responses

Aphids respond to volatiles both from plants and from other aphids, but the mechanisms are dynamic and complex, and not yet well understood (Chapter 8, this volume). Walking apterae respond to host-plant odours in olfactometers (e.g. Pettersson, 1970, 1973, 1994; Nottingham *et al*., 1991b; Pettersson *et al*., 1994). Host finding by walking adult apterae and nymphs is perhaps unusual in the field, but it can be hypothesized that volatile plant cues also contribute to initiation of probing and that social interactions can modify feeding behaviour.

The major olfactory organs, present in all morphs and developmental stages, are the primary rhinaria, one on each of the two last antennal segments. Their responses to a variety of plant volatiles have been shown with electrophysiological recordings (Anderson and Bromley, 1987; Pickett *et al*., 1992; Visser and Piron, 1997; Park and Hardie, 1998, 2004). These rhinaria contain receptors for common leaf volatiles, and might also detect low-volatility hydrocarbons on the leaf surface (van Giessen *et al*., 1994; Park and Hardie, 2002, 2003, 2004).

Comparisons have been made between electroantennogram (EAG) responses of different aphid species and morphs to plant volatiles. The EAG records the voltage response across all of the antennal olfactory receptors. Visser and Piron (1997) compared EAG responses from the cabbage specialist *Brevicoryne brassicae* (cabbage aphid) and the generalist *Myzus persicae* (peach–potato aphid) reared on the same host plant. They found that responses differed between species for 35 of 80 tested plant volatiles. Eleven of 54 and six out of 50 test volatiles, respectively, showed different responses between winged morphs from two *M. persicae* clones and between apterous *M. persicae* reared on a host plant or artificial diet. The EAG responses to fewer test compounds differed between *M. persicae* clones, and there were no differences between these data and those collected for alate and apterous morphs of a single clone of this species, or between

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individuals reared on different host plants. The differences between morphs may be species dependent, as in a comparison of EAG responses of the polyphagous alate summer virginoparae and the monophagous autumn gynoparae of *A. fabae*: no differences were found over 35 test volatiles or between alate and apterous virginoparae (13 test volatiles) (Hardie *et al*., 1994a). A similar comparison with *R. padi*, using a more sensitive EAG technique, showed a significant difference in EAG responses between the winged virginoparae and the gynoparae. The former had a larger EAG response to benzaldehyde, which was a prominent volatile from bird cherry (*Prunus padus*), the winter host of *R. padi* (Park *et al*., 2000), but only the gynoparae responded behaviourally to benzaldehyde in olfactometer studies (Pettersson, 1970; Park *et al*., 2000).

Winged adults usually have further groups of olfactory receptors, the secondary rhinaria, predominantly on the third antennal segment. In most aphid species, these secondary rhinaria are fewer, less well developed or absent in adult apterous individuals and absent in nymphs. This corresponds to the predictions that winged aphids are more adapted to the colonization of new plants, while apterae and nymphs develop and reproduce close to where they are born. However, the precise role of the secondary rhinaria in host selection is still unknown. EAG studies indicate that they contribute little, if at all, to the overall EAG response to plant volatiles in winged females (van Giessen *et al*., 1994; Park and Hardie, 2002), and more sensitive electrosensillogram studies (DC recordings of receptor potentials from individual placoid sensilla of the secondary rhinaria) revealed no response to 31 common plant volatiles (Park and Hardie, 2004). The latter study showed that secondary rhinaria of *A. fabae* males and gynoparae were specifically sensitive to sex pheromone components, and concluded that in winged virginoparae, they might be sensitive to unknown/untested plant volatiles (Chapter 8, this volume).

Recent olfactometer studies have shown the role of odour blends as key stimuli indicating host and non-host plants for aphids. While individual common plant volatiles could be considered repellents for *A. fabae*, when combined in a blend mimicking the plant odour, they became components of an attractant (Webster *et al*., 2010a). It has also been shown that volatiles released by a plant vary across day and night, and between individual plants, and that certain volatile pairs remain in a constant concentration ratio within these perturbations (Webster *et al*., 2010b). Thus, it appears that volatile blends can be important in host-plant discrimination and settling (Webster, 2012; Ninkovic *et al*., 2013b; Webster *et al*., 2013).

Olfactometer studies with walking aphids have examined preferences for certain plant odours (e.g. Nottingham *et al*., 1991b; Hori, 1999). However, the responses of flying aphids have so far not been studied sufficiently to permit general conclusions. Studies with flying *A. fabae* and *B. brassicae* showed that non-host odours reduced landing frequencies, but host odours did not increase landing (Nottingham and Hardie, 1993). In field experiments, flying individuals of *Cavariella aegopodii* (willow–carrot aphid) were caught more frequently in traps releasing volatiles typical of the summer host plants than in empty control traps (Chapman *et al*., 1981).

Winged *A. fabae* took off from a suitable host plant if presented with a non-host odour immediately after landing. This response, however, seems to switch off after some time on the plant (Storer *et al*., 1996) and suggests a role for plant volatiles as part of a rapid host-plant screening mechanism in the field. There is an obvious risk of sensory adaptation of antennal receptors when aphids walk on a suitable host plant constantly exposing them to positive volatile stimuli. Thus, it has been postulated that the antennal waving exhibited during walking may reduce habituation by taking the olfactory receptors beyond the boundary layer of odoriferous air at the plant surface (Hardie and Powell, 2000). During periods of stylet insertion into plant tissue, aphids tend to hold the antennae stationary and laid back over the thorax/abdomen (Hardie *et al*., 1992). Such an action is open to the interpretation that internal plant chemical cues have taken over as more relevant to aphid behaviour than odours at this point.

There is experimental support for the hypothesis that aphid host-plant selection and settling is affected by olfactory semiochemicals released both by potential host plants and by the aphids themselves (Pettersson, 1993, 1994; Hardie *et al*., 1994b; Chapter 8, this volume). Volatiles supporting the identification of optimal settling sites offer rapid information on specific situations such as plant responses due to feeding of competing species (Gosset *et al*., 2009) and the presence of predators at a potential feeding site (Ninkovic *et al*., 2013a).

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Plant Contact after Landing

Plant surface characters, such as 'hairiness' and the structure of the epicuticular wax, may restrict aphid walking. The importance of structure and chemistry of the wax for host-plant preferences has been shown (Klingauf *et al*., 1978; Powell *et al*., 1999). In studies of *Lipaphis pseudobrassicae* (mustard aphid) and *B. brassicae* on genotypes of *Brassica* with different plant cuticular wax (Åhman, 1990), it was found that the tarsal claws of *L. pseudobrassicae* were too short to cope with the cuticular wax particles and the aphids fell off the leaves. The physical entrapment of aphids by glandular trichomes producing repellent volatiles has been studied extensively (Lapointe and Tingey, 1986; Tingey, 1991). The sticky membrane and volatile effects can be removed temporarily by washing, and the aphids then seem to probe cultivars with trichomes as easily as those without them (Chapter 22, this volume). Plant breeding and genetic modification (GM) can be used to promote the release of aphid alarm pheromone from plant surface structures, potentially creating a semiochemical barrier to aphid settling (Chapter 8, this volume).

Some aphid species show preference for specific parts of the host plant, depending on the host-plant developmental stage. Thus, *R. padi* prefer settling close to the soil surface early in the summer, but later in the summer the upper leaves and ears of cereals are preferred (Wiktelius *et al*., 1990). Similar seasonal movements have been found for *B. brassicae* on *Sinapis alba* (Gabrys *et al*., 1997). Mechanisms for continuous evaluation and rejection of suboptimal feeding sites maximize aphid reproduction success by inducing mobility and search for better feeding sites.

Contact chemoreceptors are important after arrival on a potential new host plant. However, in comparison to other phytophagous insects, in aphids the number of external contact chemoreceptors appears extremely low. The sensory pegs on the labial tip could be contact chemoreceptors, but all 16, as well as the other labial trichoid sensilla, have only mechanoreceptors (Wensler, 1977) and seem to be used mainly to detect the concave borders of epidermal cells where stylet penetration commences. At the tibial–tarsal junction is one trichoid sensillum with four neural dendrites within the shaft, typical of a contact chemoreceptor (J. Hardie, unpublished; Fig. 9.1). There is ultrastructural evidence that the apical antennal hairs may be contact chemoreceptors (Bromley *et al*., 1980), and in *A. fabae* it was shown behaviourally that they could detect the antifeedant polygodial on a leaf surface (Powell *et al*., 1995). As aphids walk on a leaf, the antennal tips can touch the surface and detect non-volatile chemical cues associated with the cuticle. Such surface contact by antennal tips has been demonstrated using fluorescent powder as a marker (Powell *et al*., 1995). It has also been shown that non-volatile plant epicuticular lipids could be detected by aphids (Powell *et al*., 1999), but the location of the chemoreceptors is unknown.

Prior to actual plant penetration, aphids may secrete watery saliva from the stylets on to the plant surface. This has been assumed to contribute to the detection of soluble surface chemicals by the pharyngeal gustatory organ after ingestion (Wensler and Filshie, 1969; Wensler, 1974).

Feeding apterous aphids are exposed to disturbance from other aphids, natural enemies, rain, wind, other herbivores, etc., and can move both within and between plants (Mann *et al*., 1995). However, aphid movement on a micro scale has also been shown to be affected by atmospheric pressure changes (Pellegrino *et al*., 2013). The readiness to move can be morph specific, and in *A. fabae*, apterous adults and nymphs destined to be wingless adults left the host plant more readily than nymphs destined to be winged (Hardie, 1980). Studies on the importance of colony density for the movement of *R. padi* apterae showed that olfactory cues lowered the threshold and also contributed to a spaced settling pattern (Pettersson *et al*., 1995; Quiroz *et al*., 1997). So far, the factors modifying host-plant search and acceptance by alates after landing have received some interest (see the section above on olfactory responses; Storer *et al*., 1996).

Feeding by a moderate colony density of *B. brassicae* increases food quality of the leaf favouring settling and development of conspecifics, and it has been hypothesized that there is an optimal size for this feeding group initiating the improved food quality (Way and Cammell, 1970; Way, 1973; Miles, 1999). However, two different aphid species using the same host plant will potentially create a host-plant-mediated competition for plant resources. Hypothetically, this is related to adverse specific dietary changes induced by the competing aphid species. Experiments with *Sitobion avenae* (English grain aphid) and *R. padi* lend support to this concept of interspecific competition (Gianoli, 2000).

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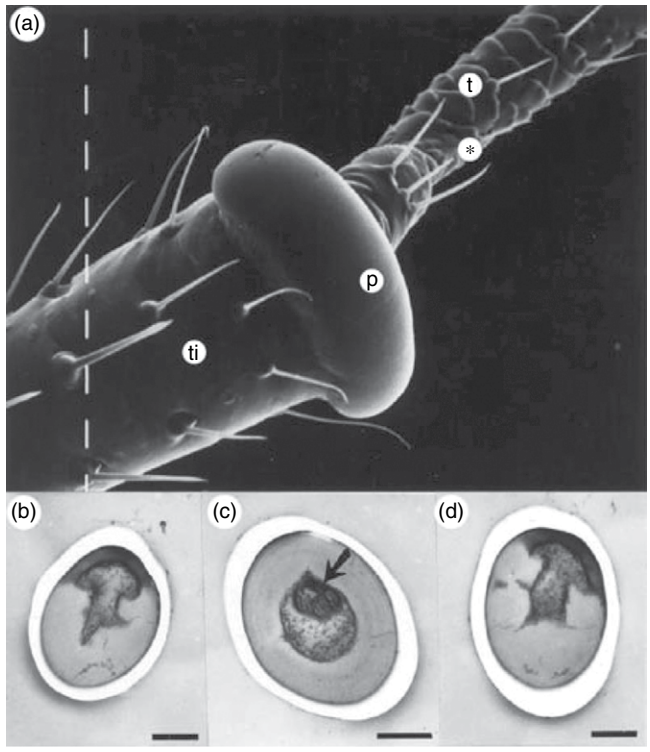

Fig. 9.1. (a) Scanning electron micrograph showing part of the lower tibia (ti) of an adult apterous vetch aphid, *Megoura viciae*, showing the everted pulvillus (p) and the tarsus (t). The first segment of the tarsus bears three trichoid sensilla, two longer outer hairs and a central shorter hair (asterisked). Scale bar = 10 μm. (Micrograph courtesy of J. Hardie.) (b, c and d) Transmission electron micrographs showing transverse sections through the shafts of the outer hairs (b and d) and central hair (c). The central hair has four dendrites running along the shaft (arrowed, c) and is typical of a contact chemoreceptor, while the outer hairs do not and are mechanosensory in function. Scale bars = 0.5 μm. (Micrograph courtesy of J. Hardie.)

There was a reciprocal negative effect on performance and host-plant acceptance by either species when fed on young wheat plants infested with the other aphid species. However, apterae of *S. avenae* preferred air containing the odour of feeding apterae of *R. padi* to clean air (Johansson *et al*., 1997). In other olfactometer experiments, alate individuals of *Lipaphis erysimi* and *B. brassicae* avoided individuals of other species that had settled on a plant (Pettersson and Stephansson, 1991).

Probing – Plant Penetration

Aphid stylets consist of two mandibular and two maxillary stylets that form a bundle with two canals; one for food and one for saliva, fused close at the stylet tips. Probing seems the most appropriate term for all activities while the stylets are inside the plant, and three probing phases can be distinguished behaviourally; pathway, xylem and phloem phase (Fig. 9.2). During these probing phases, the structural and chemical information from the plant tissue is monitored by gustatory receptors. The stylet tips have mechanoreceptors, and all fluids ingested during probing pass the pharyngeal gustatory organ, with eight epipharyngeal and six hypopharyngeal papillae, containing more than 60 taste cells in total (Wensler and Filshie, 1969). Moreover, the pathway and phloem phases (see below) have each been associated with several periods of saliva excretion.

The EPG technique (Box 9.1) allows monitoring of stylet activities in the plant tissue. In the pathway phase, the stylets actively penetrate the tissues intercellularly with frequent brief intracellular punctures. In the xylem and phloem phases, which

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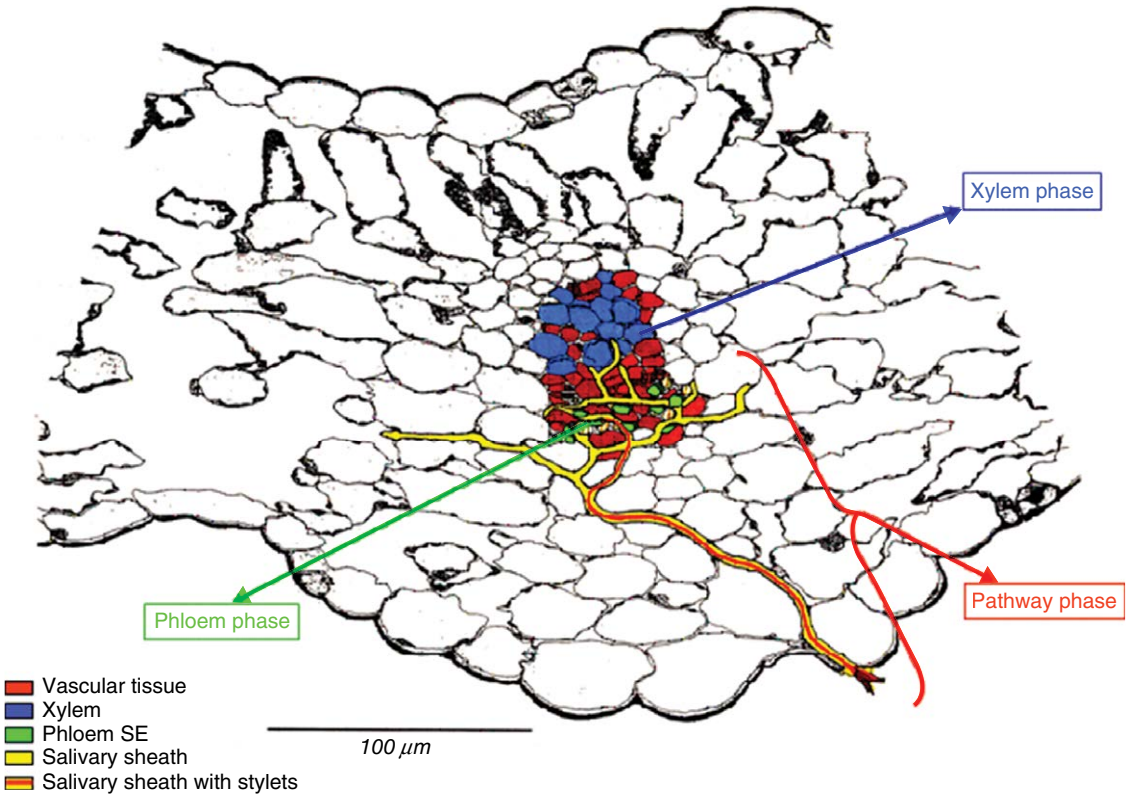

Fig. 9.2. Reconstruction of a complete stylet pathway by *Aphis fabae* on a broad bean plant, *Vicia faba*, based on a series of transmission electron micrographs. (Courtesy of W.F. Tjallingii and Th. Hogen Esch.)

follow, the stylets are at rest inside the xylem vessel or the phloem sieve element (SE). The combination of EPG recording with other techniques, such as transmission electron microscopy (TEM), isotope-labelled diets, using viruses as markers, honeydew clocks, etc., has contributed substantially to the understanding of aphid probing.

Pathway phase

During the intercellular stylet pathway phase, frequent brief intracellular punctures (pds) can be observed (Fig. 9.3). Initially, short 'test probes' of 0.5–3 min occur, showing only pathway phase waveforms that often include one brief cell puncture. These punctures, or pd waveforms, are recognized by a sudden drop of the voltage signal, reflecting the cell membrane potential when the stylet tips penetrated the plasmalemma due to the fact that the stylets act as a microelectrode, recording the voltages at the tips. After 5–10 s, the pd waveform shows a fast return when the stylets withdraw from the punctured plant cell (Table 9.1, Fig. 9.3). Later, as the probes last longer, many of theses pds are shown at irregular intervals. During a pd, first saliva is injected into, and then a sap sample is taken from, the punctured cell and evaluated by the pharyngeal gustatory organ. Nearly all cells bordering the stylet track are punctured, but the stylets themselves otherwise clearly continue intercellularly after withdrawal from the neighbouring cells (Tjallingii and Hogen Esch, 1993). The EPG from aphids feeding on synthetic diets with radioactive tracers have shown that the sampled sap reaches the pharyngeal organ within 0.1–0.2 s, (Spiller *et al.*, 1990). The stylets appear to penetrate mostly between the cellulose and hemicellulose fibres of the secondary cell walls and not along or through the middle lamella. Although the role of saliva seems important during the penetration phase, there seems

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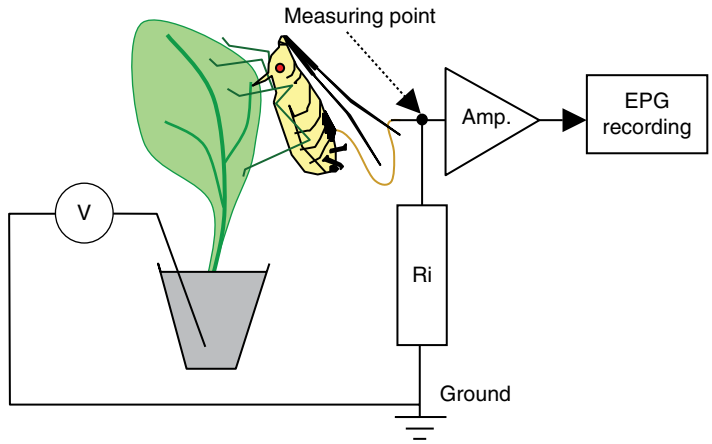
Box 9.1. The electrical penetration graph (EPG)

In the EPG technique, an aphid and a plant are made part of an electrical circuit by connecting a plant electrode, inserted into the soil, and an insect electrode (gold wire, 10–20 µm diameter) glued to the insect. The circuit also incorporates an electrical resistor (Ri) and a voltage source (V). An amplifier – not being part of the circuit and having no effect on it – is connected to this circuit at the measuring point. As soon as the aphid stylets penetrate the plant, the circuit is completed and a fluctuating voltage of the EPG signal is recorded. The voltage fluctuations appear in a number of distinct patters, referred to as waveforms. The major waveforms that have been distinguished for aphids are given in Table 9.1 with their experimental correlations to probing activities and stylet tip positions in the plant tissues.



Electrical origin of the signal

The fluctuating voltages have two electrical origins: (i) electrical resistance (R) fluctuations; and (ii) fluctuating voltages generated in the insect–plant combination, called electromotive forces (emf).

The respective signal constituents are referred to as R- and emf-components, which are superimposed at the measuring point. The R-components are due mainly to valve movements in the food and salivary canals within the maxillary stylets and to sealing of the stylet tips by the plasmalemma of a plant cell, just before being punctured at the start of a pd waveform (see main text), and also to resistance changes in ion channel conduction during intracellular stylet tip penetration (so far, hypothetical). The emf-components originate mainly from 'membrane potentials' of plant cells – when their plasmalemma is punctured by the stylets – and from 'streaming potentials' caused by the fluid movements in the two capillary stylet canals. Muscle and neural potentials in the insect do not contribute significantly to the EPG signal.

Measuring systems

The original EPG system (McLean and Kinsey, 1964) used an alternating current (AC) voltage applied to the plant, and amplitude modulation signal processing (as with AM radio signals). However, this system was only sensitive to the R-components, not to the emf-components. An optimized version of this original system is still used sometimes and has been referred to as an 'R-EPG system'. Later, Tjallingii (1988) developed an EPG system using a direct current (DC) voltage source and an appropriate input resistor ($10^9\Omega$) to record both R- and emf-components equally, which could be referred to as a full-EPG system. This is the most widely used system at present. A special version of this system, with a very high input resistor ($Ri > 10^{12}$–$10^{15}\Omega$) is only sensitive to emf-components and can be referred to as an emf-EPG system. Thus, there are three EPG systems: (i) the (regular) full-EPG system that records both signal components; (ii) the emf-EPG system that only records the emf-components; and (iii) the R-EPG system that only records the R-components. The full-EPGs contain the widest range of biological information, and therefore the signals are more complicated than the signals from the emf- and R-amplifiers, which have been used only in special studies. Neither the separate emf- or a combined full- and R-signal have as yet contributed significantly to better knowledge or correlations between waveform and with the aphid activities or plant properties (Tjallingii *et al*., 2010).

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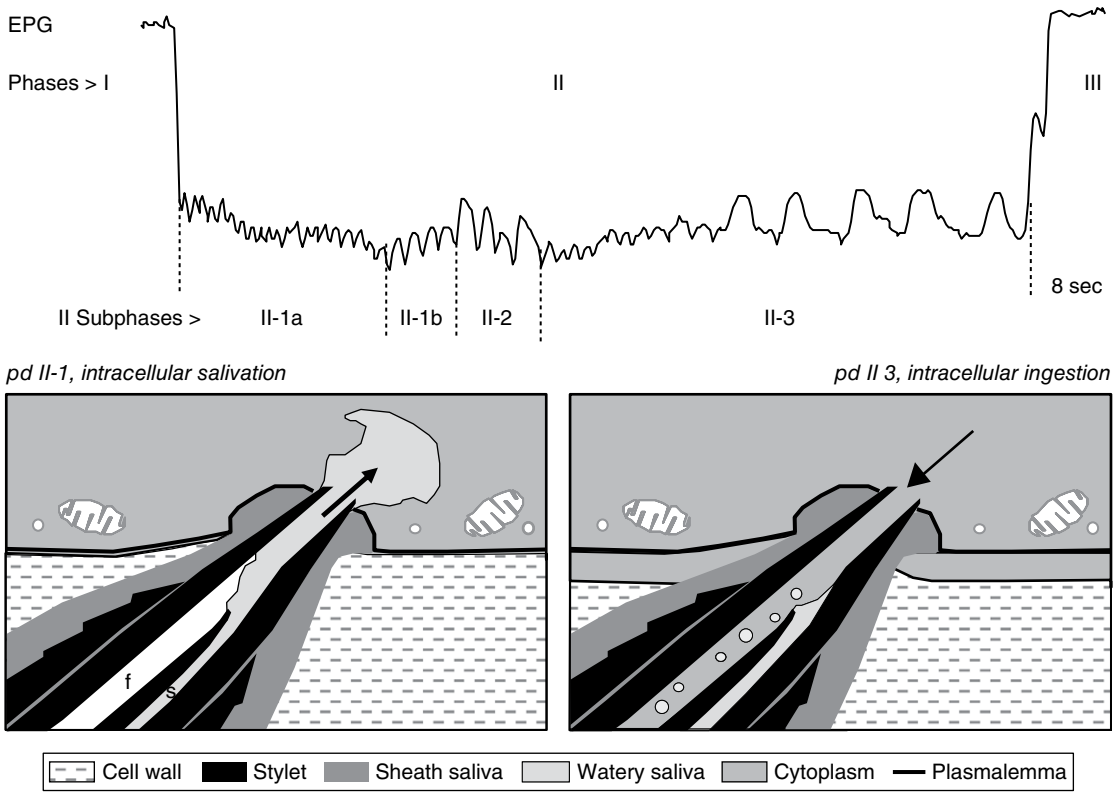

Fig. 9.3. Electrical penetration graph of intracellular stylet puncture (top) and related stylet activity diagrams (bottom). The food (f) and the salivary canal (s) are fused near the tips of the maxillary stylets. The voltage difference between the high phase I and III intercellular level and the phase II intracellular level represents the transmembrane potential of the stylet-punctured plant cell. The phase III edge represents stylet withdrawal from the cell. During subphase II-1 (1a, 1b, or 1a and 1b), watery saliva is injected over a few seconds, confirmed by the transmission of non-persistent viruses, whereas at the II-3 subphase, cytoplasm (sap) is actively ingested from the cell. (From Martin *et al*., 1997.)

Table 9.1. Electrical penetration graph (EPG) waveforms and corresponding aphid activities. (From Tjallingii, 1987.)

EPG Waveform	Behavioural phase	Activity
A, B, C	Pathway	Intercellular penetration
Pd	Pathway	Intracellular puncture
E1	Phloem	Saliva secretion
E2	Phloem	Sap ingestion, passive
F	Pathway	Derailed stylet mechanics
G	Xylem	Sap ingestion, active

specifically to be a clear role for pectinases (Cherqui and Tjallingii, 2000). It cannot be excluded that the intercellular fluid is sampled, but so far there is no direct evidence for this.

Most pd waveforms last for 5–10 s and comprise three waveform patterns or phases: (I) before the plasmalemma puncture, stylet tips extracellular signal at high voltage level; (II) stylet tips intracellular, signal at 80–150 mV; and (III) after stylet withdrawal from the cell, at the same voltage level as in phase (I); stylet tips return to an extracellular position. During the intracellular phase II, a sequence of waveform 'subphases' occurs II-1, II-2 (Fig. 9.3; Powell *et al*., 1995; Tjallingii *et al*., 2010). Subphase II-1 represents watery saliva injection into the punctured cell; the activity during subphase II-2 is still unknown; and subphase II-3 represents ingestion of cell contents (Martín *et al*., 1997). The separation of subphases is not always distinct, and subphase II-1 may show two separate waveforms (Tjallingii *et al*., 2010). Which one is

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related to the watery salivation is still unknown. During these brief cell punctures, only the maxillary stylets are used to pierce the plasmalemma, and presumably also the vacuole membrane (tonoplast). TEMs (Fig. 9.4) show that cells remain intact and survive puncturing by the stylets with no disrupted vacuoles, mitochondria or chloroplasts (Tjallingii and Hogen Esch, 1993).

In contrast to herbivores with chewing mouthparts, aphids sample and taste the secondary metabolites directly from the cell's storage compartments. This avoids the mixing of allelochemicals with their related converting enzymes, which is the main mechanism in the plant to produce repellent and toxic defence against chewing herbivores; for example, the conversion of glucosinolates to isothiocyanates (Mathile, 1984; Mullin, 1986). Allelochemicals can act as 'token stimuli' affecting pathway activities in aphids (Chapter 22, this volume). In Brassicaceae, glucosinolates such as sinigrin (Gabrys and Tjallingii, 2002) and sinalbin (Gabrys *et al*., 1997) have been used to study host-plant recognition by *B. brassicae*. Sinalbin in epidermal cells of the flower stalks of *S. alba* is higher than in the epidermal cells of old leaves (Gabrys *et al*., 1997). In settling experiments, *B. brassicae* preferred the flower stalks, whereas *M. persicae*, known to tolerate glucosinolates up to certain concentrations only (Nault and Styer, 1972), preferred old leaves with lower glucosinolate levels. On old leaves, EPGs by *B. brassicae* showed short probes (<2 min) no deeper than the epidermis, while initial probes on flower stalks lasted longer (>10 min) and often included phloem feeding. This suggests that sinalbin in epidermal cells is an important probing stimulus for *B. brassicae*. When this aphid was given a choice between diet with and without sinigrin, and between excised leaves of non-host plants with their petioles in water with and without sinigrin, the glucosinolate treatments were preferred (Gabrys and Tjallingii, 2002). However, it remains unclear how the added sinigrin was distributed in the plant and where it might be sampled by the aphid; that is, from the xylem vessels, from the intercellular space in contact with the xylem transport system, or from the cytoplasm of mesophyll or phloem cells after (active) transport into these cells. One or more of the three sites is possible, and sampling will then be during EPG waveform G, xylem drinking, pd II-3 sampling from a cell, or E2 ingestion after phloem contact, respectively.

Intracellular fluid ingestion/sampling during subphase II-3 was inferred from experiments on transmission of non-persistent plant viruses (Martin *et al*., 1997). Sufficient virus was acquired during one pd puncture in an epidermal cell of a virus-infected plant (Fig. 9.3) to achieve subsequent transmission to a healthy test plant. Aphids are the most important vectors for non-persistent plant viruses, even for non-host plants. Thus, the cereal aphid *R. padi* is an important vector for *Potato virus Y* to potato (Chapter 15 and 29, this volume). Evidence for the importance of short probes on non-hosts also comes from close-up video recordings in combination with EPGs (Hardie and Powell, 2000) of adult *A. fabae* gynoparae on broad bean (*Vicia faba*). Within 5 min, 75% of the gynoparae departed from the summer host, and the majority

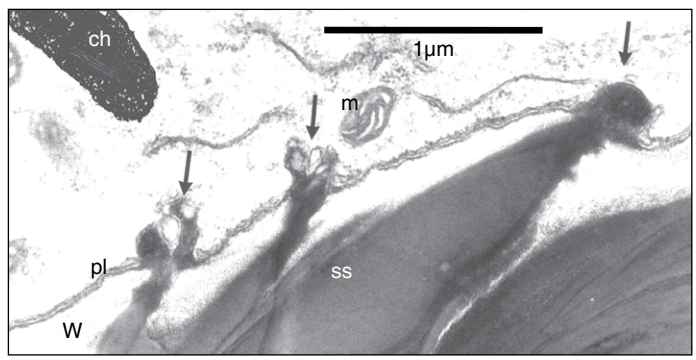

Fig. 9.4. Remnants of three intracellular punctures (arrows) with dark sheath saliva (ss) in the electron lucent material of the cell wall (w) (tissue fixation 1.5 h after puncture). The damage is restricted to the plasmalemma (pl) around the sheath material. Mitochondria (m) and chloroplasts (ch) are intact after a puncture. (Micrograph courtesy of W.F. Tjallingii and Th. Hogen Esch.)

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of these did so after a short probe during which brief cell punctures (including sap sampling) occurred, presumably causing rejection.

Plant tissue cues may stimulate or inhibit stylet pathway progress, resulting in shorter or longer times being required to reach the phloem. In wheat, DIMBOA encountered in the sheath cells of the vascular bundle (Massardo *et al*., 1994) prolongs the pathway phase and delays the phloem phase initiation, although the phloem phase as such is not affected during 8 h experiments (Givovich and Niemeyer, 1991; Givovich *et al*., 1994). It seems plausible that the brief pd cell punctures contribute to this effect, but these punctures are also essential in locating the phloem sieve elements. In EPG recordings from whiteflies (Aleyrodidae), no or very few pd punctures occur, but their efficiency in phloem finding does not differ from that in aphids. Although the external labial taste receptors of whiteflies, which are missing in aphids, may collect sufficient information from the plant surface for host discrimination (Walker and Gordh, 1989), intracellular cues to direct stylet penetration towards the phloem SEs seem not essential for the whiteflies. It has been suggested that gradients in the plant tissues could present phloem-finding cues in the form of differences in sucrose levels and pH between mesophyll and phloem cells. However, such differences, though present between mesophyll, vascular parenchyma and SE cell contents, do not change progressively cell by cell towards the phloem and so cannot be 'followed' during pathway progress. Moreover, apart from the whitefly anomaly, a possible symplasmic sugar gradient will presumably be inverted diurnally and depend on the source–sink relationship; it is therefore not a reliable indication of phloem position.

It has been shown that a significant majority of both alate virginoparae and gynoparae of *A. fabae* and *R. padi* reproduce prior to phloem feeding, although all make brief cell punctures (pd waveforms in the EPG) before reproducing (Tosh *et al*., 2002; Nam and Hardie, 2012). In addition, a potent parturition stimulant has been isolated from the winter host plants that induces larviposition in gynoparae, but not in virginoparae, of these species (Powell and Hardie, 2001; Nam and Hardie, 2014). Without this stimulant, there is little or no reproduction. It now seems that parturition, in general, is stimulated prior to the aphid reaching the phloem elements and feeding (Powell *et al*., 2004). The interpretation is that the chemical cues identified in the peripheral plant cells are used by the aphids to identify suitable hosts on which to reproduce. Other aphid species may differ in the mechanisms and cues for such a crucial decision, although similar conclusions are being drawn from work with *Acyrthosiphon pisum* (pea aphid) (Caillaud and Via, 2000; Nam *et al*., 2013). The chemical identification of the specific reproductive stimulants for gynoparae of *A. fabae* and *R. padi* is still lacking, but the stimulant is present in winter host leaves throughout the growing season (Powell and Hardie, 2001; Nam and Hardie, 2014)

Phloem phase

The phloem phase of probing (Fig. 9.5) is characterized by EPG waveform E1, indicating SE salivation, and waveform E2, indicating SE ingestion with salivation – hereafter named 'E1 salivation' and 'E2 ingestion'. Once the aphid's stylets have punctured the SE, analyses of many EPG experiments have shown that there are three important activity/waveform transitions that can be considered to reflect the three most important decisions aphids then need to make: (i) switching to E1 salivation; (ii) switching from E1 salivation to E2 ingestion; and (iii) sustaining E2 ingestion for longer than 10 min (see below).

E1 salivation

Several brief pd punctures into phloem SE may precede the first E1 salivation period, either in a previous or in the same probe as E1 occurs for the first time. In general, all E1 waveform periods start with pd waveform subphases II-1 and II-2 (Fig. 9.5, arrow), but subphase II-3 (sampling) is mostly missing, which may indicate that gustatory cues have already been evaluated during earlier pd punctures in the SE or companion cell. After these pd features, the typical E1 peaks, increasing in amplitude and frequency, develop (Fig. 9.6). As determined from the EPG recordings made during the probe of Fig. 9.2, the first E1 salivation occurred in the last SE out of 11 previously punctured SEs during this TEM-assessed probe.

There seem to be no clear waveform differences between an SE pd puncture and a pd in any other type of cell so that (based on the EPG recording) these two cannot be discriminated. However, some aphid species show repetitive pds, which, in comparison to normal pds, last longer (15–25 versus 5–10 s) and occur with more constant intervals (30–35 s),

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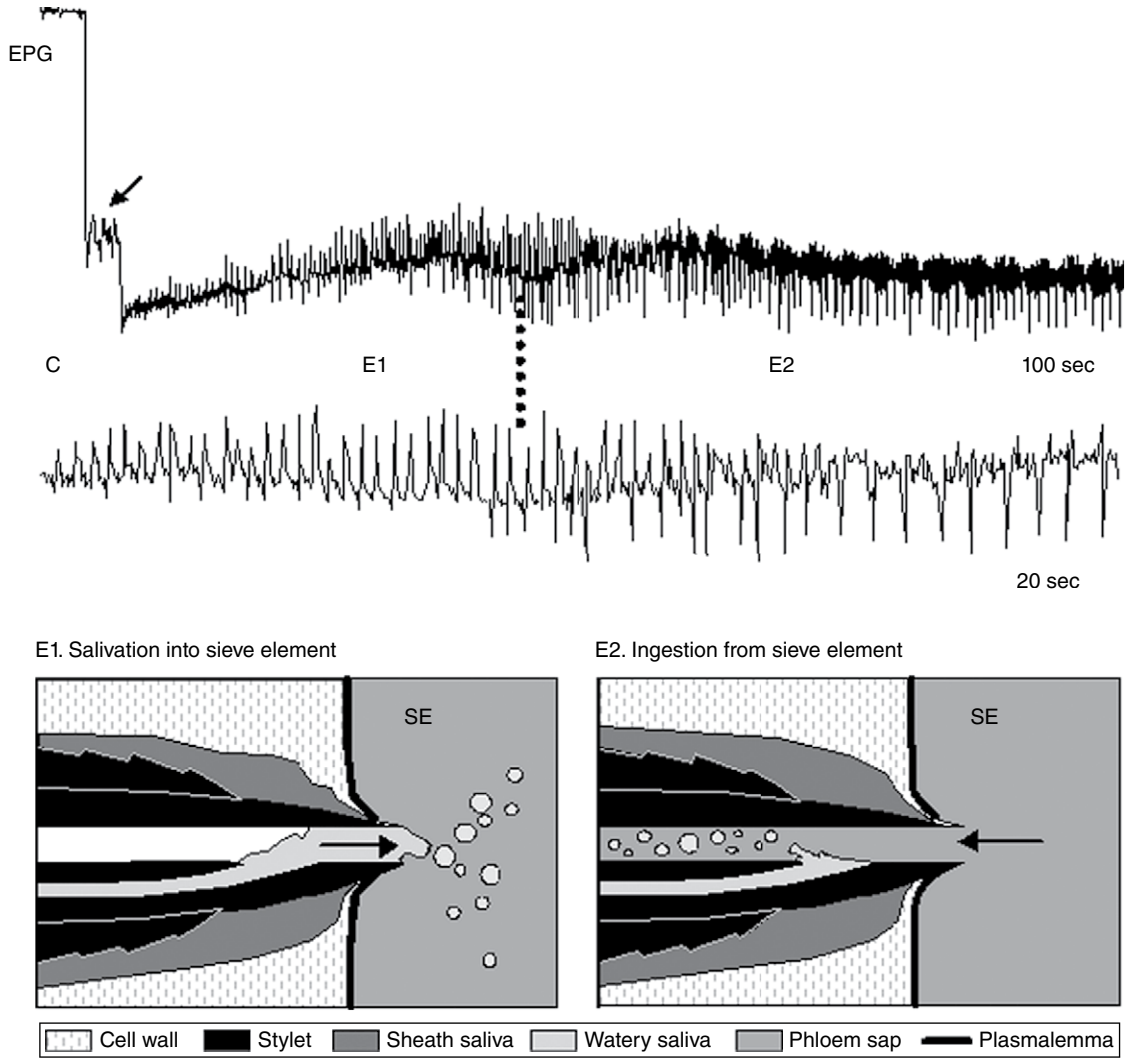

Fig. 9.5. Electrical penetration graph showing phloem-phase waveforms (top) at different timescales. From waveform C, first regular pd subphases II-1 and II-2 (arrow) are shown, then E1 and E2. Bottom left, diagram showing when the cibarial valve is closed, the fusion of the food and salivary canals near the stylet tips allows injection of saliva, E1, into the phloem sieve element (SE). Bottom right, phloem ingestion when the cibarial valve is open during E2, the high hydrostatic pressure forces the saliva into the food canal with the phloem sap. (From Prado and Tjallingii, 1994.)

show more distinct subphase II-2 features and show reduced membrane potentials (Tjallingii and Gabrys, 1999; Fig. 9.6). A bout of repetitive pds is mostly followed by E1 phloem salivation, and is supposed to represent multiple punctures in one and the same SE. Repetitive pds have been found in a few Aphidinae (e.g. *B. brassicae*, *A. pisum*, *Therioaphis trifolii maculata* – spotted alfalfa aphid) and in many tree-feeding species from other taxonomic groups.

The aphid species that show repetitive pds also show normal pd punctures, rarely followed by E1 salivation. Between the normal pds in these aphids, individual pds occur with the same features as the repetitive ones, and are thought to reflect early SE punctures. In conclusion, decision 1 to switch from pd to E1 salivation in an SE is not taken automatically when the SE is reached (Fig. 9.6).

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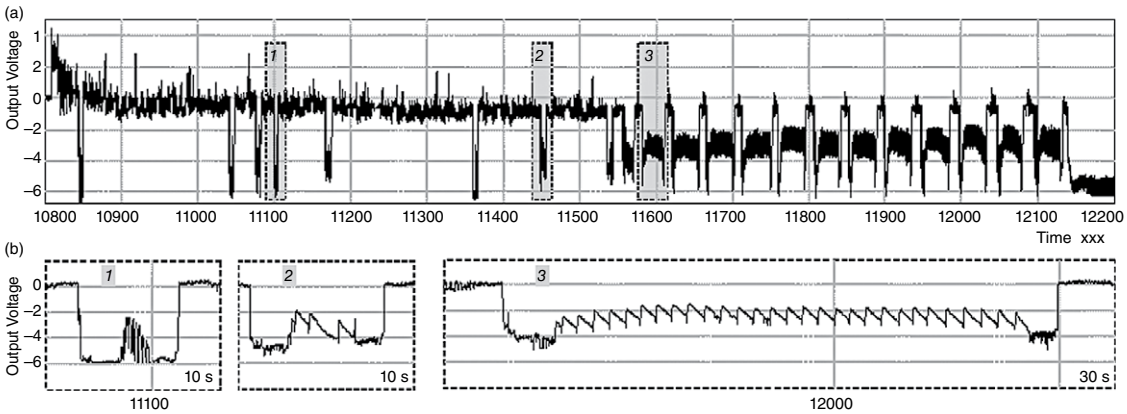

Fig. 9.6. Repetitive sieve element punctures by *Therioaphis trifolii maculata* on lucerne. (a) Electrical penetration graph of a probe (starting from the 0 volt, pre-probing level, shortly after ~10,800 s) with a period of repetitive potential drops (~11,550–12,150 s). The beginning of that period indicated that the stylets certainly reached a sieve element about 12 min after the probe started. Sometimes, the period before which repetitive pds occurred is much longer. Subsequently (~12,150–12,200 s), a period of E1 salivation and E2 ingestion occurred. During the initial pathway phase, mainly normal pds are observed, such as pd *1*, but also some smaller pds are shown; pd *2*, for example, as well as the pd following pd *1* (at ~11,180 s). These smaller pds show similar subphase II-2 details to the repetitive pds, such as repetitive pd *3*. These are now thought to reflect isolated, short phloem contact, suggesting that a sieve element (or other phloem cell with the same membrane potential, which is lower than in mesophyll cells) was punctured as early as ~11,170 s, i.e. about 6 min after the probe started. (b) Details of a normal pd (*1*), a proposed 'early phloem' pd (*2*) and a repetitive pd (*3*). The latter two pds reveal distinctly different waveform features to the normal pd: a lower membrane potential (~80% of a normal pd), longer duration (about 25 s in repetitive pd *3*) and a much lower frequency of subphase II-2 signal elements.

Functionally, the E1 saliva has been proposed to bind calcium in the SE, thus inhibiting the coagulation of phloem protein and subsequent sieve plate occlusion, which is the normal SE wound reaction. This inhibition was shown for forisomes, a specific Fabaceae phloem protein (Knoblauch and van Bel, 1998; Knoblauch and Peters, 2004; Walker and Medina-Ortega, 2012; Medina-Ortega and Walker, 2013). Calcium added *in vitro* to isolated forisome crystals resulted in dispersion, the sieve plate occlusion state, whereas subsequently added EDTA (a calcium-binding agent) caused forisome contraction, restoring its small crystalline shape and, *in vivo*, the opening of SE connections between cells across the sieve plate. Adding aphid saliva, collected from artificial diet after mass feeding by aphids, had the same effect as the EDTA application. However, it has recently appeared that the function of E1 salivation in disabling the SE occlusion reaction of the plant is not as clear as it seemed. First, stylet insertion by *A. pisum* into an SE of its host, *V. faba*, does not trigger forisome dispersal, suggesting that E1 salivation is not needed to prevent sieve plate occlusion (Walker and Medina-Ortega, 2012). It may be that forisome dispersal does not occur because the stylet damage is too small to trigger it or that the initially injected salivation, the pd subphase II-1 activity always preceding E1 salivation (Fig. 9.5, arrow), is preventing the SE occlusion. In another experiment, induced forisome dispersal by applying a heat shock was not reverted any faster by E1 salivation than by the plant itself (Medina-Ortega and Walker, 2013). Heat shock (Will *et al*., 2007) or caterpillar feeding (Salvador-Recata *et al*., 2014) causes propagated SE depolarizations with associated calcium influx. Aphids feeding on a phloem SE reacted to depolarizations by switching back from E2 ingestion to E1 salivation. After a few minutes, the SE membrane was repolarized, and 10–15 min later E2 ingestion was resumed. Although there is an apparent relationship between the calcium concentration, the membrane polarization and the E2 to E1 waveform changes, it remains unclear whether these small calcium concentration differences, or any other concurrently occurring SE activities, have a role in the waveform switches or not.

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During E1 salivation, the saliva can only reach the SE if it is pumped out at a higher pressure than that of the SE sap, and if no sap in the common apical part of the stylet ducts is moving into the food canal and thus dragging the saliva into the aphid (Fig. 9.5; bottom left). This will not occur as long as the cibarial valve is closed.

E2 ingestion

Opening the cibarial valve reflects the switch from E1 salivation to E2 ingestion, which is supposed to be a mainly passive process on the part of the aphid. It seems likely that the switch is triggered by SE cues after E1 saliva creates sufficient suppression of SE occlusion. The nature of these cues is as yet unclear. Also, although this suppression may be effective at the stylet insertion site, additional anti-clogging seems needed to prevent protein clogging the narrow stylet food canal. After stylectomy during E2 ingestion, the phloem sap exudation from the stylet stump usually stops after some time (one or a few hours), and clogged proteins in the food canal are shown in TEM micrographs (Tjallingii and Hogen Esch, 1993). During E2 ingestion, concurrent E2 salivation occurs, and this saliva mixes with the incoming phloem sap flowing directly into the food canal and will not reach the SE (Prado and Tjallingii, 1994; Fig. 9.5, bottom right) but prevents blockage of the food canal. Electromyograms from regions in the head close to the salivary pump and close to the cibarial (suction) pump suggest that in the E2 waveform (Fig. 9.5; 20 s fragment), the downward E2 spikes are related to salivary pump activity, whereas the smaller and faster (6 Hz) waves are related to cibarial valve/pump muscle activity.

Sustained phloem feeding

Sustained E2 ingestion can be continued for hours, and even days, indicating final phloem or host acceptance for feeding. As it is not prudent to record EPGs longer than 6–8 h (due to increasing wire effects; Tjallingii, 1986; van Helden, 1995), only relatively short periods of sustained E2 ingestion can be recorded reliably. However, a threshold duration of about 10 min, called 'committed/sustained phloem feeding', can be used as an indicator for phloem/host-plant acceptance (Tjallingii, 1990; Montllor, 1991; Prado and Tjallingii, 1994). The time between plant access and committed phloem feeding is usually several hours and often includes many separate probes with or without phloem phases (Fig. 9.7). Many early E2 ingestion periods do not last longer than 10 min, and it remains unclear why. In *A. fabae* on *V. faba* leaves, the average time to committed phloem ingestion was 5.2 h (Tjallingii, 1994). The monophagous *Drepanosiphum platanoidis* (sycamore aphid) on a leaf of sycamore (*Acer pseudoplantanus*) took about 4 h before sustained E2 occurred (W.F. Tjallingii, unpublished). The generalist alate virginoparae and the specialist gynoparae of *A. fabae* showed a similar time, 4 and 4.5 h, respectively (Tosh *et al.*, 2002). The time lags quoted here are averages of 15–20 individuals; the minimum time is often shorter, sometimes only 25 min. Phloem or host acceptance does not follow automatically once E2 ingestion is reached, as the final decision depends on SE cues.

Quantitative regulation of E2 ingestion is not well understood, but possibly the pharyngeal valve regulates the throughput of sap forced into the food canal. Excretion data from 'honeydew clocks' showed a constant droplet size and interval during long E2 ingestion periods. In the laboratory, free,

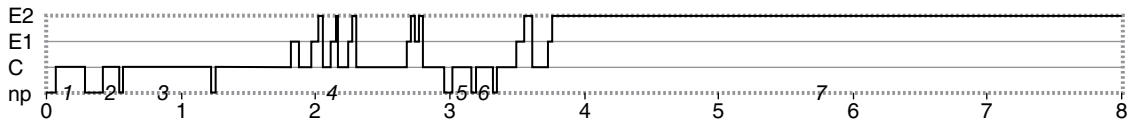

Fig. 9.7. Schematic representation of aphid-probing activities during the first 8 h of plant contact by *Brevicoryne brassicae* on mustard leaves, *Sinapis alba*. The activities are represented as category levels on the *y*-axis, with time (h) on the *x*-axis. Italic numbers indicate the successive probes. Some probes (*1*, *2*, *3*, *5* and *6*) show only pathway activities (C). Two probes (*4* and *7*) include phloem phases. Probe *4* includes only phloem salivation (E1) in the first sieve element penetrated, while all others show phloem feeding (E2) as well as salivation. The last phloem phase in probe *4* switches from E1 to E2, back to E1 and then to E2 again. The last phloem phase in probe *7* has an E2 period >10 min, i.e. 'committed phloem ingestion' considered as phloem or host-plant acceptance after 4 h.

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non-wired aphids also showed long and constant honeydew excretion independent of the diurnal light–dark periodicity of ingestion rate. Ingestion periods longer than 10 min are interrupted regularly, even on suitable hosts, and the regulating mechanism of phloem sap uptake may be via the duration of ingestion periods, rather than by the ingestion flow rate (Tjallingii, 1995). The feeding rate and ingestion periods under field conditions needs further study.

Salivary secretions during probing

Aphids have been thought to secrete two types of saliva, 'gelling saliva' from the principle glands and 'watery saliva' from the accessory glands (Miles, 1999). The gelling saliva forms the stylet sheath, supporting stylet movement, and the watery saliva is injected into plant cells during pd punctures and during E1 and E2 salivation (Fig. 9.3 and 9.5, respectively). However, the gelling process depends on both the saliva composition and the presence of oxygen in the secretion location (Will *et al*., 2012), while 'watery saliva' appears to be excreted continuously, including during the pathway phase (Moreno *et al*., 2011). Thus, no distinction can be made between the two types of saliva in terms of secretion time and location. Moreover, saliva contains many proteins (Rao *et al*., 2013) and the principle salivary glands contain several different types of secretory cells (Ponsen, 2012), presumably making different contributions to the composition of the saliva.

In aposymbiotic aphids (i.e. lacking symbionts), an increase in EPG waveform F was shown, reflecting disrupted stylet mechanics (Tjallingii, 1987; Machado-Assefh *et al*., 2015), presumably due to a deficient saliva composition. The saliva contains enzymes such as pectinases, cellulases, polyphenol oxidases and peroxidases (Miles, 1999), but whether the absence of these or other components interferes with stylet mechanics remains to be studied.

The role of E1 salivation in calcium binding is discussed above, and this appears very aphid–plant species specific (Medina-Ortega and Walker, 2013). Also, disabled phloem phase activity has been reported from gene knockout or RNAi treatments to change the saliva protein composition (Navdeep *et al*., 2006; Chapter 2, this volume).

Mechanical damage caused by stylet penetration is minimal, but in non-hosts, or in less preferred plants, the salivary secretions can cause damage expressed as growth disturbance, necrosis, discoloration and other effects on plant tissues (Chapter 14, this volume). Even moderate aphid numbers can have serious effects, and an initial infestation of 15 *A. fabae* or *A. pisum* per plant killed broad bean plants with 4–5 true leaves in 1–2 weeks (Tjallingii, 2004). Hypersensitive plant symptoms were wilting and necrotic areas on leaf petioles or plant stems, resulting in dried, dead plants and yield loss. The same plants infested by *Megoura viciae* (vetch aphid) were only affected after a much longer period and larger populations. It is hypothesized that the *M. viciae* saliva is compatible with SE factors in *Vicia* species due to their co-evolutionary history, whereas the saliva of *A. fabae* and *A. pisum* is incompatible with *Vicia* species, as these are not their natural hosts.

Xylem phase

Aphids are primarily phloem feeders, but they also ingest xylem (Spiller *et al*., 1990), recognized as waveform G in EPGs, and especially recorded from desiccated and starved aphids (Ramirez and Niemeyer, 2000). In contrast to phloem ingestion, xylem ingestion hardly contributes to nutrition (Kulhmann *et al*., 2013), but compensates for dehydration and water deficit. As the xylem sap has a low or negative hydrostatic pressure in contrast to phloem, xylem drinking should be an active ingestion (sucking). Xylem ingestion has received moderate attention, for two reasons: (i) EPG studies are generally not done with starved or desiccated aphids; and (ii) when it occurs, the durations are very variable, depending on the individual water-deficit condition.

Winged morphs of *A. fabae* landing after a flight frequently showed more xylem ingestion than walking apterous aphids, presumably with a greater need to redress their water balance (Powell and Hardie, 2002). A high percentage showed xylem ingestion on their appropriate host plants: 65% on broad bean for winged virginoparae and 60% on spindle for gynoparae. They also ingested xylem on the non-preferred host; that is, 85% of the alate virginoparae on spindle (the winter host) and 20% of gynoparae on broad bean. Increased xylem ingestion often occurs on less suitable plants due to postponed phloem feeding, a delay which will also increase water deficit.

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Incompatible Aphid–plant Interaction (Plant Resistance)

In the search for new aphid-resistant plant cultivars and reduced virus transmission, incompatible aphid–plant combinations are now widely investigated (see also Chapter 22, this volume). The resistance to *M. persicae* in 20 *Solanum tuberosum* (potato) cultivars and related species was screened by Alvarez *et al.* (2006). After a no-choice screen for survival and reproduction with free-moving individuals on each plant, 6 h EPG recordings were made to identify resistance factors and their tissue location. Two plants having glandular trichomes showed an increased time to the first probe, while aphid survival and reproduction was reduced. However, when the leaf surface with trichomes was washed with water-soaked cotton wool, probing started as rapidly as on susceptible plants. Several other plants showed resistance factors in the epidermis and superficial mesophyll, as indicated by larger numbers of short (<3 min) probes, indicating a maximum stylet penetration depth of about three cell layers, possibly limited by deterrent chemicals in these cells.

Other EPG variables indicated resistance at different locations in the plant. Long E1 salivation periods alone or followed by brief E2 ingestion found in the potato cultivar 'Kardal' occurred exclusively in young leaves, indicating an age-dependent phloem resistance. In a different study, the melon cultivar 'TGR' (*Cucumis sativus*) showed that melon aphids (*Aphis gossypii*) had increased numbers of single E1 salivation periods that lasted longer on young than old leaves before a switch to E2 ingestion (Garzo *et al.*, 2002; Tjallingii, 2006). Survival and reproduction on old leaves confirmed that resistance was lost with leaf ageing. Occlusion of SEs can be triggered when punctured by aphids on non-host plants (Medina-Ortega and Walker, 2014), which presumably can be considered as a suitable feature to be used in host-plant resistance programmes. In other cases, (host) plant resistance was characterized by difficulties in sustaining E2 ingestion, presumably due to other SE incompatibility factors (van Helden and Tjallingii, 1993; Klinger *et al.*, 1998; Kaloshian *et al.*, 2000). It is becoming clearer that incompatible interactions at mesophyll and at phloem level, especially, are playing a crucial role in aphid–plant interactions, and therefore the co-evolution of these interactions may be considered a major factor in the predominant monophagy in aphids (Hogenhout and Bos, 2011).

In some plants, classified as aphid susceptible based on insect survival and reproduction, resistance features were found in EPG recordings. These plants would have been discarded in traditional plant-breeding research. Also, some plants classified as resistant, based on aphid survival and reproduction, showed no resistance features at all in EPGs, indicating that plant penetration behaviour as such was not affected. This may be due either to early factors, during landing or during plant surface exploration, or to factors encountered later, such as plant toxins, antibiosis in the true sense (Alvarez *et al.*, 2006).

Secondary plant substances, constitutive or induced, may play a role in each of the decisions aphids make during probing, as discussed in previous sections. But at the phloem level, the nutritive quality of the SE sap will play a role as well. This is a quality that changes with plant age, differs between plant parts and shows diurnal/seasonal fluctuations (McClung Robertson, 2006; Chapter 6, this volume). Diurnal fluctuations of amino acids in SE exudates from excised aphid stylets have been shown by Winter *et al.* (1992). More *Nasonovia ribisnigri* (currant–lettuce aphid) individuals stopped feeding on lettuce (*Lactuca sativa*) and withdrew their stylets more frequently at night than during the day (van Helden and Tjallingii, 1993). Similar observations were made with video on *A. fabae* feeding on their host plants (J. Hardie, unpublished).

Overpopulation seems a well-established reason to leave a host plant. Walking colony members increased tactile disturbance (crowding) in *D. platanoidis*. Also, in *R. padi* colonies, increased movement of conspecifics, or disturbance by natural enemies, rain and wind, has been attributed to increased volatile semiochemical concentrations (Quiroz *et al.*, 1997; Chapter 8 and 11, this volume).

Host Alternation and Changes in Host-plant Preference

Seasonal host alternation occurs in a limited number (*c.*10%) of aphid species (Blackman and Eastop, 1984; Chapter 4, this volume). Changes of host-plant acceptance and its effects on migration have an obvious importance in the population biology of these species.

The host-plant preference of the winged autumn gynoparae of *A. fabae* changes at the final moult,

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and all larval stages prefer to settle on the natal summer host (Hardie and Glascodine, 1990). In this species, the readiness of the adult gynoparae to take off and leave a summer host seems to be related to the extended period of initial migratory behaviour, during which the insect will not land on a green, plant-like visual target (David and Hardie, 1988; Nottingham and Hardie, 1989; see also the section above on orientation and host-plant finding).

A similar situation was also found for the gynoparae of *R. padi* moving to bird cherry (Nottingham *et al.*, 1991a). By contrast, spring migrants and alate summer morphs of both species did not show such a prolonged migratory flight phase.

Host-plant specificity of the different morphs of *R. padi* varies, and gynoparae exclusively accept *P. padus* as a primary host on which to reproduce. Sloe (*Prunus spinosa*) sometimes grows alongside *P. padus* and is accepted as a host plant by spring morphs developing on the winter host, but not by the gynoparae migrating specifically to *P. padus*. In the autumn, *R. padi* gynoparae and males migrate from grasses to leaves of bird cherry, and host-plant components enhance the behaviour of males approaching sex pheromone sources (Hardie *et al.*, 1994b). Gynoparae and oviparae feed on senescing leaves, but staying too long on the senescing leaves carries the risk of falling to the ground. In field experiments, oviparae were found to be capable of monitoring the leaf ageing process and left the leaves in due time to avoid this risk (Glinwood and Pettersson, 2000c).

Aphids feeding on bird cherry leaves cause damage that induces the production of methyl salicylate (Chapter 8, this volume), which acts as a key promoter for spring migrant take-off (Glinwood and Pettersson, 2000a, 2000b). The application of methyl salicylate to barley produced a significant reduction of infestation in cereals by *R. padi* in field experiments (Ninkovic *et al.*, 2003). A similar effect of methyl salicylate has been shown for the damson-hop aphid, *P. humuli*, when this species is leaving its winter host, *Prunus cerasifera* (Campbell *et al.*, 1990).

The overwintering eggs of *R. padi* hatch on the winter host, bird cherry (*P. padus*), and colonies develop on the young leaves and shoots. Alate spring migrants are produced as a response to increased crowding in the first 2–3 generations (Wiktelius *et al.*, 1990) and leave the winter host for different grasses. This migration means a definitive change in host-plant acceptance of the spring migrants, so that a return to the winter host is excluded (Sandström and Pettersson, 2000; Glinwood and Pettersson, 2000b).

Plant Predisposition to Aphid Probing

Studies on induced aphid resistance in three aphid–plant combinations showed that after 4 days induced resistance was only manifested in leaves not pre-infested, while the aphids probed and settled on pre-infested leaves as easily as on clean plants (Prado and Tjallingii, 2007). EPG recording showed that the induced and systemically spread resistance appeared to be phloem located. Hypothetically, the systemic resistance can be linked to phloem-transported E1 salivary components from the pre-infested leaves, whereas the resistance suppression in infested leaves is local and may be due to pathway phase salivation, inter- or intracellularly in mesophyll and parenchyma tissues. Not only suppression/avoidance of induced resistance takes place in a colonized plant part: it may even enhance plant suitability to the same or higher level than in uninfested plants. Individuals of *A. fabae* on a *V. faba* leaf monitored by EPG inside an established small colony reached the SEs earlier and started E2 ingestion sooner than on a clean plant leaf. So, the colony individuals have mutual benefit (Prado and Tjallingii, 1997).

Plants usually coexist with other plants, and plant–plant interactions can influence aphid host-plant acceptance. Volatiles from a barley plant infested with *R. padi* induced a change in neighbouring uninfested plants, making them significantly less acceptable to *R. padi*. The induced plant response was systemic, and non-preference (antixenosis) seems to play a significant role; the mechanism behind this effect is, however, not known (Pettersson *et al.*, 1996).

The results of laboratory and field experiments indicate that a tritrophic perspective is relevant for ecological implications of plant–plant interactions and aphid host-plant ecology (allelobiosis *sensu* Pettersson *et al.*, 2003; Vucetic *et al.*, 2014). The transmission of allelobiotically active plant substances affecting the aphid ecosystem has been reviewed by Birkett *et al.* (2000), and some specific stress-related substances have been tested (Chamberlain *et al.*, 2001). Allelobiotically active substances from couch grass (*Elymus repens*) and exudates from thistle (*Cirsium arvense*) cause a significant reduction of aphid acceptance of exposed barley plants (Glinwood *et al.*, 2003, 2004; Chapter 8, this volume).

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Direct volatile interactions between undamaged plants of different species can also initiate responses in receiving plants that may have implications for aphids. Potato plants exposed to onion volatiles released higher concentrations of the terpenoids (*E*-)nerolidol and TMTT (4,8,12-trimethyltrideca-1,3,7,11-tetraene), which are significantly repellent to *M. persicae* (Dahlin *et al*., 2014) and reduce aphid immigration into potato fields when onions are present (Ninkovic *et al*., 2013b). Reduced aphid settling was also found when individual plants of a specific genotype were exposed to air passing another barley plant in a twin cage arrangement (Fig. 9.8) with a compressor-controlled airflow. This effect was related to specific combinations of barley cultivars (Fig. 9.9; Pettersson *et al*., 1999; Ninkovic *et al*., 2002). Plants influenced by neighbouring plants with aphid infestations showed a temporal change in biomass allocation, favouring root growth, which could indicate a systemically mobilized resistance barrier (Ninkovic *et al*., 2003).

An aphid attack evokes local and successively systemic plant responses and promotes plant responses similar to those caused by other herbivores and plant diseases (Forslund *et al*., 2000).

Increased CO_2 and an endophyte-infested host plant initiated reduced settling on host plants of *R. padi* (Ryan *et al*., 2014). Changes in four amino acids in the phloem partially explained the effect of plant nitrogen fertilization and elevated CO_2 on aphids. The results indicate the complexity of different host-plant acceptance factors affecting aphids in complex ecosystems.

Conclusions

Host-plant selection, mainly relevant to alate aphids, is initially dominated by visual cues, superseded by olfaction. During this initial plant approach, the effects of semiochemicals from natural enemies and interspecific aphid competition call for further interest.

After landing, tasting for shorter or longer probes is initiated. A probe is a complex activity, encompassing stylet penetration, saliva excretion, sap sampling, xylem ingestion and ultimately phloem feeding. Probes may include three distinct basic behavioural phases: pathway, xylem, and phloem shown by distinct EPG waveforms. Rejection of

Fig. 9.8. Twin cage arrangements where a plant in one cage is exposed to volatiles from another plant in an upwind cage. The airflow through the two cages is provided via tubing connecting the second cage to a vacuum tank. (Photograph courtesy of Velemir Ninkovic). Settling bioassay results are given in Fig. 9.9.

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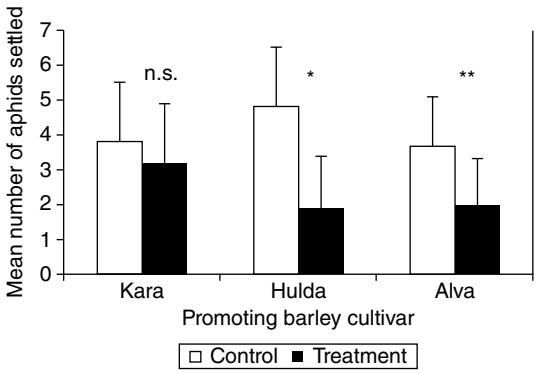

Fig. 9.9. Aphid settling on barley plants, cv. Kara, after exposure to volatiles from cv. Kara (control), and cvs. Hulda and Alva in twin cages. Bars show means ± SD. Comparison of the number of aphids settled on control and treated plants was made with paired t-tests (n = 20) in all experiments. **P <0.01; *P <0.05; n.s. P >0.05. (From Pettersson *et al*., 1999.)

non-host plants may occur at any time during, and even before, probing.

The stylet track followed during the pathway phase is intercellular, but most cells along the track are punctured briefly while saliva is injected and sap sampled. Plant damage by probing is minimal, which allows virus transmission and prevents the activation of deterrent allelochemicals, as are commonly induced by chewing herbivores. Aphid saliva is complex, and several extra- and intracellularly secreted components are active in preventing plant wound responses or inducing plant susceptibility as well as resistance. At the level of phloem sieve elements, aphids have to make three important decisions: (i) to start E1 salivation once the stylets have punctured a sieve element; (ii) to switch from E1 salivation to phloem feeding (E2 ingestion); and (iii) to switch subsequently to committed phloem feeding (arbitrarily taken as longer than 10 min E2 ingestion). It is largely unknown what cues play a role in these decisions.

Plant–aphid interactions change plant properties, thus influencing plant acceptance/rejection cues. In aphid colonies, the changes are different from those in uninfested, systemically connected plant parts. Such effects are not restricted to the individual plant, but are observed in neighbouring plants as well. Also, cultivars of the same species may interact with each other and influence properties of neighbouring cultivars with respect to aphid acceptance or rejection. More aspects of how plants react to ecosystem-sharing species are presently being investigated below as well as above ground.

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10 Aphid Movement: Process and Consequences

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Introduction

This chapter reviews the movement of agriculturally important aphids. It includes information on how different morphs and life stages redistribute themselves in response to intrinsic factors and extrinsic perturbations over time and through spatial scales that span walking behaviour on individual plants to aerial transport over very long distances. The chapter explores the economic consequences of aphid movement and weaves the multiple roles of movement into the tapestry of pest management, providing insight into ways of manipulating aphid movement and thereby mitigating the negative economic impacts resulting from it.

Pest Status

Some aphids are pests because they feed on the phloem of crop plants (Chapter 14, this volume). This feeding is associated with honeydew excretions that reduce leaf gas exchange and impair photosynthesis, resulting in yield decreases, sometimes of considerable proportions. The timing of aphid arrival on new hosts can influence plant health and yield. Many aphids achieve pest status because they transmit plant-debilitating viruses that can, in turn, wreak havoc on a crop and its potential harvest.

Globally, around 5000 species of aphid have been described (Remaudière and Remaudière, 1997); most are confined to the north and many to the south temperate regions, and very few are native to the tropics (Dixon *et al*., 1987). Individual species are usually restricted to one or a few plant species and often move between primary (generally perennial) and secondary (mostly herbaceous) hosts (Dixon, 1998) at defined points in their life cycles. Most aphid species have, at most, a marginal impact on agriculture, with around 450 species (less than 10%) colonizing the world's food and fibre crops (Chapter 1, this volume).

Blackman and Eastop (2000) consider only 18 of the 450 aphid species found on the world's crops to be truly polyphagous, i.e. propagating on hosts from several plant families. Their definition of polyphagy excludes the grain aphids (e.g. *Rhopalosiphum padi*, *Rhopalosiphum maidis*, *Sitobion avenae*, *Schizaphis graminum*, *Diuraphis noxia*, *Metopolophium dirhodum*) that feed on multiple grass hosts, some of which (e.g. maize, wheat, rice, sorghum and barley) are among our most widespread and important crops. Thus, aphids that directly impact agriculture comprise about 24 highly polyphagous and multi-grass feeders, or 0.5% of the known aphid species, the majority of which are cosmopolitan and highly efficient *r*-strategists (Leather and Walters, 1984; Robert, 1987). A handful of additional aphid species are direct pests of specific crops, even though they have narrow host ranges (e.g. *Aphis glycines* (soybean aphid) or *Nasonovia ribisnigri* (currant–lettuce aphid)). Thus, worldwide, relatively few species are

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direct pests of agriculture. Many of these same multi-host aphid species are notable pests of crops and vectors of plant viruses (Dixon, 1988).

While aphids are unquestionably important as crop pests in their own right, their greatest impact on agriculture is as vectors of potentially crippling plant viruses. Vector colonization and movement patterns influence the timing and pattern of virus epidemics, which, in turn, are linked to yield losses. Timings and patterns of virus epidemics differ substantially depending on transmission mode. Below, we explore aphid movement as it impacts the transmission of: (i) persistent and semi-persistent viruses, which, because of the considerable time required to acquire, process and transmit the virus, are primarily vectored by the relatively few species of aphids that colonize the crop; and (ii) non-persistent viruses, which are acquired and inoculated by many aphid species during brief stylet probes (see Irwin and Nault, 1996; Nault, 1997; Chapter 15, this volume).

Contrary to the aphid behaviours necessary for successful semi-persistently and persistently transmitted virus epidemics, lengthy aphid feeding and reproduction on the plant are counter to rapidly escalating epidemics of non-persistently transmitted virus diseases because these behaviours reduce retention of viruses in the aphid mouthparts (Collar *et al*., 1997) and limit aphid movement within a crop (Halbert *et al*., 1981; Thomas, 1983; Gray and Lampert, 1986; Harrington *et al*., 1987; Sigvald, 1987). Importantly, numerous aphid species well beyond those that are severe direct crop pests can be implicated in the spread of non-persistently transmitted viruses (Kennedy *et al*., 1962; Halbert *et al*., 1981).

The Nature of Aphid Movement

Aphids often appear sedentary. As a general rule, aphids, even those that are winged as adults, spend a considerable period of their lives unable to fly. Wing muscles of alatae (winged morphs) of most host-alternating species begin to autolyse a few days after adults eclose (Haine, 1955; Dixon, 1988; Dixon *et al*., 1993), confining the opportunity for flight to a narrow window shortly after the moult to the adult stage (Liquido and Irwin, 1986; Kobayashi and Ishikawa, 1993; Levin and Irwin, 1995; Zhang *et al*., 2008). Furthermore, flight initiation is primarily, though not exclusively, restricted to daylight hours (Taylor, 1958; Johnson, 1969; Dixon, 1988; Isard and Irwin, 1993; Isard and Gage, 2001) and to instances when atmospheric conditions favour take-off (Jensen and Wallin, 1965; Walters and Dixon, 1984; Isard and Gage, 2001). Thus, when considering the entirety of an aphid's life cycle, the amount of time spent moving appears minimal, especially over spatial scales greater than a single plant. Nonetheless, aphids are predisposed to move in response to intrinsic stimuli (Kidd, 1977) and extrinsic perturbations (Bailey *et al*., 1995; Mann *et al*., 1995; Müller *et al*., 2001; Smyrnioudis *et al*., 2001; Zhang, 2002), and such movement can be of profound importance. Aphid movement, in particular migration (Loxdale *et al*., 1993), may be perceived by some as minimal and inconsequential, but such a perception seriously understates and grossly oversimplifies the ecological consequences of movement and ignores the profound economic impact aphids have, through the act of moving, on managed ecological systems.

Evidence supporting the hypothesis that migratory aphids often colonize crops can be found in several publications that list the species most often trapped aloft (Glick, 1939; Berry and Taylor, 1968; White, 1970, 1974; Irwin and Thresh, 1988). Because this book deals with aphids as pests of managed ecosystems, it seems fitting to treat both appetitive movement and migration (see below) as equally important categories of movement.

Conceptual Framework for Aphid Movement

A conceptual framework best facilitates a pragmatic evaluation and assessment of aphid movement. Such a framework should take into account the forces that cause, and the mechanisms that result in, movement. Movement by different life stages and morphs should also be addressed. Finally, the scales of movement must be identified and linked with causal displacement forces and mechanisms. Through such a framework, a more realistic appraisal of movement can be gained, and the framework can serve as a conceptual model to link aphid movement more easily to risk assessment and resulting economic losses and pragmatic management solutions.

Modes of transport

An aphid moves from its point of origin (source) towards some other place (sink) by one of two types of transport mechanism, either through 'inadvertent' (Fig. 10.1a) or 'intentional' (Fig. 10.1b)

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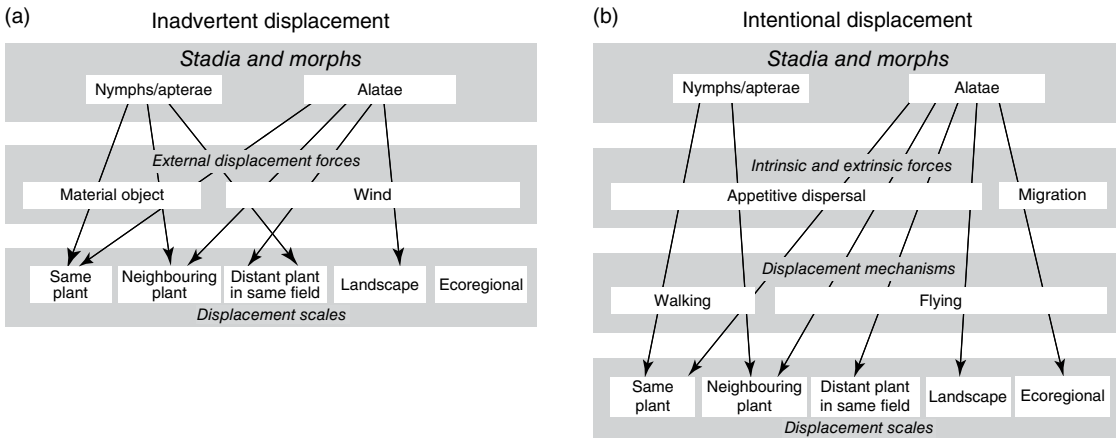

Fig. 10.1. (a) Movement patterns during inadvertent displacement. The schematic takes into account the stadia and morphs of aphids, the external displacement forces that cause movement and displacement scales. (b) Schematic of movement patterns during intentional displacement. The schematic takes into account the stadia and morphs of aphids, intrinsic and extrinsic forces that cause movement, displacement mechanisms involved and displacement scales.

displacement. Inadvertent displacement is an involuntary act, leaving the aphid few options regarding its translocation; it is propelled by the force of impact, gravity, air currents, or a combination of these, or it can be transported by animals, farm machinery, automobiles, or aircraft. As a result, the aphid is transported involuntarily towards a sink. Inadvertent displacement by rising air currents might leave the aphid somewhat battered but, if it survives, it is often able to reproduce and transmit diseases (Zúñiga, 1985; Bailey *et al*., 1995; Fereres and Moreno, 2009). The inadvertently displaced aphid may, during the act of being displaced, purposefully intervene by righting itself, walking, or flying, thus shifting the displacement mechanism from inadvertent to intentional.

Intentional displacement (Fig. 10.1b) is a voluntary act, being prompted by intrinsic forces or extrinsic perturbations. Intrinsic forces that result in aphid movement are preprogrammed; that is, they are governed by the genetics of the organism (Liu *et al*., 2008). Extrinsic perturbations that result in aphid movement are governed by reactions to sensed stimuli in the environment. Movement can result from a combination of extrinsic and intrinsic forces.

Intentional displacement manifests itself in either the intrinsically induced phenomenon known as migration (*cf*. Loxdale and Lushai, 1999) or in 'appetitive dispersal' (Wenks, 1981; *cf*. 'dispersal' of Loxdale and Lushai, 1999), the extrinsically or intrinsically induced dispersal mechanism that evokes a search response for specific resources (e.g. food, mate, oviposition target) or triggers an escape response (e.g. from natural enemies, chemical changes of senescing hosts, overcrowding) (*sensu* Loxdale and Lushai, 1999, concept of dispersal).

Scales of displacement

When an aphid is displaced or actively moves, it is translocated from some source to a sink, in not only three-dimensional space but within a temporal context as well. The horizontal and temporal scales can best be visualized in terms of the relative magnitude of movement by aphids to adjacent plant parts, whole plants, fields, landscapes, ecoregions, continents and transcontinental landmasses (Fig. 10.2). The movement scale that an aphid is able to achieve depends to a considerable extent on the height (vertical displacement) that an individual attains during the movement process. Although an aphid can be blown off its host plant and carried into the atmosphere, it rarely moves horizontally beyond the scale of neighbouring plants (Fig. 10.3). This is unless it is dislodged or otherwise propelled from a considerable height (tall tree, cliff face), is caught up in a strong convective air current, or actively flies and thereby increases or maintains its height above ground (Isard and Gage, 2001). Individuals descending from dramatically different heights would, in fact, quite likely achieve different

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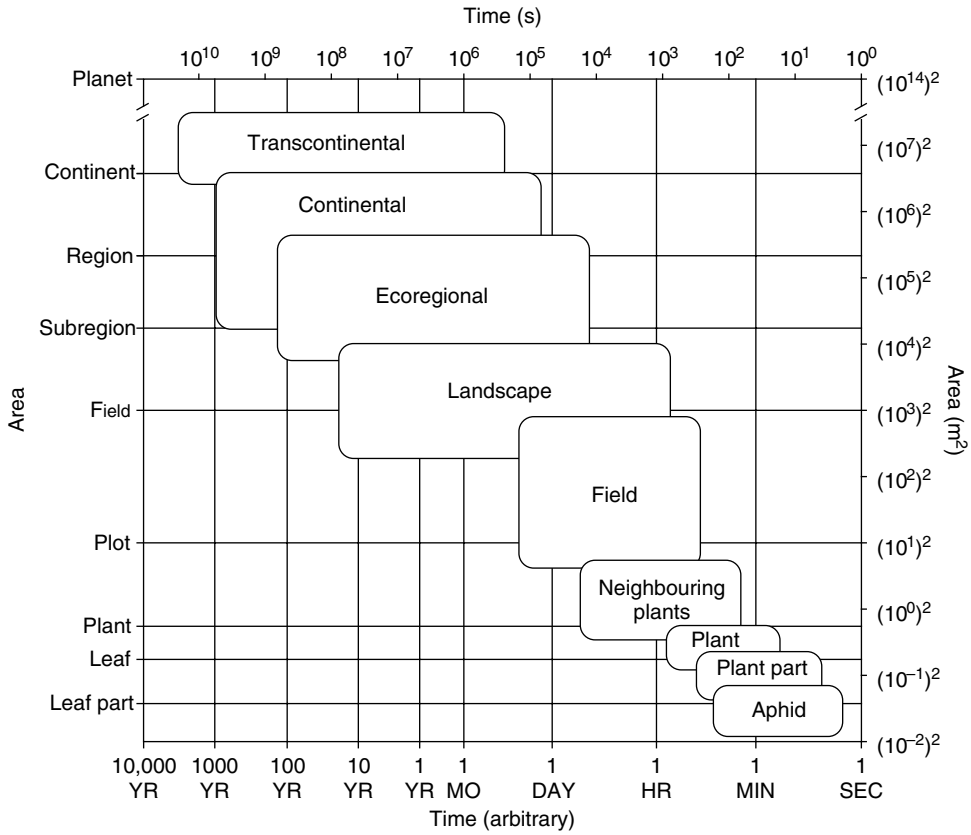

Fig. 10.2. Scaling temporal and spatial displacements that involve and affect aphid movement. Note that both the temporal and spatial scales are logarithmic.

scales of movement. However, the differences probably would not be great (Fig. 10.1a) unless alatae actively take flight, where the differences in scales of movement can be dramatic (Fig. 10.1b), depending on the inclination of the aphid, the altitude individuals attain and the atmospheric motion systems active at the time.

The time it takes an aphid to reach a destination, and the duration of occupancy, provide the range of temporal backdrops for these scales. The duration of occupancy may be transient to alight, probe briefly and move on, or encompass colonization and maintenance at the sink. In a larger temporal scale, spanning seasons of hospitable and inhospitable climate or boom-or-bust resources, metapopulations, or generations of aphids, may also oscillate in space, moving, for example, into previously inhospitable territory after a harsh winter, and later southward as the day length decreases and resources deteriorate. For example, a dramatic epidemic of *Maize dwarf mosaic virus* in Minnesota (USA) was linked to long-distance transport of aphids from the southern states (Zeyen *et al.*, 1987).

Aphid life stages, morphs

Two categories of individual are considered in this chapter: flightless morphs and flight-capable alatae. Thus, we seek to characterize the active mode of intentional displacement rather than the life stages and morphs that are moving. For flightless individuals, there is a single active mode: walking. For flight-capable individuals, there are potentially two such modes: walking and flying. These statements imply that all life stages and morphs walk the same and that all flight-capable morphs fly in the same manner – a faulty assumption.

Petrovskii *et al.* (2011) found that individual aphid dispersal due to walking was generally diffusive in nature, but because the length and duration

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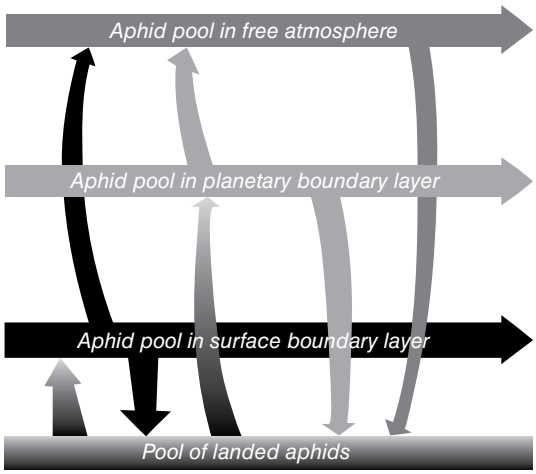

Fig. 10.3. Vertical movement patterns by pools of aphids in the atmosphere. Note that the atmosphere has been divided into three distinct layers; the free atmosphere, the planetary boundary layer and the surface boundary layer. Most long-distance translational movement by aphids takes place in the planetary boundary layer.

of walks vary among individuals, the overall impression was of Lévy flight (a random walk in which the step-lengths had a probability distribution that was heavy-tailed) (Viswanthan *et al*., 1996). Therefore, generalizing behaviour based on individuals can seriously underestimate the dispersal of the aphid population, and thus the rate of colonization or of an epidemic.

Nevertheless, researchers have been able to identify propensities of movement for various life stages. Ferrar (1969) found that aphid nymphs were predisposed to greater interplant movement prior to moulting, particularly during the last instar. Such movement can result in a less crowded and less plant-stressed environment for the next generation; it might also reduce predation and parasitism, because the dispersed aphids would be scattered and less apparent to most natural enemies. A series of greenhouse experiments enabled Zhang (2002) to characterize the walking behaviour of wingless life stages and morphs of *R. padi* (bird cherry–oat aphid). When perturbed by modest wind gusts, or when their host plants were brushed, fewer earlier nymphal instars than later instars or adult apterae tended to move from their hosts. In fact, the more mature the aphid, the farther it tended to move. Furthermore, when testing movement patterns of non-alatoid and alatoid fourth-instar nymphs, no difference was detected in the proportion of individuals that moved or in the distances they walked. Walking aphids may reach plants as much as 13.5 m away from the release point. The walking distances were affected by age (adults versus nymphs) and by environmental conditions (Ben-Ari *et al*., 2015). Interplant movement of aphids is a function of not only the aphid morph but also the season of the year. *Nasonovia ribisnigri* (currant–lettuce aphid) apterae, for example, showed a greater potential to disperse from one plant to another in the spring over such movement in the autumn, independent of population density. During the spring, apterae were thus able to colonize more plants than were winged morphs (Diaz *et al*., 2013).

Winged morphs also differ in movement behaviours. In a series of laboratory studies, Nottingham *et al*. (1991) found that three distinct alate morphs of *R. padi* responded differently to an intermittent resource target during their maiden flights. Autumn-produced gynoparae had a greater initial climb rate than both summer exules and spring emigrants. Gynoparae also flew for a longer period than summer migrants before responding to a resource target, while spring migrants responded after an intermediate time interval.

The Migratory Process

Aphid migration is predicated on innate behaviour and results in directed, undistracted movement (Kennedy, 1985; Dingle, 1996; Irwin, 1999), often culminating in dramatic displacements abetted by atmospheric motion systems (Irwin and Thresh, 1988; Gage *et al*., 1999; Irwin, 1999; Irwin *et al*., 2000; Isard and Gage, 2001). The concepts of 'long-distance' movement and aphid 'migration' are interwoven in the literature and often erroneously considered as synonymous (*cf*. Johnson, 1969; Robert, 1987, for reasons why these are not synonyms). Through a series of laboratory studies that determined when an aphid's flight trajectory could be altered by the presence of resource items (e.g. light of the same wavelength as a potential food source), Hardie (1993) experimentally disentangled the two terms and demonstrated the behavioural distinction between them. 'Long distance' refers to an aphid that has moved far (from several to thousands of kilometres). This movement can be achieved in one of two ways. An aphid can actively seek a resource item during appetitive

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dispersal and encounter atmospheric conditions (e.g. thermals) that propel it upward, where it is then subject to horizontal translocation by atmospheric motion systems (i.e. inadvertent displacement over long distances). The other, more common, way is through the act of 'migration', during which an aphid actively flies towards an ultraviolet light source. It ignores all cues associated with resource items and climbs high into the atmosphere, where it is then positioned to move great distances by the prevailing atmospheric motion systems. Thus, migration is only one, albeit a more common, way in which an aphid can move long distances. Sometimes, the migratory urge does not coincide with favourable atmospheric conditions to promote a take-off angle that will allow successful ascent into the atmosphere, and this can result in rather short-distance dispersal events, demonstrating that not all migratory events end up in long-distance dispersal (Isard and Irwin, 1996; Isard and Gage, 2001).

The migratory process is complex. When an alatoid nymph moults, becoming an adult alata, it may already be physiologically primed to migrate. Such an aphid, given the appropriate environmental setting, will actively ascend into the atmosphere, where it continues flying as the air currents displace it horizontally. The process terminates when the aphid actively begins to descend and land. The migratory process, then, can be delineated by four phases: (i) events leading to take-off; (ii) take-off and ascent; (iii) horizontal translocation; and (iv) events leading to behaviour switching that culminate in descent and landing. Alighting behaviour, which is manifest in descent and landing events, occurs once the migratory process has been switched off and is treated under 'appetitive dispersal' below.

Events leading to take-off

Several factors govern which aphids are able to take flight and when they are able to do so. Migrants will take longer to develop, incur delayed reproductive development, smaller gonads and reduced fecundity as costs of flight (Dixon and Wratten, 1971; Dixon and Kindlmann, 1999; Müller *et al*., 2001). They fuel their flight with sequestered energy reserves (Liquido and Irwin, 1986; Dixon *et al*., 1993). Because aphids that migrate have a low probability of survival (i.e. few migrants find and colonize new hosts), the migratory strategy seems based on the notion that enough will encounter more favourable environments to colonize, reproduce and make up for losses. When aphids are not physiologically primed to take off, they will not voluntarily do so (Dixon, 1977).

Host-plant physiology

The phenological stage and quality of the host plants during the aphid's development are considered primary among environmental factors, but Müller *et al*. (2001) discovered in retrospective examination of the literature that not all species appear to react to the same stimuli. *Myzus persicae* (peach–potato aphid; green peach aphid), in particular, was generally unaffected by host-plant quality, and many of the experiments detailing this subject used *M. persicae* as a model. However, other well-known pest species did not respond to host plant cues, including *Aphis fabae* (black bean aphid) and *Aphis gossypii* (cotton aphid; melon aphid). Common pest species tested that responded to deteriorating host-plant conditions included *Aphis craccivora* (black legume aphid; cowpea aphid; groundnut aphid), *Brevicoryne brassicae* (cabbage aphid), *Macrosiphum euphorbiae* (potato aphid), *R. padi* and *S. avenae* (English grain aphid). In addition, flight apparatus (wing size and flight muscle) of *Tuberculatus quercicola* varied depending on sex and the nutritional quality of host plants. When the nutritional status of *Quercus dentata* deteriorated, the flight muscles of winged females were reduced (Yao, 2012a). Clearly, it is important to know which aphid species react to deteriorating host conditions in targeted cropping systems.

Crowding

Explosive population growth results in severe crowding, which induces alata production and increases the chances of apterae purposefully moving or being jostled off their host plants (Robert, 1987). Although crowding nearly always appears to induce wing production, species are affected differently by the timing of the crowding event, with some species affected only by prenatal crowding, some by postnatal crowding in the first two instars and some by crowding at both stages (Müller *et al*., 2001). Such priming can also precondition the eclosing alatae for flight take-off (Walters and Dixon, 1984; Dixon, 1988).

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Presence of natural enemies

Acyrthosiphon pisum (pea aphid) increases the proportion of winged morphs among its offspring when exposed to foraging predaceous ladybird beetle larvae and adults (Dixon and Agarwala, 1999; Weisser *et al*., 1999; Mehrparvar *et al*., 2013), hover fly (Fig. 10.4) and lacewing larvae (Kunert and Weisser, 2003), or aphidiid parasitoids (Sloggett and Weisser, 2002). Similar results have been obtained with *Uroleucon nigrotuberculatum* (Mondor *et al*., 2004) and *A. gossypii* (Mondor *et al*., 2005). In contrast, neither *A. fabae* nor *Megoura viciae* (vetch aphid) increased alata production when placed in tubes or on plants previously infested with ladybird larvae and conspecifics (Dixon and Agarwala, 1999). With respect to the mechanisms responsible for wing induction in the presence of natural enemies, an early study indicated that a chemical cue contained in ladybird larval tracks caused *A. pisum* to produce more alatae (Dixon and Agarwala, 1999). Aphid alarm pheromone has been shown to play a crucial role in wing induction, both under laboratory (Kunert *et al*., 2005) and field (Hatano *et al*., 2010) conditions. The release of the alarm pheromone, (*E*)-ß-farnesene, by foraging predators or parasitoids reinforces movements in the aphid colony. The resulting increase in the number of physical contacts among individuals leads to the observed increase in winged morph production in the presence of natural enemies, i.e. the 'pseudo-crowding mechanism' (Weisser, 2001; Weisser and Sloggett, 2004; Kunert *et al*., 2005).

Fig. 10.4. *Sphaerophoria scripta*, a male on the stem of a coriander plant. The larvae are common predators of aphids found in lettuce fields and other vegetable crops in the Mediterranean basin. (Original colour photograph by A. Fereres.)

Ant tending

Aphid-attending ants are well known for guarding their aphids from attack by predators and parasitoids in return for honeydew. This otherwise mutualistic relationship is found to influence negatively the likelihood that the attended aphids will disperse. Ant attending may suppress alarm pheromones, which can encourage the production of alatae in *A. fabae* (Tegelaar and Leimar, 2014). Yao (2012b) demonstrated that *T. quercicola* exhibited extremely low dispersal rates when tended by ants, but developed much stronger flight muscles when ants were excluded. Mehrparvar *et al*. (2013) found the ant-attended *Metopeurum fuscoviride* (pink tansy aphid) produced winged offspring predominantly at the beginning of the season, while the unattended *Macrosiphoniella tanacetaria* (tansy aphid) produced winged individuals throughout the season. Tokunaga and Suzuki (2008) showed that movement was greater in the non-ant-attended *A. pisum* than in the ant-attended *A. craccivora*. They concluded that disparity in ant attendance influenced the morphological and behavioural traits that led to differences in aphid dispersal rates. Kindlmann *et al*. (2007) discovered in suction-trap data that ant-attended species began their long-distance dispersal activity significantly later in the season than did non-ant-attended species.

Take-off and ascent

Physiological factors

Alate aphids that are in a migratory mode are physiologically primed to take flight towards an ultraviolet light source (Fig. 10.5). Alatae have a relatively narrow window of time during which they can actively take off and ascend in migratory flight. This window opens within 12 h of the aphid moulting to the adult stage and begins to deteriorate about 2 days later, effectively closing 4 days after moulting to the adult stage (Liquido and Irwin, 1986; Kobayashi and Ishikawa, 1993; Levin and Irwin, 1995; Zhang *et al*., 2008).

The angle of aphid flight trajectories is physiologically regulated by the age of the aphid at take-off. Within a day of becoming adult, winged *R. padi* leave the canopy at a mean angle of 34° above horizontal; between 1 and 2 days old, the angle decreases to 24°; and by 2–3 days, the angle is only half what it was within the first 24 h (Isard and Irwin, 1996; Isard and Gage, 2001). Combined with the wind profile at the

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Fig. 10.5. An alate *Nasonovia ribisnigri* just initiating take-off towards an ultraviolet light source. (Original colour photograph by A. Fereres.)

time of take-off, predictions may be made about the success of alatae of different ages and of their trajectories in enabling ascent into the planetary boundary layer (PBL; atmospheric layer situated above the surface boundary layer and below the free atmosphere). This layer varies in depth with the time of day, from as shallow as 0.3 km above the Earth surface at night to as deep as 3 km during the day (Isard and Gage, 2001). If an aphid flies upward and reaches this layer, it can be translocated long distances along with the horizontal air currents.

Many agriculturally important aphids are in a migratory mode during their maiden flights, at least for a short period (Hardie, 1993). The amount of time an aphid spends in purposeful, unobstructed, upwardly directed flight provides a measure of how high into the atmosphere it can ascend. Ascent rates of aphids in a migratory mode are initially rapid; for example, 20–30 cm/s for *A. fabae* (Kennedy and Booth, 1963) and 22–67 cm/s for *S. graminum* (greenbug) (Halgren, 1970). Voluntary long-distance air transport is probably only achievable during an aphid's maiden flight, both because the rate of climb on subsequent flights is less (Isard and Irwin, 1996) and because the aphid tends to shift sooner from an upward, UV-directed, migratory flight mode to a host-seeking, appetitive mode. This decreases the possibility of entering the PBL and drastically reduces the duration of flights subsequent to the initial one (Kennedy and Booth, 1963).

Atmospheric influences

The nature of the atmosphere directly influences whether an aphid will take off and ascend into the PBL. Two interactive atmospheric forces govern the ability of aphids to take flight and ascend into the PBL. Inertial forces sustain movement of air parcels (i.e. small, cohesive volumes of air) in a horizontal plane and permit aphids within them to move long distances, essentially riding the surrounding air currents. Buoyant forces, both positive and negative, allow air parcels, because of density differences, to move upwards or downwards in a vertical plane. Given the backdrop of a typical warm spring through autumn day, the interaction between these two forces throughout a diel cycle provides windows of opportunity for aphids to ascend and dictates how high they will ascend into the atmosphere. Aphids will not take off voluntarily in the presence of strong winds. But in the absence of these, aphids are much more likely to ascend during times when the buoyant forces are neutral or positive (rising air parcels).

Unstable atmospheric conditions occur during daylight hours as the sun's energy heats the Earth's surface. In turn, that energy warms the air nearest it, which becomes less dense than the air above and begins to rise. The cooler, denser air then descends (negative buoyancy), replacing the warmer, less dense air. This unstable atmospheric situation provides an excellent opportunity for aphids to take off and ascend into the PBL, where they can be moved far by inertial forces. The atmospheric mixing process continues throughout the daylight hours, driven by the solar heating of the Earth, and results in an expansion in the depth of the PBL. As the air parcels rise, however, they are slowed by friction (another force acting on the system) as the vertically moving air parcels are dragged horizontally by inertial forces.

In the transition between unstable (daytime) and stable (night-time) atmospheric conditions, the ratio of buoyant to mechanical forces approaches zero, becoming neutral. This condition generally occurs in the early morning hours after sunrise, or for a shorter period around sunset. Under neutral conditions and when wind speeds are low, aphids primed for long-distance flight can ascend and reach the PBL. Their trajectory when escaping the

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surface boundary layer to the PBL is likely more shallow than that afforded during unstable atmospheric conditions, because buoyancy neither aids (unstable conditions) nor hinders (stable conditions) their ascent (Isard and Gage, 2001).

Interactions of physiological and atmospheric influences

Aphids delay maiden and subsequent flights when wind speeds are high, usually preferring winds closer to their own flight speed of less than 1 m/s (Haine, 1955; Robert, 1987; Kennedy, 1990; Bottenberg and Irwin, 1991); however, adverse wind conditions may delay but not prevent take-off (Walters and Dixon, 1984; Robert, 1987). Mixed cropping systems can form barriers that reduce wind speeds in the shorter crop (Castro *et al*., 1991), allowing aphids to depart more readily than from canopies of uniform height (Bottenberg and Irwin, 1991). Both upper and lower temperature thresholds will inhibit aphid take-off, although these temperatures vary by species and season (Wiktelius, 1981). With the exception of *S. graminum*, which can initiate flight at temperatures as high as 41–42°C (Berry, 1969; Dry and Taylor, 1970; Halgren, 1970), the lower threshold for most species varies between 13 and 16°C (Johnson and Taylor, 1957; Jensen and Wallin, 1965; Dry and Taylor, 1970; Walters and Dixon, 1984; Zhang *et al*., 2008), while the upper threshold is generally around 31°C. Light intensity also affects the likelihood of aphid take-off, with few species ever initiating flight in the absence of light or during moonlight, which is up to 1 lx. According to Robert (1987), take-off usually occurs at intensities greater than 1000 lx, with no apparent upper limit (Berry, 1969).

Horizontal translocation

Differences achieved in horizontal scales of displacement are related directly to the layering of the lower atmosphere (Fig. 10.3). The angle of ascent will determine whether the aphid will succeed in reaching a horizontal transport layer in the PBL. Alatae taking off under unstable atmospheric conditions, whether predisposed to migratory or appetitive flight, are more likely to be transported longer distances than if they initiate flight in stable atmospheric conditions. When conditions are stable, aphids in neither flight mode are able to escape the surface boundary layer and thus are unaided by positive atmospheric forces and cannot be moved long distances (Isard *et al*., 1994; Isard and Gage, 2001). Once attaining the PBL, horizontal transport of an organism is largely governed by the stratification of the wind layers. Meteorological conditions favourable to long-distance transport within the PBL are seasonal in occurrence (Scott and Achtemeier, 1987; Isard and Gage, 2001), setting up migratory opportunities during specific periods of the year (usually spring, summer and autumn) in association with certain types of meteorological events.

The most notable of these events is the 'low-level jet', which commonly occurs in mid-latitudes. These horizontal air currents form after dusk, when the Earth's surface begins to cool, and the PBL begins to stabilize and becomes compressed horizontally with air currents of different speeds and temperatures trapped and stratified within it. It is not known if aphids actively seek out low-level jets or if they are passively concentrated within them. Due to a lack of turbulence from below, these strong, horizontally directed, relatively warm air strata retain the aphids trapped after sundown. These aphids may then be transported great distances before dawn, when the rising sun begins to heat the Earth and mixing deprecates the integrity of the low-level jet; this is when the aphids trapped in those strata begin to descend (Isard and Gage, 2001).

Successful migratory flights, abetted by air currents in which they are embedded (Fig. 10.3), allow aphids to attain a more linear directionality, faster ground speed and, consequently, greater distance traversed than would be possible solely under their own power (Kennedy, 1985). In climates nearer the poles, when night temperatures become too low to sustain aphids in active flight overnight (i.e. flapping their wings and remaining aloft), the aerial transport of aphids seems limited to daytime movements. In climates where night-time temperatures remain relatively warm, overnight transport is common and can result in displacements of hundreds, even thousands, of kilometres (Isard and Gage, 2001). Knowledge of the history of the wind speed and direction of these jets enables researchers to do back trajectory analyses to determine the probable source regions of the migrant populations (Scott and Achtemeier, 1987; Drake and Gatehouse, 1996).

Reynolds and Reynolds (2009) tested a Lagrangian stochastic mechanistic model of aphid flight behaviour to predict the densities and distances travelled of migratory aphids in atmospheric boundary layers with stabilities ranging from almost

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purely convective (no wind shear) to strongly stable. The model predicts that aphid densities diminish with height and that windborne migration of aphids is distinctly different from the aerial dispersal of seeds and wingless arthropods. Therefore, they suggest that the term 'passive', frequently applied to aphid flight, is misleading and should be abandoned, because atmospheric turbulence serves to amplify rather than 'dampen' the aphid's own movements. The same model predicts that aphids aloft within a convective boundary layer can travel as much as 6 km/h downwind, while those aloft within a boundary layer of neutral stability can travel as much as 30 km in a single hour. Once they cease flying, most aphids are predicted to fall out of the atmosphere with a speed close to their fall speed in still air, although a small proportion of aphids can remain airborne for as much as 3 h after they cease flying.

Given the vagaries of weather and of physiological priming, one might presume that migration is a rather rare event. On the contrary, it can be a common, though seasonal, phenomenon, one that at times fills the sky with countless billions of aphids in long-distance transport (Grossheim, 1914; Dewar *et al*., 1980; Irwin and Hendrie, 1985; Marking, 2002).

Switching off the migratory urge

At some point during its journey, although the mechanism is unknown, the aphid's behaviour switches and, in an effort to obtain specific resources, it will be attracted by cues other than ultraviolet light. When that occurs, the aphid ceases its migratory phase and enters an appetitive mode. The timeliness of its success in descending and landing may also depend on meteorological conditions. Those aphids whose transport was abetted by favourable, low-level jet winds may be forced to remain flying until this horizontal transport layer breaks down in the early, post-dawn morning hours, when they can once again perceive landing sites and terminate their flight (Isard *et al*., 1990; Isard and Gage, 2001). When the migratory phase has ceased, the aphids will begin the process of leaving the atmosphere in search of resources, and all future flights appear to be appetitive in nature.

Appetitive Dispersal

Appetitive dispersal encompasses that set of behaviours, other than migration, which span the interval between leaving a host that is deemed undesirable and seeking a host that is desirable. It also encompasses movement to seek a primary host or mate, or even a nearby secondary host after overseasoning (Mackenzie and Dixon, 1991), although Ward *et al*. (1998) estimated that the success rate of *R. padi* finding its primary host can be less than 1%. Our definition of appetitive dispersal includes the causal mechanisms for leaving and settling, as well as those of the dispersal event. Thus, appetitive dispersal must take into account both the stimuli that cause aphids to leave their feeding position on a plant and the cues that motivate them to cease their searching for a new feeding position or mate.

Stimuli that cause aphids to disperse in an appetitive manner

Extrinsic cues that stimulate aphids into an appetitive dispersal mode might be host-plant mediated or physical in origin, and could result from natural perturbations or crop management practices. Appetitive dispersal may even occur without any apparent external stimulus; alternatively, it might result from an innate strategy to make the best use of plant resources (Hodgson, 1991). Appetitive dispersal often occurs at the smallest scale herein considered, on a single plant, where an aphid might walk from one part of a plant to another to escape undesirable weather conditions, crowding, or natural enemies. However, this displacement mode includes plant-to-plant dispersal within fields, and even encompasses short duration, field-to-field movements via walking or flight.

Physical mechanisms

Aphids residing in agricultural fields may be inadvertently displaced. Mostly circumstantial evidence suggests that this sort of displacement is rather routine. Farm machinery passes through a field and brushes against an aphid or vibrates the plant on which the aphid resides (Ferrar, 1969; Schotzko and Knudsen, 1992; Bailey *et al*., 1995). Raindrops pelt an aphid directly or hit the plant, jarring the aphid from the plant (Zúñiga, 1985), or gusts of air lift and propel an aphid from an exposed plant part (Schotzko and Knudsen, 1992; Bailey *et al*., 1995; Mann *et al*., 1995). Once dislodged, the aphid either falls to the ground, where it then dies or rights itself and walks to a new (or the original) host plant, or if an alata, begins to flap its wings. If in the proper

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physiological mode, it then ascends in active, controlled flight. Thus, if not incapacitated, an inadvertently displaced aphid invariably switches to an intentional displacement mode by seeking a host plant to recolonize or by fleeing a perceived threat. Intentional displacement, that is, purposeful movement from one site to another, emanates from other environmental and agriculturally related cues, including, but not limited to, light intensity, light spectrum (Ben-Yakir *et al*., 2012; Legarrea *et al*., 2012), day length, temperature, humidity, crop canopy structure (Bottenberg and Irwin, 1992a,b) and plant density (Bottenberg and Irwin, 1992b).

The results of research into displacement responses to physical perturbations by nymphs, adult apterae and alatae appear inconsistent. The contrasting results may be, in part, a reflection of the inherent differences in the aphid species being studied. Inconsistencies in the relative magnitude of the influence remain controversial. As an example, according to Mann *et al*. (1995), increased wind duration extends the average distance apterous *S. avenae* walk; similarly, when these aphids were exposed to gentle gusts of air, they travelled less than when exposed to steady wind or strong gusts. However, while conducting a series of wind experiments, Zhang (2002) found that intensity and duration had little differential effect on the movement of *R. padi*. Indeed, almost all aphid movement ceased until the wind had subsided, and the proportion that moved and the mean distances they travelled after wind cessation were influenced neither by wind intensity nor duration.

Regulated precipitation events provide another example of inconsistent results among studies. Mann *et al*. (1995) concluded that increased duration of a precipitation event correlated positively with an increase in the proportion of dislodged and displaced apterous *S. avenae*. Also, under heavy precipitation, the proportion of *S. avenae* dislodged and the distances they travelled were greater than when exposed to a drizzle or light rain. Under regulated precipitation events that were perhaps less extreme, Zhang (2002) found that apterous *R. padi* remained on the plants throughout the precipitation event, and both Bailey *et al*. (1995) and Zhang (2002) found that, once the precipitation event had ceased, similar numbers of apterae left the plants and, irrespective of the intensity or duration of the event, travelled about the same distances.

Zhang (2002) also found that although the intensity and duration of physical perturbations each influenced dispersal, neither was able to influence movement patterns once a disturbance threshold was reached. These findings comparing brushing, wind and precipitation events suggest that physical perturbations affect the numbers of *R. padi* that move, and the distances they travel, to similar degrees up to a peak movement threshold.

Host-plant influences

Biotic stimuli that cause aphids to move are frequently initiated by changes in host-plant quality (Hodgson, 1991; Bailey *et al*., 1995; Zhang, 2002), including differences in plant structure and changed plant chemistry, the latter often attributed to plant stress (Haile, 2001). Direct, as well as indirect, factors can modify plant quality. Direct factors include relative host preferences; that is, which plants and their cultivars are less preferred and thus abandoned more readily by an aphid (Ferrar, 1969; Zhang, 2002). Both chemical and physical attributes of plants can cause this exodus. Physical attributes include plant architecture (Hodgson and Elbakheit, 1985), hairiness (Gunasinghe *et al*., 1988; Irwin and Kampmeier, 1989), leaf waxes (Powell *et al*., 1999), leaf colour (Döring *et al*., 2009) and the availability of desirable feeding sites (Kobayashi and Ishikawa, 1993, 1994).

Aphids can be prone to abandon one plant species more readily than they do another, perhaps due to physical or chemical plant differences. Zhang (2002) found that late-instar nymphs and adult apterae of *R. padi* abandoned a wheat plant more readily than either oats or barley, but that the numbers that relocated from three distinct cultivars of oats were similar. Likewise, aphids might abandon their host plant more readily during different times of the plant's life cycle. As plants mature and senesce, a mass exodus of aphids often occurs, presumably signalled by changes in plant chemistry (Parry, 1978; A'Brook, 1981).

Indirect factors that alter plant chemistry are brought about by plant stresses such as drought (Bailey *et al*., 1995; Haile, 2001; Zhang, 2002), infection by plant pathogens (Bailey *et al*., 1995; Fereres *et al*., 1999; Zhang, 2002; Fereres and Moreno, 2009), plant injury (Irwin and Thresh, 1990; Delaney and Macedo, 2001) and aphid crowding (Kidd, 1977; Hodgson, 1991; Bailey *et al*., 1995; Zhang, 2002). Bailey *et al*. (1995) investigated the impacts of drought and crowding on the movement of nymphal and adult apterous *R. padi* under greenhouse conditions and

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found that, although these indirect biotic factors tended to increase the movement of aphids, the differences between treatments were minimal and often insignificant. These results differed from those obtained by Zhang (2002), who found that the numbers of nymphs and apterous *R. padi* that relocated were considerably higher when perturbed by crowding, followed closely by drought, but that aphids travelled farther from the original host plants when these plants were subjected to drought rather than to crowding. The results of both Bailey *et al.* (1995) and Zhang (2002) indicated that host-plant-induced disturbances were generally not strongly differentiated from physical perturbations. Furthermore, their results suggested that the number of *R. padi* that moved and the distances they traversed after colonizing *Barley yellow dwarf virus*-infected hosts were similar to distances moved when colonizing hosts that were non-infected. This indicates that virus infection may not be a factor in relocation for this species.

Natural enemies and alarm pheromones

Aphids have evolved many behavioural defences in response to selection pressures exerted by predators and parasitoids (Klingauf, 1967; Gardner *et al.*, 1984; Dixon, 1988; Gerling *et al.*, 1990). Although coating natural enemies with fluids released from the siphunculi works well against small predators, the most effective reaction to both predators and parasitoids is escape, either by walking from the feeding site or by dropping or flying from the host plant (Dixon, 1958; Klingauf, 1967; Stadler *et al.*, 1994; Weisser, 1995). Such escape reactions do not require direct contact with the predator; they may also be initiated in response to direct communication among conspecific aphids by means of aphid alarm pheromones (Montgomery and Nault, 1977a,b, 1978; Roitberg and Myers, 1978a; Wohlers, 1981; Gut and van Oosten, 1985; Shah *et al.*, 1999; Chapter 8, this volume). Aphids also respond to visual, tactile and vibrational cues associated with the presence of natural enemies on a plant (Klingauf, 1967; McAllister *et al.*, 1990; Losey and Denno, 1998b; Braendle and Weisser, 2001)

The dislodging of aphids by predators has been shown in many studies (Roitberg *et al.*, 1979; McConnell and Kring, 1990; Sewell *et al.*, 1990; Minoretti and Weisser, 2000), leading almost always to emigration from the host plant, except when dislodged aphids fall into leaf axils or onto leaves (McConnell and Kring, 1990). In *A. pisum*, a certain proportion of aphids that walk away from the feeding site also walk from the host plant, and some individuals that at first escape by walking, drop off the plant after a few steps (Minoretti and Weisser, 2000; Braendle and Weisser, 2001). The numbers of aphids emigrating from host plants often exceed the numbers being killed by predators (Fig. 10.6; Minoretti and Weisser, 2000). For *S. graminum*, the numbers dislodged for each individual consumed by adult *Coccinella septempunctata* (7-spot ladybird) ranged from 1.8 to 7.2 in experiments over a wide range of aphid and predator densities (McConnell and Kring, 1990).

Foraging parasitoid wasps also cause aphids to drop or walk from the host plant (Tamaki *et al.*, 1970; Gowling and van Emden, 1994; Weber *et al.*, 1996). In addition, aphids parasitized by braconid wasps generally are more mobile (Weber *et al.*, 1996) and are more likely to drop from the plant when encountered by a predator (McAllister and Roitberg, 1987; McAllister *et al.*, 1990). Parasitism can also affect the wing development and flight behaviour of some aphid species. Even though all *A. glycines* (soybean aphid) fourth-instar alatoid nymphs parasitized by the small wasp, *Aphelinus varipes*, eclosed as normal alatae, only 35% of the third-instar alatoid nymphs produced normal winged adults. However, the flight performance of adults declined sharply when parasitized as fourth-instar alatoid nymphs 72–96 h prior to being tested (Zhang *et al.*, 2009).

Several studies have quantified the effects of natural enemy action on aphid distribution at a larger spatial scale. In arenas with several host plants, the presence of predators resulted in significant dispersal and a more even distribution of aphids among plants (Niku, 1975; Roitberg *et al.*, 1979; Sewell *et al.*, 1990; Bailey *et al.*, 1995). In a more recent study, Claflin *et al.* (2015) found that predation, host-plant abundance and plant spatial distribution interactively affected aphid distribution and virus prevalence. They also found that when increasing the number of vector non-host plants in the experimental arena, the distance and frequency of aphid movement were increased.

In the field, aphids walking on soil between plants may be exposed to additional biotic and abiotic mortality factors (e.g. ground predators, high ground temperatures) as they search for a new host plant (Roitberg and Myers, 1979; Losey and Denno, 1998a). Even though a large proportion

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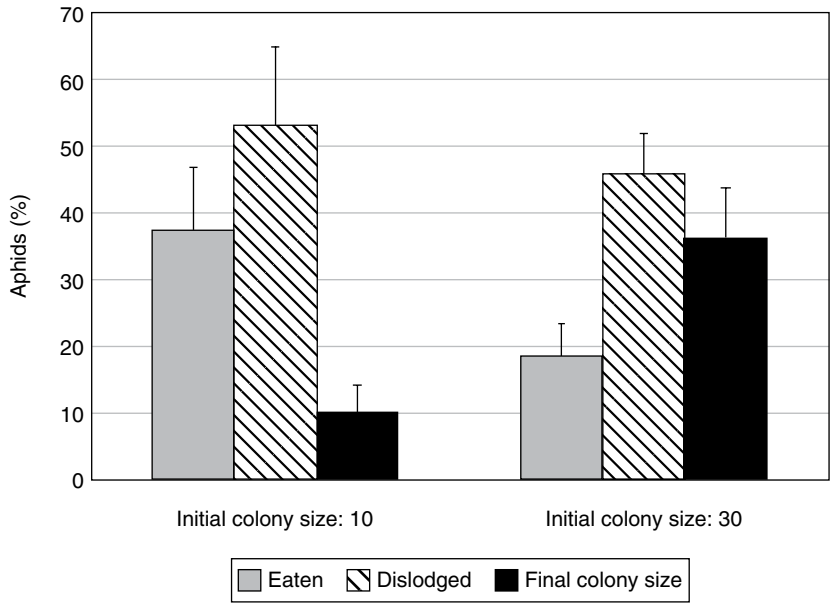

Fig. 10.6. Fate of aphids after a *Coccinella septempunctata* foraged on a broad bean (*Vicia faba*) plant. Initial colony sizes were 10 or 30 aphids when a ladybird with standardized hunger level (fed until satiation, then starved for 24 h) was introduced to the plant. Colonies consisted of a predetermined mixture of instars. The ladybird was free to leave the plant whenever it wanted and was observed continuously. Sample sizes were 6 (10-aphid colonies) and 8 (30-aphid colonies). Shown are means + SE. (Redrawn from Minoretti and Weisser, 2000.)

of aphids walking on the ground may die before settling on a new plant, evidence suggests that predators positively affect both aphid redistribution and the spread of aphid-borne plant pathogens under field conditions (Niku, 1972; Roitberg and Myers, 1978b; Annan *et al*., 1999). Annan *et al*. (1999) observed a positive correlation between the rate of within-field spread of *A. craccivora* and the incidence of natural enemies in cages placed in cowpea fields, but a number of other factors such as wind speed also influenced aphid dispersal. When estimating the effects of natural enemies on aphid populations in the field, both their positive effect at reducing aphid numbers and their effect on aphid dispersal and the subsequent spread of plant viruses need to be taken into consideration. Long and Finke (2015) found that the presence of predators reduced the prevalence of *Cereal yellow dwarf virus* because predators stimulated greater plant-to-plant movement of its vector, *R. padi*, which likely diminished vector feeding time and reduced the transmission efficiency of this persistent pathogen. They found that the reduction in disease incidence was not due to the suppression of aphid vector populations by predators but rather to the risk-avoidance behaviours of vectors.

Response to multiple perturbations

When a chemical (e.g. a herbicide) that is not directly toxic to the aphid is applied to a field, the aphids that have colonized the crop are subjected to two independent types of perturbation, those related to the direct physical act of chemical application and those related to indirect changed host-plant chemistry as a consequence of chemical absorption or adsorption by the plant. Studies by Bailey *et al*. (1995) and Zhang (2002) determined that the application of such chemicals resulted in movement to the same degree and in the same manner as did the act of physically brushing colonized plants. This led Zhang (2002) to a series of interactive experiments that compared movement under single and multiple perturbation scenarios and concluded that there was no interaction between perturbations; aphids simply moved in accordance with the most potent of those multiple stimuli.

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Landing and alighting cues

Many abiotic processes can account for undirected deposition of aphids, including the subsidence of convection currents, turbulence and rain (Isard and Gage, 2001). Generally, however, if aphids do not actively flap their wings, for example when totally exhausted (Irwin and Hendrie, 1985), gravitational forces will take over and the aphids will descend. When aphids terminate migratory behaviours, losing their attraction to short wavelength and ultraviolet (UV) light (Robert, 1987) and responding to cues that elicit what Hardie (1989) calls 'attack flight', they begin to act similarly to appetitive dispersers and are governed by the cues of potential host plants. Favret and Voegtlin (2001) examined the landing preference of alate aphids that were not native to the crop or natural habitat in which they landed. In studies that spanned 4 years in one location with row-cropped (soybean or maize) agriculture and restored prairie, more species and greater numbers of aphids landed in agricultural plots than in the nearby natural habitat. In a second location monitored for 3 years, again with similar agricultural plots but this time within a wooded area, migrant aphids once again landed more frequently in row-cropped agriculture each year. Clearly, cues to land are not random, and the preference for landing in agricultural fields has significant implications for the spread of non-persistently transmitted viruses.

Observations on the numbers of aphids alighting in habitats lacking potential host plants suggest that discrimination of hosts from the air has less to do with chemical than with visual cues (Fereres *et al*., 1999). Aphids are attracted to the shape, size and colour of a landing target (Kennedy *et al*., 1961; Fereres *et al*., 1999), and seem especially attracted to edge effects (A'Brook, 1968; Schultz *et al*., 1985). Landing aphids tend to respond to certain colours, particularly those reflecting strongly in the yellow-green wavelengths (520–580 nm) (Robert, 1987; Fereres *et al*., 1999; Kirchner *et al*., 2005), and many species are sensitive to saturated yellow colours (Broadbent, 1948; Moericke, 1955; Kennedy *et al*., 1961). The plants on which they alight may or may not be potential hosts; the discrimination appears to be sensed after landing and probing (Kring, 1972), or perhaps within centimetres of landing, in a 'sniffing' behaviour described by Kennedy *et al*. (1961). Wu *et al*. (2004) highlight Chinese research on *A. glycines*' attraction to soybean plants by odour. The visual, olfactory and gustatory stimuli involved in aphid host-plant-finding behaviour have been reviewed by Pickett *et al*. (1992), Powell *et al*. (2006) and more recently by Döring (2014).

The density of vegetation and its proportion in relation to bare ground are other factors that influence landing rates (A'Brook, 1968; Irwin and Goodman, 1981; Schultz *et al*., 1985; Kring and Kring, 1991). For most pest species, *Aphis spiraecola* (spiraea aphid or green citrus aphid) being a notable exception (Halbert and Irwin, 1981), the amount of ground cover present is inversely proportional to aphid landing rates. Thus, aphids are often more attracted to young or widely spaced plantings (Kennedy *et al*., 1961; Smith, 1976; Halbert and Irwin, 1981; Irwin and Kampmeier, 1989; Irwin *et al*., 2000), or will infest margins more readily before the interior of fields. Barriers such as windbreaks, hedgerows, forested areas and mixed cropping of plants of different heights (Kenny and Chapman, 1988; Irwin and Kampmeier, 1989; Bottenberg and Irwin, 1991, 1992a,b; Hooks and Fereres, 2006) can increase the number of aphids landing on the leeward side of such obstacles. This skewed distribution of landed aphids is hypothesized to result from both the behavioural attraction to these contrasts (Robert *et al*., 1976) and the enhanced physical control over flight direction as the aphids approach a barrier (Isard and Gage, 2001).

Incorporating Aphid Movement into Pest Management Strategies

The implications of aphid movement for the quality and quantity of harvestable products vary considerably among crops, with impacts resulting from interactions between the immigrating aphids and the crop on which they alight. Also of importance are the timing of the landing events relative to crop phenology, the aphid's reproductive potential, its abilities to transmit viruses to the crop, the residence time of the aphid on the plant and in the field, the types and impact of viruses it may transmit and the rates of ensuing virus epidemics. Aphid movement patterns and the potential implications of those patterns at multiple scales (Fig. 10.2) are requisite sets of information when considering the control of aphids within an integrated pest management (IPM) programme. Where aphids are potential pests, either in their own right or as vectors of plant viruses, crop, cropping systems-based,

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landscape-scale, area-wide and ecoregional IPM packages should consider incorporating components to manage aphids and to track their movements.

Knowing the pest status of aphids that are found within agriculturally cropped settings is enormously valuable when considering how to manage them. Aphids entering a field and landing on a crop can be placed conveniently into one of four categories, depending on the relationship between the aphid's colonizing potential and the way it is apt to damage the crop:

- A transient non-vector – a species of aphid that alights on a crop, cannot colonize it and lacks the potential to transmit viruses to it.
- A transient vector – a species of aphid that alights on a crop, is incapable of colonizing it but is able to transmit viruses that can infect it.
- A colonizing non-vector – a species of aphid that alights on a crop, can colonize it but is incapable of transmitting viruses to it.
- A colonizing vector – a species of aphid that alights on a crop, can colonize it and has the potential to transmit viruses to it.

These four categories of alighting aphids impact the crop in different ways and call for differing management practices.

Components of IPM programmes

Three functional components, fundamental, tactical and strategic (see Irwin, 1999), delineate the stages necessary to develop and hone an IPM programme. These same components are essential for managing aphids that are potential pests.

Fundamentals

To manage aphids, no matter what the crop or cropping system or the scale of the endeavour, the identity of the species that alight and the biologies of those that can colonize the crop or transmit viruses to it are fundamental. Species identification is no easy task given that, in a number of agricultural regions worldwide, often more than 40 (Halbert *et al*., 1981) and as many as 80 (M.E. Irwin and G.E. Kampmeier, unpublished results) species of aphid can alight on plants within an annually cropped field in temperate climates in most growing seasons.

There are apt to be no more than 4 or 5 aphid species that colonize any given crop in a particular area of the world, and fewer than 35 species that are confirmed vectors of any of the viruses known to infect that crop. This renders the task of identification considerably less arduous, because it narrows the potential list of species that need to be determined to a more manageable few dozen, which will likely differ by both crop and region. Blackman and Eastop (2000) can aid in determining whether any of the identified aphid species are potential colonizers or vectors of viruses capable of infecting the crop(s).

The choice of sampling schemes can be key because they supply basic qualitative and quantitative information needed to execute an IPM programme successfully (Chapter 16, this volume). Sampling schemes for aphids most often reflect components of their population dynamics within the crop (e.g. Heathcote, 1957a,b; Heathcote *et al*., 1969; Irwin, 1980). Other schemes provide evidence of the aerial diversity and density of alate aphids at specific heights above the ground (Johnson, 1957a,b; Taylor, 1977; Isard *et al*., 1990, 1994), while still others document landing rates that point to aerial movements into and within fields (e.g. Irwin, 1980; Irwin and Ruesink, 1986; Raccah and Irwin, 1988; Nebreda *et al*., 2004). It is also important to consider where the sampling takes place. Visually monitoring primary hosts, for instance, can help predict the probability of significant outbreaks of aphids in small grains in England (Leather and Walters, 1984). Each of these sets of sampling or monitoring schemes provides complementary information about aspects of aphid biology and management.

Those schemes that emphasize population dynamics can help predict the potential direct damage caused and measure the impact of persistently (and semi-persistently) transmitted viruses vectored by those species of aphid that colonize the crop. Those methods that monitor aerial densities, particularly where the sampling devices are situated at a considerable height above the ground (i.e. those positioned within the PBL) provide a measure of long-distance aerial transport. Those that emphasize alighting within the crop canopy provide information pertinent to the indirect damage aphids can cause as vectors of both non-persistently and persistently transmitted plant viruses, i.e. information useful to help forecast rates and timings of virus epidemics.

Suction-trap networks, operated to monitor aerial densities of aphids within the PBL, are used widely in many parts of the world (Chapter 16,

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this volume), particularly with a view to helping forecast incoming infestations of aphids in fields of small grains, potatoes, sugar beet and soybeans. Assuming the traps monitor within the PBL, reasonable data on numbers, sexes, morphs and species determinations are all possible products of this type of sampling scheme. Within this context, these networks are capable of helping to determine when, and in what numbers, various species of aphid are moving within the atmosphere over fixed land targets. However, because the collecting orifices of these traps are at a static height, and because the PBL is dynamic, shifting in height and depth with time of day, it is probable that the traps capture aphids within the PBL only some of the time. Also, because the insects are usually concentrated within specific parts of the PBL, some of the time the traps are sampling appropriate areas and some of the time they are not. Thus, it is difficult to describe the density characteristics of the taxa sampled by such trapping networks. Recent aphid dispersal modelling efforts suggest, however, that suction-trap data can provide a proxy for aphid colonizing rates in the field. Fabre *et al.* (2010) developed a hierarchical Bayesian model by fitting long-term data from eight suction traps located in north-western France with densities of winged morphs of *R. padi* colonizing barley fields in the autumn. This model predicts aphid crop colonization based on suction-trap count data; in this case, a reliable alternative to crop sampling.

Tactics

Tactics are practices that can help reduce the threats posed by pests to crops. Those practices available for managing aphids usually can be placed into one of five groupings: chemical control, biological control, host-plant resistance, habitat manipulation and legal control (note that genetic control is woven into the fabric of several of these groupings). These tactics are discussed below in relation to how they are affected by aphid movement.

Chemical control (Chapter 18, this volume) entails the introduction of chemically based compounds that kill or alter the behaviour of pests. Some juvenile hormones and ecdysone inhibitors can retard aphid development so that movement potential is restricted (Tamaki, 1973; Kuldova *et al.*, 1998) or flight is prevented in morphs that possess normally developed wings and flight muscles (White and Lamb, 1968). Although pesticides are not the best solution for the long-term control of aphids, intervention at critical points in the growing season may prove successful in stalling or reducing movement. In cropping systems where aphids are not the sole pests of interest, regular and frequent pesticide applications can cause pests, including aphids, to become resistant (Chapter 19, this volume), allowing pest populations to expand rapidly. Moreover, slower-acting pesticides agitate aphids, causing them to move more readily, increasing the likelihood that they will spread non-persistently transmitted viruses to new plants before becoming incapacitated (Irwin and Kampmeier, 1989; Collar *et al.*, 1997; Irwin, 1999).

Biological control (Chapter 20, this volume) lowers populations of pests by introducing, augmenting, or inundatively releasing the pests' natural enemies, e.g. pathogens or their by-products, predators, or parasitoids. Classical biological control, for example using introduced parasitoids to control the invasive *Therioaphis trifolii maculata* (spotted alfalfa aphid) (Schlinger *et al.*, 1959a,b), if at the source and not the sink, can retard aphid build-up successfully and therefore diminish their collective movement to a sink. This may reduce virus problems resulting from aphid movement. *Aphidius colemani* has the potential to reduce in the long term the spread of both non-persistently and persistently aphid-transmitted plant viruses (Dáder *et al.*, 2012). Over the short term, however, certain aphid–parasitoid combinations may result in the increased transmission and spread of non-persistent viruses (Hodge *et al.*, 2011).

Host-plant resistance (Chapter 22, this volume), an effective measure for the long-term control of pests, deploys crop cultivars that are resistant to colonizing aphids, deters aphids from landing or probing, or provides protection from the viruses they carry (Gunasinghe *et al.*, 1986, 1988; Martin *et al.*, 2003). In theory, the restlessness of aphids on resistant plants might be expected to increase the spread of non-persistent viruses, but this is not borne out in practice.

Habitat manipulation (Chapter 21, this volume) is perhaps the most versatile and potent of the tactics available for managing aphids and their movement. However, employing it requires considerable knowledge of the cropping systems, including the aphids and viruses they transmit, and it is undoubtedly the most complex and difficult of the tactics to execute properly. Habitat manipulation may be key to making a crop less attractive or

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unapparent to both transient and colonizing aphids (Irwin *et al*., 2000). Species of aphid that are potentially damaging to crops often fly in large numbers and alight in fields during specific, predictable times of the season (A'Brook, 1981). Because aphids alight preferentially on isolated plants and, whenever possible, avoid alighting on closed or nearly closed canopies (A'Brook, 1968; Irwin and Kampmeier, 1989; Irwin *et al*., 2000), selecting planting dates and planting densities that provide the greatest canopy cover during peak flight periods can stave off colonizers and transients alike. Narrower row spacing can reduce the time between sowing and canopy closure significantly, rendering plants less attractive much sooner (Halbert and Irwin, 1981; Harvey *et al*., 1982). The incidence of both non-persistently- and persistently-transmitted plant viruses was much lower under current commercially used close-row spacing than under wider in-row spacing of potato crops (Davis *et al*., 2015), probably because lower plant densities enhanced aphid landing rates. Reflective surfaces and coloured mulches can also help reduce aphid landings (Smith and Webb, 1969; Kring, 1972).

Locating newly planted fields upwind of and away from the flight pathways of aphids emigrating from older, senescing crops that are apt to harbour them and the viruses they transmit is another way to avoid infestations and restrain virus epidemics. Exclusion covers can keep aphids from landing on and colonizing crops or spreading viruses within fields and, because of the added costs, are especially effective in fields planted to cash crops such as peppers (Avilla *et al*., 1997). Trap crops that are planted more sparsely or are sown later in the season than the main crop can help lure aphids, diverting them from a valued field. Barrier crops are modified trap crops that can be used as natural sinks for viruses transmitted in a non-persistent manner. Once viruliferous aphids land and probe on the virus-immune barrier crop, they lose most of their virus charge, and their ability to spread the virus to the susceptible crop is reduced significantly (Hooks and Fereres, 2006). Moreover, on a landscape scale, multiple cropped systems may provide greater biodiversity, different microclimates (Castro *et al*., 1991, 1992), non-virus hosts and barriers that can influence movement in the canopy, resulting in altered landing and colonization rates (Bottenberg and Irwin, 1992b). The use of banker plants provides a very good opportunity to enhance the biological control of aphids in both enclosed (Jandricic *et al*., 2014) and outdoor (Nakahira *et al*., 2012) crops.

Legal control measures are usually enacted on a scale larger than that of a single field. When growers look beyond their own fields for sources of aphids and disease, communication through local or regional networks and cooperation among growers on an area-wide or regional basis provide important tools (Giles *et al*., 2008). When government agencies or regional grower associations decide that measures beyond providing information and communication are necessary, policies that range from quarantine to mandated land- and water-use practices might be introduced. The foundations of the temporal and spatial aspects of these measures must be based firmly on knowledge of aphid movement. They are enacted for the common good of the growers of the area covered and for consumers and society at large. Although legal controls inevitably restrict individual freedoms, such measures are particularly applicable to highly mobile pest species, including agriculturally important aphids and the viruses they carry.

The strategic component

An IPM programme is ultimately founded on a strategy, the spatial integration and timely deployment of carefully selected, compatible tactics. Many IPM programmes are based primarily on remedial measures. Under such programmes, active sampling plans are used to monitor the densities of various pests, and when they exceed economic injury levels (i.e. pre-established thresholds), they signal that some tactic or set of tactics should be implemented to reduce pest populations to levels below established thresholds. Of the five classes of tactics described above, only biological, chemical and legal controls normally function in a remedial mode, and remedial IPM is often most appropriate for managing aphids that fall into either the 'colonizing non-vector' or 'colonizing vector' pest status category, because this mode can lower population levels. In situations where an aphid species is potentially carrying viruses, population reductions cannot always occur before the targeted aphids are able to spread the virus. Thus, practices to manage populations of aphids that transmit viruses into and within a field, by either transients or colonizers, should be anticipated and initiated before the crop is planted. Remedial IPM is generally ineffective for managing transient aphids.

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Preventative measures attempt to contain potential pests before they become actual pests by anticipating and intervening to thwart their build-up. When protecting annual crops, preventative measures are almost always invoked before the crop is planted. Each of the five tactical categories can be executed in a preventative manner. Preventative IPM can alter an aphid's potential to move, the way it moves, its alighting behaviour and its subsequent rate of increase.

Strategies need to be scaled to the movement potential of the target pest. If the focus is on colonizing non-vectors that move mainly within a field or between fields, a field- or landscape-scale circumscription is adequate. If, however, the aphid is migratory and capable of moving great distances, the IPM programme should be robustly large scaled, even ecoregional, in circumscription (Irwin, 1999).

The larger the programme circumscription, the more anticipatory it must be. Large-scale programmes should incorporate approaches that envisage the timing and abundance of pest influxes, including the use of predictive models that can forecast the movement, direction, distance and timing of key aphid species. Much research has gone into developing simulation models of aphid movement (Taylor *et al*., 1979; Stinner *et al*., 1983; Ruesink and Irwin, 1986; Scott and Achtemeier, 1987; Kendall *et al*., 1992; Leskinen *et al*., 2011; Macfadyen and Kriticos, 2012). To date, however, few predictive models have been developed, and the success of forecasting aphid displacements is limited (Chapter 16, this volume).

Outbreaks of aphid pests originating from afar (Hodson and Cook, 1960; Wallin *et al*., 1967; Wallin and Loonan, 1971; Kieckhefer *et al*., 1974; Zeyen *et al*., 1987; Pedgley, 1993; Schmidt *et al*., 2012) can be unexpected and explosive. Yet, of the few forecasts that currently exist to alert growers to the timing and density of influxes of key aphid species into areas downwind of a source (Chapter 16, this volume), the IPM strategies being developed are grappling with ways to take full advantage of those forecasts. To attune the management strategy better, tactical activities to reduce populations or alter the timing of alatae production need to be initiated at the source areas, so that flight activities are suppressed and flight timings offset from particularly vulnerable stages of the crop being protected.

Predictive models depend on coupling atmospheric motion systems, especially those of the PBL, with the maiden take-off timings of alatae, thus linking source areas with sinks and vastly expanding the area under scrutiny. Such anticipatory models require greater knowledge of the population dynamics of aphids at their sources than at their sinks. This highlights the importance of research aimed at pinpointing the source areas of aphids that might move into areas of concern.

The source area of an aphid in flight or alighting in a field is probably one of the most difficult pieces of the movement puzzle to decipher, let alone predict. Radar has been used to detect aphids (Hendrie *et al*., 1985; Irwin and Thresh, 1988; Leskinen *et al*., 2011) and aphid predators (Jeffries *et al*., 2013) in the atmosphere. However, unlike the radar signature of larger insects such as locusts and moths, that of aphids is less reliable, and the identity of the species flying cannot be ascertained without directly sampling them in the atmosphere. Aircraft-mounted sampling devices (Glick, 1939; Berry and Taylor, 1968; Isard *et al*., 1990; Hollinger, *et al*., 1991) can provide a quantitative measure (numbers per volume of air sampled) of aphids that can be identified, and some of the more sophisticated systems can provide data on the height at which they are flying (Hollinger *et al*., 1991).

Mapping the meteorological features and where in the atmosphere aphids are located is only part of the puzzle in determining the possible sources of migrants. Calculating the flight energy reserves to match the amount of time spent in active flight from a source to a sink (Cockbain, 1961; Liquido and Irwin, 1986; Irwin and Thresh, 1988) provides information on the amount of time the aphid is airborne. This, coupled with the trajectory, provides a rough approximation of source area. Matching specific genetic markers of various species of aphid from a sink with population markers obtained at many potential sources is another, independent, way of determining potential source areas (Steiner *et al*., 1985; Voegtlin *et al*., 1987; Chapter 3, this volume). This complementary set of procedures provides a powerful tool for developing predictive models of source areas of immigrants.

Categories of aphids as agricultural pests

The unique aspects of managing each of the aphid pest categories mentioned earlier involve all three components of an IPM programme: fundamental, tactical and strategic.

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Transient non-vectors

On any given day, vast numbers of transient aphids can enter a field, land on a myriad of plants while moving through it, and make their way out of the field. These transients go undetected with sampling schemes that emphasize visual inspection of population dynamics in the field and aerial densities. Aphids that are transient in a field and do not transmit viruses to that crop will not impact the crop's potential harvest negatively, even though they might be extremely numerous. This category often has the highest numbers of aphid species in the field at any given time. Therefore, their presence, when detected by IPM practitioners and crop managers, can spur growers to take remedial action unnecessarily, e.g. apply pesticides. As a result of this action, production costs can increase, side effects can impact human health negatively and other management practices can be severely disrupted. Aphids in this category, once identified and properly categorized, should be left alone. They are not true pests, at least of the crop being monitored.

Transient vectors

Transient vectors pose a serious threat to crops because, as they repeatedly alight, probe and fly across a field, they are capable of rapidly spreading debilitating, non-persistently transmitted viruses. In many crops, potential vectors of these viruses are, for the most part, inadequately known, making the pest status categorization of those species problematic. Methods to test aphids for their potential to transmit non-persistent viruses are provided by Irwin and Ruesink (1986), Raccah and Irwin (1988) and Chapter 15, this volume. Slightly modified versions of these same methods can also aid in determining the vectoring potential of persistently and semi-persistently transmitted viruses (e.g. infectivity index, Plumb, 1986).

Because transient aphids often go undetected, growers can be taken by surprise when non-persistent virus epidemics sweep through fields and across the landscape in a matter of days, devastating the crop and, if poorly timed, severely reducing its potential yield. By the time the epidemic has been detected, the damage will have already occurred.

Monitoring aphid movements into and within fields cannot provide information useful for curtailing non-persistent virus epidemics. Liquid-filled pan traps, especially those that are neutral with respect to crop canopy colour (Irwin, 1980; Irwin and Schultz, 1981), provide valuable data for quantitatively tracking the movement of aphids, by species, into and through a field (Irwin and Ruesink, 1986; Raccah and Irwin, 1988). These monitoring devices aid researchers in developing simulation models of aphid movement relative to chronological occurrence, crop phenology, crop canopy closure and virus epidemics. Models (Ruesink and Irwin, 1986) can also help in understanding and predicting yield reductions attributable to virus epidemics resulting from aphid movement into and within the crop.

Theoretically, non-persistent virus epidemics can best be avoided by altering the aphids' time of appearance, controlling their frequencies of alighting, using virus-resistant genotypes and by intercropping. Non-persistent virus epidemics can be managed through tactical measures enacted at either the aphids' source (i.e. where they mature) or at their sink. No matter where the measures are to be applied, they must be enacted in a preventative manner, before the crop is planted and well before the aphids can be detected by any sampling scheme placed at the sink.

Most pesticides are slow acting and unable to control transient aphids. The application at the sink of quick-acting contact pesticides, such as synthetic pyrethroids, on the one hand might increase, like slow-acting pesticides, the spread of non-persistently transmitted viruses by increasing the likelihood that viruliferous vectors will move among plants and probe and transmit the virus before dying. On the other hand, quick-acting pesticides, unlike those that are slow acting, might help to curb epidemics, because although such pesticides do not inhibit the acquisition or inoculation of such viruses, they can diminish the aphid's ability to accomplish both and to move to inoculate successive plants (Irwin *et al*., 2000).

Biological control cannot effectively halt transient aphids nor greatly reduce their ability to spread non-persistent viruses at a sink. Theoretically, introducing biological control agents or inundatively releasing natural enemies at the source, where the aphids mature, could effectively lower populations, thus reducing and retarding influxes of aphids at the sink.

Deploying plant genotypes resistant to aphids can influence the rapidity with which aphids move through a field by changing the rate of probing once the transient aphid has alighted on a leaf. Virus resistance can be even more effective in influencing the ability of the aphids to transmit viruses

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within a field. When a viruliferous aphid probes a virus-resistant plant or a plant that is not a host of the virus it may be carrying, the probability of the virus being transmitted is close to nil. Therefore, the probability of transmission the next time that aphid lands and probes, if on a non-infected, susceptible host of the virus, is greatly diminished. This concept is extendable to mixed plantings (e.g. intercropping), where the viruses that can infect one crop are not the same as those that infect the other, or mixtures of susceptible and resistant cultivars planted in a field. By so planting, the spread of non-persistent, aphid-borne viruses in that field can be constrained (Gunasinghe *et al*., 1986; Martin *et al*., 2003). Moreover, barrier crops that reduce the load of viruliferous aphids (Hooks and Fereres, 2006), and physical barriers to probing (e.g. leaf pubescence) by viruliferous aphids, effectively reduce the probability of inoculation (Gunasinghe *et al*., 1988). Reflective mulches (Jones, 1991; Silva-Filho *et al*., 2014) and plastic films and nets that manipulate insect vision can also reduce the spread of non-persistently aphid-transmitted viruses (Diaz *et al*., 2006).

Colonizing non-vectors

Although the pattern of settling may differ among colonizing species, when an immigrant encounters a suitable host, it will add to the infestation at its sink. Some species alight on a host plant in a field, begin producing nymphs and form a colony there. Others alight, produce a few nymphs, then fly to neighbouring plants, where they produce more nymphs, thus dispersing their offspring more widely and, at the same time, probing more host plants. Regardless of the settling pattern, many species of colonizing aphid tend to spread from field margins to their interiors and from plant to plant along, rather than between, rows (Bottenberg and Irwin, 1991; *cf*. Wu *et al*., 2004, for an exception). Once the initial colonies are formed, they expand, and subsequent spread within the field is often by plant-to-plant movements of nymphs, adult apterae and even alatae. Thus, aphid infestations often become randomly patchy within a field.

The colonizing non-vector category of aphids can be managed in much the same way as other potential insect pests. Because virus spread is not a concern, the aphids should be managed solely in accordance with the damage they might cause the crop and its potential yield. Establishing economic injury levels, monitoring established aphid populations at the sink and applying measures to limit infestations once populations exceed economic thresholds form appropriate remedial responses to this category of pest.

Colonizing vectors

Aphids that can colonize a crop and are potential vectors of plant viruses pose a serious, ongoing threat to crops they colonize, often more so because they are capable of transmitting persistent and semi-persistent viruses than because they are a threat on their own. The timing of aphid movement relative to plant phenology must be taken into account when predicting the impact of viruliferous aphids. The distinction between the movement of already infective vectors and those that must first acquire the virus is critical for predicting the longer-term effects on the host plants. Early infections have a greater impact on yield parameters and the plant's ability to act as a source of inoculum for subsequent spread at the sink. Because aphids generally retain persistent viruses for long periods, a reasonable likelihood exists that aphids will transport them to a sink from quite distant sources. If, however, potential vectors are not yet infective when they arrive at a sink, these aphids must first settle on a virus-infected host and their offspring must then move and colonize a non-infected host to spread the virus. Therefore, epidemics of persistent viruses often proceed at a slower rate than those of non-persistent viruses.

Unlike transient aphids that vector non-persistent viruses, colonizing vectors can be managed more successfully at the sink. Monitoring local primary or over-seasoning hosts to gauge the developmental stages of the aphids; deploying liquid-filled pan traps to confirm landings; analysing data from a regional network of suction traps to determine what is currently flying; and periodically assessing the population build-up of aphids and their natural enemies at both the source and the sink all provide important information on which to base a management strategy. The tactics one might employ are many; a few are mentioned below.

Pesticides, even those that target aphids but are slow acting, function rapidly enough to disable an aphid before it can successfully move to and inoculate a neighbouring plant with a persistent or semi-persistent virus (Kennedy and Connery, 2012). Pesticides, therefore, can effectively reduce

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populations of colonizing aphids without the concomitant spread of persistent viruses. Even under these circumstances, pesticide use can have negative consequences. Beyond the added cost of chemicals and their application and of aphid genotypes becoming resistant to the chemicals, the sensitivity and susceptibility of natural enemies to some pesticides greatly impedes biological control efforts.

Minimizing row spacing and synchronizing planting dates at the sink to confront incoming colonizing vectors with as complete a canopy cover as possible will reduce the probability that the incoming aphids will alight in the field. Sparsely planted trap crops may also divert arriving aphids. For those aphids that do land, the conservation and augmentation of natural enemies and the use of plant genotypes resistant to either the aphids or the viruses potentially being transmitted are also possible tactics that can be applied at the sink.

Conclusions

Given that aphids are sedentary for most of their lives, it seems ironic and somewhat counter-intuitive that their ability to move is so pivotal in elevating them to the status of super pests. Even though only a small fraction of the extant species comprises pests, it is their ability to move over large spatial scales that allows aphids, through their vectoring capacity, to devastate crops over a very short timespan. If aphids did not move much, or if they move over only very small spatial scales, even those species that are excellent vectors would play a much-reduced role in spreading plant pathogenic viruses. That certain aphid species do range widely, transcending continental land masses and even crossing oceans, propels them, in an agricultural context, not only to super pest status but also to the status of potential super vectors. To forecast the impact of aphids in an agricultural setting can be difficult and often requires knowledge of where they originated and the capacity to predict when they will arrive in the field. Thus, we believe that understanding aphid movement and how to modify it is key to shaping useful management strategies for aphids.

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11 Predators, Parasitoids and Pathogens[1]

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Introduction

Aphids occur in most terrestrial habitats. They are commonly attacked by predators, parasitoids and pathogens; often collectively termed Aphidophaga (Völkl *et al*., 2007). Predators kill their prey by feeding on them. In some families of aphid predators (e.g. ladybirds), both the larvae and the adults are predaceous, whereas in other families (e.g. hover flies, lacewings, midges), only the larvae are predaceous. Among insect parasitoids, all species in the braconid subfamily Aphidiinae and some genera in the family Aphelinidae develop as endoparasitoids, with generally one larva completing development in each aphid. At the end of larval development, the aphid is killed, and the parasitoid pupates within or below the hardened cuticle of its host (the 'mummy'). Adult wasps are free-living. Some species of fungi are entomopathogenic, infecting aphids directly through the cuticle, eventually killing the host.

In general, the impact of a natural enemy, and hence its potential contribution to a reduction in pest damage, depends on several factors. Although many aphid species are widespread and common, their density varies over space and time. To contribute to control, a natural enemy must be effective in locating its target pest. A variety of sensory cues emanating from the aphid's host plant, or the aphid itself, are used to locate hosts or prey over a wide range of distances. Once an aphid colony has been found, the potential voracity of a predator (or the potential fecundity of a parasitoid) plays an important role in determining the degree to which colonies will be suppressed. Patterns of resource use are also influenced by population structure and the degree of specialization. Although host-specific natural enemies are often better than polyphagous ones at finding aphid colonies, and hence are considered more effective for control, polyphagous parasitoids and predators can have a significant impact on aphid populations. For aphid pathogens, host location is largely passive; however, parameters affecting persistence, transmission and dispersal influence the potential of pathogens to infect suitable hosts.

This chapter is organized in four sections, with the first two sections dealing respectively with predators and parasitoids. The focus is on foraging behaviour and on cues triggering successful search. The third

[1] The authors would like to dedicate this chapter in memory of their friend and colleague, Wolfgang Völkl, who was the lead author of this chapter in the First Edition and who sadly passed away in 2015.

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section, on microbial agents, focuses on parameters affecting epizootiology; that is, the potential of a pathogen to cause an epidemic or epizootic. We discuss also the relationship between host or prey specificity and resource utilization in terms of enemy effectiveness. In the fourth section, we consider intraguild interactions and mutualistic relationships and how they may limit the effectiveness of Aphidophaga as biological control agents in the field.

Aphid predators

Ladybird beetles (Coleoptera: Coccinellidae) (Fig. 11.1)

General biology

Beetles from the family Coccinellidae comprise some 6000 species, of worldwide distribution (Seago *et al*., 2011; Nedvěd and Kovář, 2012). They are variously called ladybirds (as in this volume), ladybugs or ladybeetles, although these names are sometimes reserved exclusively for the larger and more brightly coloured coccinellids. The family includes phytophages, mycophages and entomophages (Giorgi *et al*., 2009; Hodek and Evans, 2012). Most entomophagous ladybirds feed on Sternorryncha, with many feeding predominantly on aphids. Aphidophagous species are concentrated in the tribe Coccinellini, although aphid-eating taxa can also be found in other coccinellid tribes (Giorgi *et al*., 2009).

The lifetime fecundity of aphidophagous ladybirds varies markedly with temperature and prey type, even within a species (e.g. Papanikolaou *et al*., 2013); this leads to widely differing estimates of lifetime fecundity. For example, reports for *Adalia bipunctata* (2-spot ladybird) feeding on aphids give

Fig. 11.1. Coccinellidae. (a) Eggs of *Adalia bipunctata*. (Photograph courtesy of the late S.P. Hopkin and Ardea, London.) (b) Larva of *Coccinella 7-punctata*. (Photograph courtesy of A. Stewart-Jones.) (c) Pupa of *Coccinella 7-punctata*. (Photograph courtesy of the late S.P. Hopkin.) (d) Adults of *Coccinella 7-punctata*. (Photograph courtesy of the late S.P. Hopkin and Ardea, London.)

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lifetime fecundities ranging between 39 and 1535 eggs/female (Nedvěd and Honěk, 2012). Across species, it would be safe to assume a range from less than 100 to 2000 or more (data in Nedvěd and Honěk, 2012). Most aphidophagous species lay eggs in clusters (Majerus, 1994; Nedvěd and Honěk, 2012). A number of benefits accrue from this habit, possibly related to the very small size of neonate ladybird larvae, making the initial capture of prey difficult. Larvae eating unhatched, late-hatching or possible 'trophic' eggs from the same clutch survive longer and are larger, making subsequent aphid capture more likely (Banks, 1956; Hodek and Evans, 2012). Groups of neonate larvae can also feed socially (Hemptinne *et al*., 2000a; Moore *et al*., 2012). Furthermore, fewer eggs may fall victim to predation because, when grouped together, the chemical defences they possess are more apparent to natural enemies (Agarwala and Dixon, 1993).

In keeping with other life-history characteristics, aphidophagous ladybirds develop quickly compared to coccidophagous species, as aphids constitute the more ephemeral prey (Dixon *et al*., 1997, 2011; Borges *et al*., 2011). Developmental times for aphidophagous ladybirds are typically in the order of several weeks (e.g. data in Dixon *et al*., 1997). Both sexes develop at a similar rate, although adult males are smaller than females (Dixon, 2000). Within-species developmental times are affected strongly by temperature and aphid prey species (Hodek and Evans, 2012; Nedvěd and Honěk, 2012). Thus, egg to adult development of *Coccinella septempunctata* (7-spot ladybird) on *Myzus persicae nicotianae* (tobacco aphid) varies between 71.9 days at 14°C and 22.1 days at 23°C (Katsarou *et al*., 2005), while development of the same species at 25°C varies between 17.5 days on *Myzus cerasi* (cherry blackfly) and 20.8 days on *Hyalopterus pruni*, the mealy plum aphid (Özder and Sağlam, 2003). Developmental times may even be influenced by the aphid host plant. For example, *Hippodamia variegata* exhibited developmental times varying between 12.6 days and 14.5 days on *Aphis gossypii* (cotton or melon aphid) from five different host plants (Wu *et al*., 2010). Other parameters, including mortality and adult size, are also affected by rearing temperature and diet (Hodek and Evans, 2012; Nedvěd and Honěk, 2012).

The number of generations per year is limited to one at high latitudes, but increases as latitude decreases towards the tropics. Ladybirds in temperate regions typically diapause in winter, while ladybirds in areas with hot or dry seasons may aestivate at those times: adults are generally the dormant life-history stage (Hodek, 2012).

Ladybirds have a variety of natural enemies. Many generalist predators avoid eating ladybirds due to their chemical defences, which are comprised of interspecifically variable alkaloids and are present in all life-history stages (Brakefield, 1985; Ceryngier *et al*., 2012). Populations of immature ladybirds exhibit high levels of cannibalism, especially if aphids are in short supply (Mills, 1982; Schellhorn and Andow, 1999), and may also fall victim to intraguild predation and aphid-tending ants (see below). Ladybirds are also attacked by a variety of specialized parasites, including dipteran and hymenopteran parasitoids, mites, fungi and bacteria, which can reach very high prevalences (Ceryngier *et al*., 2012). Particularly noteworthy are the group of so-called 'male-killing' bacterial endosymbionts, which are transmitted cytoplasmically through the female line. They kill male eggs before hatching, a strategy that enhances female (and their own) survival at the expense of males (Majerus and Hurst, 1997; Ceryngier *et al*., 2012).

Adult and larval foraging for aphids

How adult ladybirds find aphid-bearing plants over long distances remains poorly understood, but cues are probably visual, such as shape and colour, and olfactory, from either the aphid or the plant (e.g. Bahlai *et al*., 2008). Experience may play a role in the effective use of these cues (Wang *et al*., 2015). Larvae that begin their life in a suitable habitat chosen by their mother do not forage over long distances, although they may move between adjacent plants via the ground or overlapping leaves (e.g. Banks, 1957).

On the plant, a number of behaviours bring adult and larval ladybirds into contact with their aphid prey. Ladybirds, like aphids, exhibit positive phototaxis and negative geotaxis; their search is concentrated on leaf edges, stems and particularly veins, the latter being a focus for aphid colonies (Banks, 1957; Frazer and McGregor, 1994; Hodek and Evans, 2012). Aphid honeydew is an arrestant stimulus (Carter and Dixon, 1984), ensuring that ladybirds remain in areas inhabited by prey. Plant architecture influences the efficiency of ladybird foraging if it makes aphids more difficult to detect or catch (Kareiva, 1990; Clark and Messina, 1998). Plants with waxy surfaces may be difficult to walk on, while leaf hairs or trichomes impede movement (Shah, 1982).

Some studies suggest that visual or olfactory detection by adults or larvae occurs over only short

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distances of a centimetre or so (Nakamuta, 1984a; Hemptinne *et al*., 2000a). Aphid body fluid stimulates feeding in adults (Nakamuta, 1984b). After aphid encounter, adults and larvae switch to intensive searching behaviour whereby they search the immediate area more slowly and with frequent turns (Banks, 1957; Hodek and Evans, 2012). Larvae of *Ceratomegilla undecimnotata* are highly variable in their intensive search behaviour, which can occur prior to finding an aphid, be delayed, or not occur at all after aphid capture (Ferran *et al*., 1994). Flexibility in intensive searching behaviour is likely to be an adaptation to variable conditions, particularly prey distribution (Ferran *et al*., 1994; Dixon, 2000).

Oviposition and predatory behaviour in aphid patches

A patch of aphids is only suitable for ladybird oviposition for a short period early in its development (the so-called 'egg window') (Fig. 11.2). If ladybirds oviposit too early, then there are insufficient aphids to support the developing larvae, while if ladybirds oviposit too late, the aphids will not persist for long enough at high densities to allow the larvae to reach adulthood (Hemptinne *et al*., 1992).

It appears that the minimum density of aphids necessary for ladybird reproduction to begin is determined by the relative size of the aphid and ladybird species involved (Sloggett, 2008a). Small aphid species support oviposition by small ladybirds at lower densities than large ladybirds, because the minimum food required to support egg production in small ladybirds is lower. However, because small ladybirds cannot catch the older life stages of large aphid species, larger ladybirds can reproduce earlier at lower total densities of large aphids. A number of studies with different sized aphid species show the same size-related pattern of temporal variability in ladybird reproduction (Sloggett, 2008a).

Although a few studies have suggested that cessation of oviposition is associated with prey-related cues (e.g. Johki *et al*., 1988), such cues appear to be of very limited importance relative to cues from the ladybirds themselves (Hemptinne *et al*., 2000b). When ladybird larvae are already present on a plant, subsequent clutches of eggs are at risk from intraguild predation and cannibalism (Hemptinne *et al*., 1992; Dixon, 2000). Females avoid ovipositing when conspecific, and sometimes allospecific, ladybird larvae are present (Hemptinne and Dixon, 1991; Seagraves, 2009). This is mediated by chemical cues from larvae on the plant surface; these cues reduce the female's tendency to oviposit and increase her activity, thereby encouraging her to leave the plant (Růžička, 1997; Doumbia *et al*., 1998; Laubertie *et al*., 2006). Sentis *et al*. (2015) further showed that temperature influences the emission of these chemical cues from larvae, which in turn changes the oviposition behaviour of conspecific females. Such temperature-mediated effects on chemical communication would likely influence population processes in coccinellids.

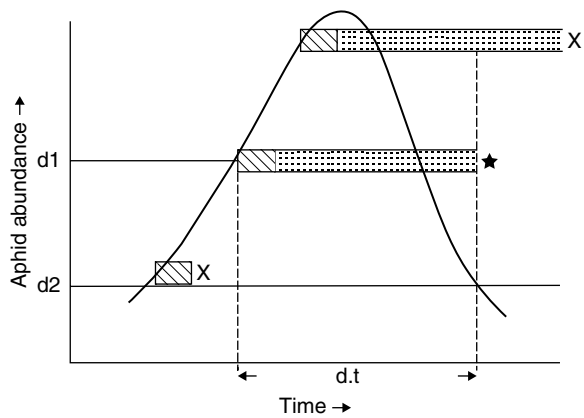

Fig. 11.2. The advantage of ladybird beetles synchronizing their reproductive effort with the early development of aphid populations. Dashed bars correspond to egg laying and dotted bars indicate larval development. Open means that larvae cannot complete their growth. (X) unsuccessful, (★) successful reproductive effort; d1 and d2 = threshold densities for the survival of first- and fourth-instar larvae, respectively; d.t. = developmental time. (From Hemptinne *et al*., 1992.)

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Prey specificity

Aphidophagous ladybird species vary markedly in aphid prey specificity. Some ladybirds only feed on a very few aphid species: *Myzia oblongoguttata* (striped ladybird) is restricted to conifer aphids, and *Anisosticta novemdecimpunctata* (water ladybird) feeds mainly on *H. pruni* in *Phragmites* spp. reed beds. In contrast, some ladybirds are generalists, such as *A. bipunctata* and *C. septempunctata*, which feed on hundreds of different aphid species (Majerus, 1994). Complex relationships occur between diet and habitat; while dietary specialists may be restricted to one or a few plant species, some habitat specialists, such as the myrmecophile *Coccinella magnifica*, consume many different aphid species (Sloggett, 2008b).

Conventionally, aphids have been divided into 'essential prey', which support oviposition and development, 'alternative prey', which can be consumed but are unsuitable for reproduction, and 'rejected prey', which are unacceptable (Hodek and Evans, 2012). However, many prey species that are not consumed in the wild will serve as essential prey in the laboratory (see Majerus, 1994). Furthermore, transitional cases exist where prey species are marginally suitable for reproduction and are, therefore, difficult to categorize (Hodek and Evans, 2012).

Although aphids are the primary diet of aphidophagous ladybirds, other food items may form a significant part of their diet. These include other Sternorryhncha, other insects including Lepidoptera, fungal spores and plant material, especially fruit and pollen (Evans, 2009; Lundgren, 2009; Hodek and Evans, 2012). Alternative food can have positive effects on oviposition, larval growth and survival, when aphids are limited (Evans *et al*., 1999; Kalaskar and Evans, 2001). Many aphidophagous ladybirds utilize these alternative foods, as well as alternative aphid prey, during periods when essential aphid prey are scarce, such as early spring or late summer in temperate regions (Sloggett and Majerus, 2000a; Hodek and Evans, 2012).

Ladybirds, aphid populations and aphid control

The impact of aphidophagous ladybirds on aphid populations remains controversial. It has been argued that ladybirds do not reproduce for long enough in a patch to provide adequate aphid control. This is because their generation time is long relative to their prey, and because aphids are patchily distributed (Hemptinne and Dixon, 1997; Kindlmann and Dixon, 2001). Additionally, cannibalism and intraguild predation can further limit aphid control. None the less, many practitioners still consider that ladybirds play an important role in aphid population control (e.g. Obrycki *et al*., 2009), although their 'popularity' has declined in recent years (Michaud, 2012). The majority of aphidophagous ladybirds considered important for biological control are generalists; but their tendency to move between prey species and habitats may limit their utility (Sloggett *et al*., 2008) and can lead to unintended non-target effects (Evans *et al*., 2011). In particular, the introduction of exotic ladybirds to new geographic regions for aphid control may have led to declines in native species, through competition and/or intraguild predation (Evans *et al*., 2011).

Syrphidae (hover flies) (Fig. 11.3)

General biology

Hover flies are one of the largest dipteran families. Larvae of about one-third of hover fly species in the subfamily Syrphinae are predators of Sternorrhyncha, usually aphids. Adults are active diurnal flower visitors and feed on pollen and nectar (Rotheray, 1989); they mimic bees and wasps.

Adult hover flies are characteristically highly fecund. In *Episyrphus balteatus*, the average lifetime production of eggs per female ranges between 2000 and 4500 (Branquart and Hemptinne, 2000). Larvae hatch after 2–5 days and almost immediately start feeding on surrounding aphids. Larvae feed by puncturing the aphid cuticle and sucking out the contents. There are three larval stages; the final instar pupates inside a puparium, usually located on the plant where the last prey was consumed. Developmental times vary between species and are influenced by prey species and temperature.

Most species are univoltine in temperate regions, while multivoltinism is common in the tropics. In northern Europe, several species are partially migratory: some individuals remain in their summer habitats and overwinter at larval, pupal or adult stages, while the rest of the population migrates over long distances to southern Europe (Raymond *et al*., 2013).

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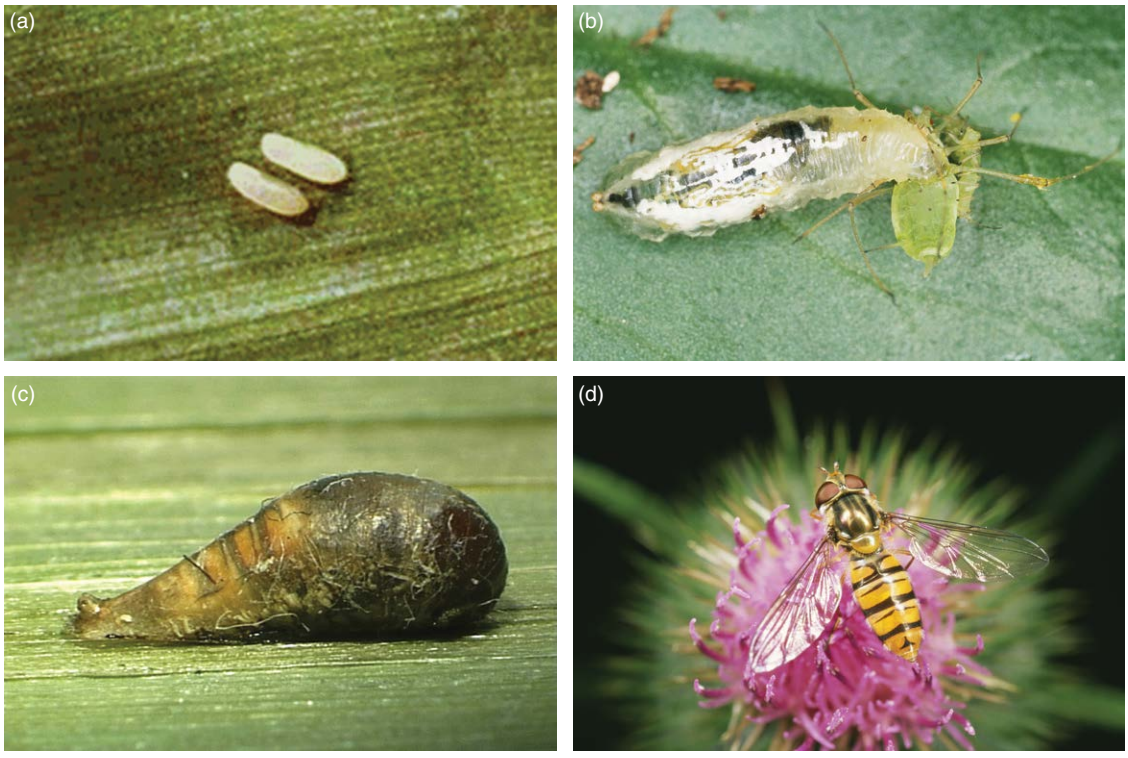

Fig. 11.3. Syrphidae. (a) Syrphid eggs, species not known. (Photograph courtesy of B. Freier and the Biologische Bundesanstalt für Land- und Forstwirtschaft, Kleinmachnow, Germany.) (b) Larva of *Episyrphus balteatus*. (Photograph courtesy of the late S.P. Hopkin and Ardea, London.) (c) Puparium of *Episyrphus balteatus*. (Photograph courtesy of U. Wyss.) (d) Adult *Episyrphus balteatus*. (Photograph courtesy of the late S.P. Hopkin and Ardea, London.)

Oviposition site selection

Oviposition in hover flies is elicited by olfactory and visual cues. Females of *Eupeodes corollae* and *E. balteatus* respond positively to stimuli from honeydew, and probably also from aphid siphunculus secretions. These stimuli may act both as long-distance kairomones and oviposition stimuli following prey location (Budenberg and Powell, 1992; Bargen *et al.*, 1998; Sutherland *et al.*, 2001). Additionally, females of *E. corollae* respond to plant structural characteristics, having a preference for vertical over horizontal surfaces and darker over lighter strips (Chambers, 1988). Eggs are often laid singly, either close to or within aphid colonies, although some species lay eggs in batches distant from the colony, or even on uninfested plants (Chambers, 1988). In the latter case, young larvae may survive by cannibalizing conspecific eggs.

Aphid colony size has an important influence on oviposition site selection. Since larvae have a limited dispersal capability, the female's decision on oviposition site is crucial to the survival of her offspring. Hover fly females adjust their egg number in relation to aphid density, behaviour considered adaptive since it both secures larval survival and optimizes the female's search effort. Generally, the number of eggs deposited increases with aphid colony size (Bargen *et al.*, 1998; Sutherland *et al.*, 2001). In contrast, there are reports that females of many hover fly species prefer smaller aphid colonies, or aphid colonies with a high proportion of early instars, for oviposition (e.g. Ito and Iwao, 1977; Hemptinne *et al.*, 1993). These females may be avoiding high aphid densities because large colonies are more likely to be subject to increased aphid emigration, rather than to continued colony growth, the latter being essential to ensure the survival of hover fly offspring (Kan, 1988). Hover fly females

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also lay fewer eggs in aphid colonies where conspecific larvae are already present (Hemptinne *et al*., 1993).

Prey specificity and larval foraging

Field and laboratory observations suggest that hover fly larvae attack a broad range of prey types (Chambers, 1988; Gilbert and Owen, 1990), but there are also truly specialized species, such as *Eupeodes nielseni*, which consumes only a few aphid species on pine (Laska, 1978). In polyphagous species, different prey in the diet may influence developmental time and pupal weight, which in turn may influence adult fecundity (Sadeghi and Gilbert, 2000).

Hover fly larvae are active between dusk and dawn. Their search is characterized by casting behaviour (Chambers, 1988) in which the hind body remains attached to the substrate while the anterior end is extended forward and laterally until a prey item is contacted. Evidence for the importance of olfactory and gustatory cues for larval foraging behaviour is inconsistent. Chambers (1988) assumed that hover fly larvae recognized aphids only by tactile cues and that they did not use directed cues for prey location. In contrast, Bargen *et al*. (1998) found that first-instar larvae of *E. balteatus* exhibited a directed search over short distances and responded to volatile olfactory cues from aphids. Rapid prey location would be especially important for first-instar larvae hatching from eggs that had been deposited at a distance from the aphid colony.

In the laboratory, hover fly larvae show great voracity. Single larvae of Syrphini consume between 250 and 500 aphids, depending on aphid size and temperature (e.g. Chambers, 1988; Soleyman-Nezhadian and Laughlin, 1998). Larvae of Melanostomini, which are considerably smaller, consume between 135 and 150 aphids (e.g. Chambers, 1988). In all studies, third-instar larvae consumed more than 80% of aphids captured. Larvae of this age class were also most successful and efficient at capturing prey. When provided with an excess of aphids, hover fly larvae often killed more than they required for development and only partially consumed killed aphids (Chambers, 1988).

Hover flies and aphid populations

Hover flies can be important antagonists of aphids, particularly in cereals (Hagen *et al*., 1999). Striking aphid population reduction was observed when high levels of hover fly oviposition and larval hatching occurred early in the season, before aphid population growth accelerated (Tenhumberg and Poehling, 1995). Besides climatic factors, their effectiveness is limited by slow immigration rates of adults into fields and in simple landscapes (Haenke *et al*., 2009; Chaplin-Kramer and Kremen, 2012). Since adults are flower visitors, their foraging activity in crops can be enhanced when field margins provide a continuous supply of flowers such as Asteraceae and Apiaceae, which have easily accessible pollen (Ruppert and Molthan, 1991; Hogg *et al*., 2011). Since cereal fields are usually characterized by a shortage of food for flower visitors, alternative agricultural practices that favour wild flowers (e.g. set-aside, herbicide-free buffer zones, conservation strips (Chapter 21, this volume) may attract adult hover flies. Besides their impact on cereal aphids, hover flies also reduce aphid populations in citrus and apple orchards (Tracewski *et al*., 1984; Michaud and Belliure, 2000), and even in tropical crops such as taro and banana (Stechmann and Völkl, 1990).

Chrysopidae and Hemerobiidae (lacewings) (Fig. 11.4)

General biology

Lacewings (Neuroptera) are polyphagous predators feeding mainly on soft-bodied insects. Species of Chrysopidae and Hemerobiidae all commonly predate aphids, and some species in the Coniopterygidae have also been recorded feeding on aphids, particularly on conifers (Canard *et al*., 1984; New, 1988).

The eggs of many lacewing species have thin hyaline stalks (egg pedicels), although this is absent in other species. The pedicel protects eggs and newly hatched larvae from cannibalism and intraguild predation (Růžička, 1997).

Lifetime fecundity in chrysopid species varies between 150 and 600 eggs/female and seems to be greatest in hemerobiids (600–1500 eggs) (Canard *et al*., 1984; New, 1988). Between 15°C and 25°C, developmental times range between 6 and 12 days for hemerobiids and between 15 and 30 days for chrysopids (Canard *et al*., 1984; New, 1988; Liu and Chen, 2001; Michaud, 2001). In both families, there are three larval instars; pupation takes place within a globular cocoon, which is attached to the plant surface. In temperate regions, most lacewings are multivoltine (Tauber and Tauber, 1982), although the biology of many species has received

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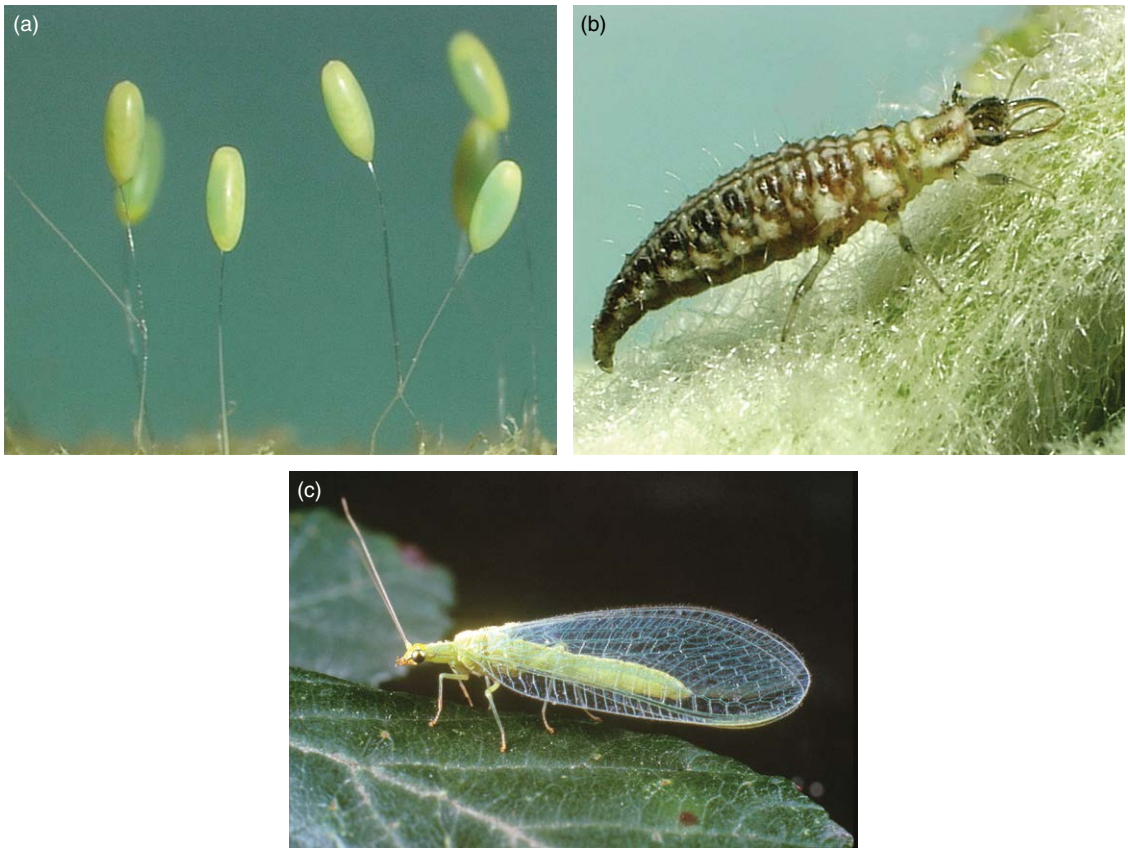

Fig. 11.4. Chrysopidae. (a) Eggs of *Chrysoperla carnea*; (b) larva of *Chrysoperla carnea*. (Both photographs courtesy of U. Wyss.) (c) Adult of *Chrysoperla carnea*. (Photograph courtesy of Rothamsted Research, Harpenden, UK.)

little research attention. Many lacewing species enter winter diapause (hibernation) either as adults (such as *Chrysoperla carnea* – common green lacewing – or *Micromus angulatus*), pupae, or even prepupae (New, 1988).

Chrysopid and hemerobiid larvae are very active predators, as are most of the adults. Some adult chrysopids, such as *C. carnea*, feed on nectar, yeasts, pollen and honeydew, the latter of which may attract them into aphid colonies. Larval voracity depends on prey size and temperature. Michaud (2001) reported a relationship between food consumption and developmental time of larval *Chrysoperla plorabunda*, which consumed between 130 and 1650 *Aphis (Toxoptera) citricidus*, depending on aphid instar. *Chrysoperla carnea* larvae also responded to changes in prey species, consuming more *A. gossypii* (292) and *M. persicae* (273) than *Lipaphis erysimi* (146) (Liu and Chen, 2001).

Adult foraging and oviposition behaviour

Chrysopid larvae are generalist predators. For example, Herard (1986) reported that *C. carnea* fed on more than 70 prey species from five insect orders including aphids, psyllids, mealybugs, leafhoppers and whiteflies. Many chrysopid species are attracted to cues associated with the presence of aphids. In laboratory experiments, *C. carnea* responded positively to volatile breakdown products of the amino acid, tryptophan, which is a common component of aphid honeydew (van Emden and Hagen, 1976), to aphid sex pheromone and to (*E*)-β-farnesene, the alarm pheromone of aphids (Zhu *et al*., 1999). *Chrysopa pallens* showed a positive response to aphid sex pheromone but not to (*E*)-β-farnesene (Boo *et al*., 1998). Plant volatiles, such as β-caryophyllene and 2-phenylethanol are also attractive (Zhu *et al*., 1999). Furthermore, larvae of various *Chrysopa* species

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mark the substrate with an oviposition-deterring pheromone, which significantly reduces both intra- and interspecific oviposition activity (Růžička, 1996).

Having selected suitable areas on a given plant, the females of many neuropterans do not search specifically for an oviposition site in the direct vicinity of an aphid colony (Coderre *et al*., 1987). For example, *Chrysopa oculata* (goldeneyed lacewing) only laid eggs on maize plants if there were aphids present; however, most eggs were found on leaves without aphid colonies. This suggests that newly hatched larvae must search intensively for prey (Coderre *et al*., 1987). Similarly, random egg laying was observed in some other chrysopid species, such as *C. carnea*, whose adults feed on honeydew (Duelli, 1984).

The first bottleneck in larval foraging is the interval between eclosion from the egg and the first prey encounter. During this period, many first-instar larvae die of starvation or predation. Plant structures such as dense trichomes dislodge small larvae (Rosenheim *et al*., 1999), thereby contributing to early larval mortality and making such plants less suitable for lacewing development.

Larval foraging

Larval foraging behaviour can be modified strongly by foliage density and plant architecture, as these affect prey accessibility. Clark and Messina (1998) found that *C. carnea* was more effective in locating *Diuraphis noxia* (Russian wheat aphid) on Indian ricegrass (*Oryzopsis hymenoides*) (which is characterized by narrow, linear leaves) than on crested wheatgrass (*Agropyron desertorum*) with its flat, broad leaves. This difference may explain the greater effectiveness of *C. carnea* in eliminating field-cage populations of *D. noxia* on rice grass than on wheatgrass (Messina *et al*., 1997). Similarly, the presence of alternative prey reduced foraging by *C. plorabunda* larvae on *D. noxia*, even on easily accessible sites (Bergeson and Messina, 1998). Larvae of *C. plorabunda* were also more effective against *D. noxia* on resistant wheat plants than on susceptible ones (Messina and Sørenson, 2001), suggesting that even a modest reduction in aphid population growth might produce synergistic effects for pest reduction by natural enemies (van Emden, 1986).

Lacewings and aphid populations

The role of Neuroptera in reducing aphid populations depends heavily on local conditions. Chrysopids have the potential to reduce aphid numbers significantly (New, 1988), but there are only a few studies dealing with their effectiveness on aphid populations. The use of lacewings in biological control has been through augmentation and conservation, for they are open to manipulation, making them particularly successful in closed environments such as greenhouses. Research is needed to determine the conditions under which lacewings are most effective against key aphid pests.

Cecidomyiidae (predatory midges) (Fig. 11.5)

General biology

Within the dipteran family Cecidomyiidae, there are at least five predatory species in the genera

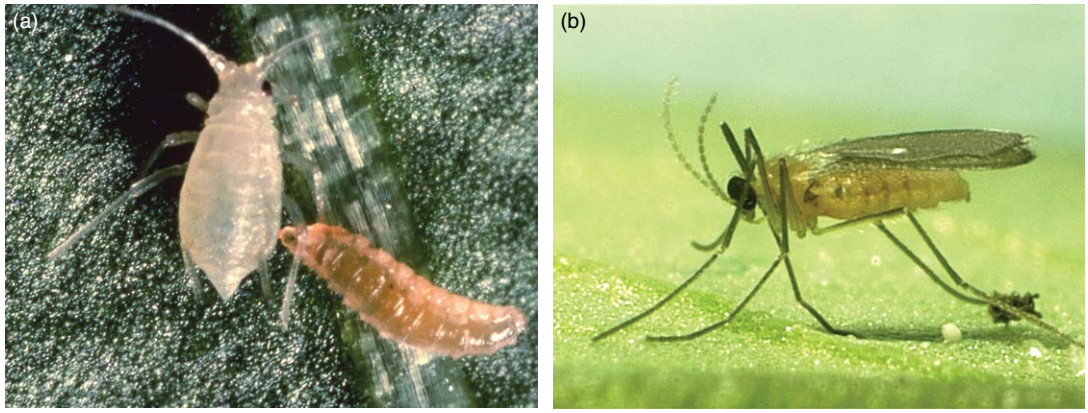

Fig. 11.5. Cecidomyiidae. (a) Larva of *Aphidoletes aphidimyza*. (Photograph courtesy of J. Bennison and ADAS.) (b) Adult of *Aphidoletes aphidimyza*. (Photograph courtesy of U. Wyss.)

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Aphidoletes and *Monobremia* whose larvae prey exclusively on aphids, while the adults feed on nectar or honeydew (Harris, 1973; Nijveldt, 1988). *Aphidoletes aphidimyza* is commonly used in biological control programmes (van Schelt and Mulder, 2000). Adult flies are nocturnal (Nijveldt, 1988). The average number of eggs laid per female during her lifetime ranges between 50 and 150; fecundity depends both on larval and adult nutrition and on geographic origin (Havelka and Zemek, 1999). Larvae hatch after 2–4 days and almost immediately start feeding on aphids. There are three larval stages; the final instar pupates in soil. Developmental time varies with temperature and nutritional condition, ranging between approximately 30 and 55 days from egg to adult (Harris, 1973; Nijveld, 1988; Havelka and Zemek, 1999). In central Europe, there are two or three generations per year (Harris, 1973). *Aphidoletes aphidimyza* hibernates in the pupal stage in the soil.

Oviposition behaviour

Females lay their eggs singly or in small clusters on foliage, usually within or close to aphid colonies. Females can discriminate between plant species or varieties, and especially between infested and uninfested plants (Mansour, 1975, 1976). The latter capability is crucial for *A. aphidimyza* survival, because neonate larvae cannot detect prey unless they are very close to them, and will die from starvation if they are more than 63 mm from food (Wilbert, 1973). Furthermore, ovipositing females respond to morphological host-plant characteristics such as leaf pubescence (Lucas and Brodeur, 1999). Evidence for a female response to varying aphid density is inconsistent, though positive correlations between clutch size and aphid density have been reported (Wilbert, 1973; Nijveldt, 1988; Lucas and Brodeur, 1999 – but see also Stewart and Walde, 1997). Additionally, Růžička and Havelka (1998) found that *A. aphidimyza* larvae secreted a species-specific, oviposition-deterring pheromone that significantly reduced oviposition in colonies already being attacked.

Prey specificity and larval feeding

Larvae of *A. aphidimyza* feed on a variety of aphid species, mainly on herbaceous plants or deciduous trees (Harris, 1973; Nijveldt, 1988). The number of aphids killed during the larval stage varies considerably. One larva needs a minimum of seven adult aphids to complete its life cycle, but may attack and partially consume as many as 80, depending on aphid size and environmental conditions such as humidity (e.g. Nijveldt, 1988). Thus, larvae may kill more aphids than they need for their development (Nijveldt, 1988), enhancing their success in biological control programmes, especially in glasshouse systems.

Other arthropod predators

Predatory bugs

ANTHOCORIDAE (FLOWER BUGS) (FIG. 11.6). Within the Heteropteran family Anthocoridae (Hemiptera: Heteroptera), species in the genera *Anthocoris* and *Orius* are common generalist predators. For example, the prey of *Anthocoris nemorum* (common flower bug) in Europe includes 34 insect species in four orders, and five mite species (Herard, 1986). Anthocorids, or flower bugs, are mainly diurnal. Females lay their eggs singly just beneath the epidermis of the prey's host plant. Mean total egg numbers of 50/female are common, but they may lay up to 200 (Hodgson and Aveling, 1988; Lattin, 1999). There are five nymphal stages. Their developmental time is influenced strongly by temperature, ranging from between 22 days at 20°C and 53 days at 14°C in *A. nemorum*. In *A. nemorum*, the number of generations per year depends on climate; the species is univoltine in Scotland, bivoltine in England and has at least three generations

Fig. 11.6. Anthocoridae. Adult *Anthocoris nemorum*. (Photograph courtesy of U. Wyss.)

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in France. Anthocorid bugs usually hibernate as adults in leaf litter, under bark, or in hollow stems (Parker, 1975).

As with many other aphid predators, anthocorid females may use herbivore-induced volatiles for prey location (Dwumfour, 1992; Scutareanu *et al*., 1997). During development, *Anthocoris* nymphs consume between 60 and 240 aphids, depending on aphid size and temperature (Hodgson and Aveling, 1988).

Anthocorid bugs are very mobile and respond rapidly to changes in prey population, thereby aggregating in areas with high prey densities (Hodgson and Aveling, 1988). In such situations, both nymphs and adults contribute to a significant reduction in aphid numbers and improved biological control (reviewed by Hagen *et al*., 1999; see also recent work by Desneux *et al*., 2006).

OTHER BUGS. Nabid and mirid bugs (Heteroptera: Nabidae and Miridae) are also aphid predators. These, like anthocorids, benefit from a diversified landscape (Müller and Godfray, 1999) and may have some impact on cereal aphid populations. Predatory bugs are considered as 'true' top predators that may disrupt biological control through intraguild predation (see below).

Chamaemyiidae (aphid flies)

This is a small dipteran family from the Brachycera whose larvae feed exclusively on aphids (Sunderland, 1988); *Leucopis* is perhaps the commonest genus. Adult flies are diurnal. Females lay eggs singly, close to or within an aphid colony, often within folded leaves (Gaimari and Turner, 1997). First instars usually attack aphids that walk over them. Second- and third-instar larvae search more actively for prey. Puparia are usually formed within the aphid colony. Larvae and puparia can be distinguished from equivalent hover fly developmental stages by the two distal siphons. Most chamaemyiid flies are habitat specialists (e.g. conifer forests) and/or associated with only a few aphid species (Tracewski *et al*., 1984; Sunderland, 1988; Mizuno *et al*., 1997). Aphid flies were recorded as particularly abundant predators in New England apple orchards (Tracewski *et al*., 1984) and in Florida citrus orchards (Michaud and Belliure, 2000), where they might have played an important role in aphid population regulation.

Polyphagous predators

Aphids are attacked by a variety of polyphagous predators such as carabid beetles (Coleoptera: Carabidae), wolf spiders (Araneae: Lycosidae) and, to a lesser extent, rove beetles (Coleoptera: Staphylinidae). These polyphagous predators are abundant at the ground level (= epigeal predators) in many temperate agroecosystems. They consume a wide variety of crop pests including aphids (see Snyder and Wise, 1999, for further references), and there is growing evidence that they contribute significantly to a reduction in aphid densities (e.g. Sunderland, 1988; Holland and Thomas, 1997; Sunderland and Samu, 2000; Firlej *et al*., 2013). Within the vegetation layer, web-making linyphiid spiders also cause high mortalities among aphids, notably in cereals and in orchards (e.g. Sunderland *et al*., 1986; Wyss *et al*., 1995, Samu *et al*., 1996). The abundance and efficiency of generalist predators is increased significantly by a diversification of cropping systems (Wratten and van Emden, 1995; Sunderland and Samu, 2000).

The European earwig *Forficula auricularia* (Dermaptera, Forficulidae) is common and sometimes an important predator of *Eriosoma lanigerum* (woolly apple aphid) in orchards. Earwigs may also reduce aphid numbers in cereal fields (Sunderland, 1988).

Aphid Parasitoids

General biology

Aphids are commonly attacked by hymenopteran parasitoids. With some 50 described genera and over 600 species, the subfamily Aphidiinae (Hymenoptera: Braconidae) is the largest (Mackauer and Starý, 1967). The majority of species are described from the temperate and subtropical zones of the northern hemisphere. Among the Aphelinidae (Hymenoptera), all species in the genus *Aphelinus* and related genera (Starý, 1988) and several species of *Encarsia* (Evans *et al*., 1995) use aphids as hosts. In addition, several species of gall midge (Diptera: Cecidomyiidae) are parasitic on aphids (e.g. Muratori *et al*., 2009); with one species, *Endaphis gregaria*, being gregarious (Mackauer and Foottit, 1979). Except for some host records, only scant information is available on the biology of the aphid-parasitic *Encarsia* and *Endaphis* species.

Aphidiinae (Fig. 11.7)

All species in this subfamily are solitary endoparasitoids (Starý, 1970, 1988). Females normally

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Fig. 11.7. Aphidiinae. Adult of *Aphidius rhopalosiphi*. Inset: mummy of *Metopolophium dirhodum* parasitized by *Aphidius rhopalosiphi*. (Photographs courtesy of G.R. Gowling.)

deposit a single egg in an aphid, although clutches greater than one or superparasitism may occur when unparasitized hosts are scarce or unavailable (Mackauer, 1990). Supernumerary larvae are eliminated by contest in the early first instar, or by physiological suppression in later instars, so that normally only one larva per host completes development (Chow and Mackauer, 1986; Mackauer, 1990). However, facultative gregarious development was observed in *Ephedrus californicus* (Mackauer and Chow, 2012). After eclosion from the egg, the larva feeds first on the aphid's haemolymph, but later feeds destructively on other tissues, thereby killing the host. There are three larval instars. The development of teratocytes, specialized cells derived from the serosal membrane of the parasitoid embryo, has been well characterized in *Aphidius ervi* (Falabella *et al*., 2009) and such cells are common in Aphidiinae. Teratocytes process host tissues in ways that greatly improve the efficiency of nutrient transfer from host to parasitoid. The mature larva spins a cocoon either inside (e.g. species of *Aphidius*, *Ephedrus*, *Lysiphlebus*, *Pauesia* and *Trioxys*) or below (species of *Dyscritulus* and *Praon*) the empty host exoskeleton, called a mummy.

Except for some thelytokous species, in which males are rare or absent (Sandrock *et al*., 2011), the majority of aphidiine wasps are bisexual. Females can determine offspring sex by controlling sperm release; unfertilized and fertilized eggs develop into sons and daughters, respectively (i.e. arrhenotoky). Because daughters achieve greater fitness benefits from increased size than sons, mothers deposit fertilized eggs selectively in large hosts that are assumed to have higher quality than small hosts (Cloutier *et al*., 1991). Most females collected in the field are mated (Mackauer, 1976); average offspring sex ratios have a moderate female bias (Singh and Pandey, 1997). Both partial sib mating, local mate competition on the natal patch, and off-patch matings among non-sibs are common features of aphidiine biology (Mackauer and Völkl, 2002; Nyabuga *et al*., 2012). Sandrock and Vorburger (2011) show that thelytoky in *Lysiphlebus fabarum* is inherited as a single-gene recessive trait. This explains in part why some populations of *L. fabarum* are sexual and some are thelytokous (Engelstädter *et al*., 2011).

Females mature eggs throughout their reproductive life. Eggs are relatively small and nutrient-poor (Le Ralec, 1991). A female may store between 100 and 400 mature eggs in her ovaries. Egg resorption does not occur in all species (Völkl and Mackauer, 1990; Le Ralec, 1991), but has been documented in sugar-fed *Binodoxys communis* held for more than 48 h without hosts (Dieckhoff and Heimpel, 2010). Lifetime fecundity is potentially very high, ranging between 300 and over 1800 eggs/female under optimal laboratory conditions (Kambhampati and Mackauer, 1989; Hågvar and Hofsvang, 1991), but fecundity is probably much lower in the field, where few adults survive for more than 2–3 days (Mackauer, 1983; Dieckhoff *et al*., 2014). Adults feed on aphid honeydew and floral or extrafloral nectaries (Tylianakis *et al*., 2004; Dieckhoff *et al*., 2014). In temperate climates, diapause is induced by both abiotic (e.g. temperature, photoperiod) and biotic (e.g. host and/or host–plant) signals (Brodeur and McNeil, 1989; Polgár and Hardie, 2000). Although parasitoids typically have higher temperature requirements than their hosts, and hence appear later in the spring (Campbell *et al*., 1974), the combination of high fecundity, short generation time and female-biased sex ratio results in a high intrinsic rate of increase (r_m), ranging between 0.2 and 0.6 females/female/day (Force and Messenger, 1964; Kambhampati and Mackauer, 1989).

Aphelinus *and related species*

These parasitoids are also solitary. Unlike aphidiine parasitoids, *Aphelinus* females must feed on host haemolymph for egg maturation, often using low-quality host stages for feeding and high-quality

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hosts for oviposition (Bai and Mackauer, 1990; Wu and Heimpel, 2007). Females rarely superparasitize (Bai and Mackauer, 1990). When few hosts are available, the relatively large and nutrient-rich eggs are resorbed, thereby prolonging the female's lifespan (Mackauer, 1982). Mature larvae pupate inside the host mummy, which is bluish-black and loosely attached to the substrate.

Aphelinid wasps are relatively small, measuring only 1–2 mm in length, which limits the female's ability to handle large aphids (Gerling *et al*., 1990). Mated females deposit fertilized and unfertilized eggs differentially in large and small hosts, respectively (Asante and Danthanarayana, 1993); this pattern of offspring sex allocation is independent of the mother's body size (Honěk *et al*., 1998). Under optimal laboratory conditions, aphelinid wasps may survive for 3–4 weeks and produce between 200 and 800 progeny (Force and Messenger, 1964; Mackauer, 1982; Honěk *et al*., 1996). However, the number of hosts killed by feeding and oviposition can be much lower, averaging only three aphids per day over 27 days in *Aphelinus flavus* (Hamilton, 1973).

Foraging behaviour and host finding

Although all parasitoids cause host mortality, the impact on the host population is determined by the parasitoid's reproductive strategy. For example, a female's between- and within-patch foraging behaviour determines the number and type of hosts parasitized in each aphid colony. Therefore, identifying the patterns and processes of foraging behaviour and of the cues involved in host finding and acceptance may help in the planning and implementation of effective biological control programmes.

Between-patch foraging behaviour

Aphidiine wasps use a variety of host-plant or host-borne cues to locate aphid colonies (Mackauer *et al*., 1996). The relative importance of these cues can vary considerably depending on the spatial scale (Völkl, 2000). When foraging between habitats or between host plants (i.e. over relatively long distances so that hosts cannot be found by walking), females often respond to olfactory cues by directed movement. Volatile host-plant compounds serving as semiochemicals can provide the parasitoid with the first information about the potential presence of aphids (Wickremasinghe and van Emden, 1992). For example, Vaughn *et al*. (1996) showed that females of *Diaeretiella rapae*, a parasitoid of *Brevicoryne brassicae*, responded to volatiles from the aphid's host plant in the Brassicaceae.

A more reliable source than plant-borne cues are aphid-borne ones, although the latter may be less detectable over a long distance. Siphuncular secretions (Grasswitz and Paine, 1992; Battaglia et *al*., 1993), alarm pheromone (Micha and Wyss, 1996) and sex pheromones (Hardie *et al*., 1994; Glinwood *et al*., 1999) are all attractive to aphidiine parasitoids. Herbivore-induced plant volatiles are also used for long-range orientation (Du *et al*., 1998; Mölck *et al*., 1999). These cues are particularly important for generalists that parasitize aphids feeding on a variety of plants. Wind tunnel and olfactometer experiments have shown that the searching behaviour of *A. ervi* was influenced by synomones released by broad beans (*Vicia faba*) infested with *Acyrthosiphon pisum* (Du *et al*., 1998; Powell *et al*., 1998; Guerrieri *et al*., 1999). The directed flights of *Aphidius rosae* within a rose bush towards branches infested with *Macrosiphum rosae* was guided by both aphid-borne cues and herbivore-induced volatiles (Völkl, 1994a). However, a parasitoid's response to plant volatiles depends on prior experience (Guerrieri *et al*., 1997); naïve females of *A. ervi* showed no directed response towards plants infested with pea aphids in a semi-natural setting (Schwörer and Völkl, 2001) and naïve *B. communis* females had a much weaker response to host-plant complexes than experienced females (Wyckhuys and Heimpel, 2007).

At the intermediate foraging scale, potential hosts can be found within walking distance or short-range flight, but outside the distance allowing visual host recognition by the parasitoid (Völkl, 1994a). Aphid parasitoids often search systematically (Li *et al*., 1992) and use gustatory and olfactory cues for rapid host location. Aphid honeydew is an important contact kairomone for both parasitoids (Bouchard and Cloutier, 1984) and hyperparasitoids (Grasswitz, 1998; Buitenhuis *et al*., 2004). Parasitoids remain longer on a honeydew-contaminated plant, which increases the probability of host location (Cloutier and Baudouin, 1990; Budenberg and Powell, 1992). Aphid alarm pheromone and secretions from the siphuncules also influence searching at the intermediate scale (Grasswitz and Paine, 1992; Battaglia *et al*., 1993). Some aphidiine species use the presence of honeydew-collecting ants as an indirect indication of potential hosts; female *Pauesia pini*, a parasitoid of *Cinara piceicola*

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(green striped spruce aphid) feeding on *Picea abies* (Norway spruce), searched spruce seedlings more intensively after contact with foraging red wood ants (*Formica polyctena*) than after contact with honeydew in the absence of ants (Völkl, 2000). Aphidiine wasps, such as *Lysiphlebus* species, exploiting aphids associated with trophobiotic ants, respond similarly and possibly even use the ants' communication system (e.g. trail pheromones) to locate their hosts (Völkl, 1997).

Within-patch foraging behaviour

For short-range detection, aphid parasitoids use distance-restricted visual and gustatory information to locate and identify suitable hosts. Visual cues, including aphid colour, shape, size and movement, can be evaluated from a short distance without physical contact (Michaud and Mackauer, 1995; Chau and Mackauer, 2000). Contact chemosensory cues (i.e. gustatory cues) located in the aphid's cuticle induce various behavioural responses in aphidiine wasps (Mackauer *et al*., 1996). In laboratory tests, females of *Aphidius colemani*, *Aphidius picipes* and *Aphelinus abdominalis* responded to aphids at a distance of 3–4 mm, independent of aphid size, but they were unable to discriminate between host and non-host aphids at that distance (Le Ralec *et al*., 2005).

Having successfully located a potential host, the female uses antennation and ovipositor probing to determine whether the host is suitable. Although females of most aphidiine species oviposit in a broad range of host sizes, including aphid embryos (Mackauer and Kambhampati, 1988), they have a preference for particular larval instars and morphs (Chau and Mackauer, 2001; Henry *et al*., 2005; Wyckhuys *et al*., 2008). When exploiting an *M. persicae* colony, *A. colemani* females attacked the more profitable hosts (large aphids) initially, but as the patch became depleted, they switched to accepting the less profitable hosts (small aphids) more frequently (Barrette *et al*., 2010).

Parasitoid preference for host size is correlated with the host's nutritional quality and handling time. Host quality is determined by both species-specific and individual-specific attributes; the latter include aphid size and age at parasitization, attributes that determine an aphid's potential growth until death (Sequeira and Mackauer, 1992). Host quality differs for female and male progeny (Mackauer, 1996). Host quality is an intrinsic property of the host that, presumably, can be evaluated according to absolute criteria, whereas host value is a relative and dynamic property that varies with parasitoid state variables such as age, egg load and prior experience, as well as with the female's mortality risks (Weisser *et al*., 1994; Mackauer *et al*., 1996) and temperature (Moiroux *et al*., 2015). For example, after several ovipositions, and hence a low egg load, a female may place a low value on a high-quality host (and reject it); by contrast, it may place a high value on a low-quality host (and accept it) if hosts of higher quality are not available (Michaud and Mackauer, 1995). However, egg load did not influence the acceptance of low-quality host species by two *Aphelinus* species (Hopper *et al*., 2013), which suggests that the ranking of host species in terms of quality may be static rather than dynamic for aphid parasitoids. One potential explanation for an insensitivity in host-choice decisions correlated with egg load is that some aphidiines are able to mature eggs rapidly, thus maintaining a relatively high egg load even after bouts of oviposition (Dieckhoff and Heimpel, 2010; Dieckhoff *et al*., 2014).

A female can increase offspring fitness by attacking a high-quality, large aphid; however, compared with small aphids, large aphids are able to defend themselves better against attack and can escape (Gerling *et al*., 1990; Chau and Mackauer, 2001; Wyckhuys *et al*., 2008). To counter escape by the host, females of *Monoctonus paulensis* hold an aphid with the forelegs for oviposition (Chau and Mackauer, 2000, 2001). Similarly, *Binodoxys* and related genera use abdominal claspers to grasp aphids during oviposition (Desneux *et al*., 2009). Although offspring developing in large hosts gained in body size and had higher fecundity, females of some species selectively attacked the smallest available aphids, i.e. ones that needed less time for handling and were less likely to escape (Chau and Mackauer, 2001). Barrette *et al*. (2009) showed that handling time was important for the estimation of host profitability when used as a predictor of a parasitoid's choice. In the case of *A. colemani* exploiting *M. persicae*, the fitness gain rate was a better currency for predicting host choice than fitness gain (Fig. 11.8). Late aphid instars were more profitable to *A. colemani* than earlier ones in terms of fitness gain, but they imposed a significant cost because of their increased capacity to defend themselves. These results suggest that parasitoid females assess host profitability from a combination of physiological characteristics and handling time. Other species do show a preference for larger hosts (Lin and Ives, 2003).

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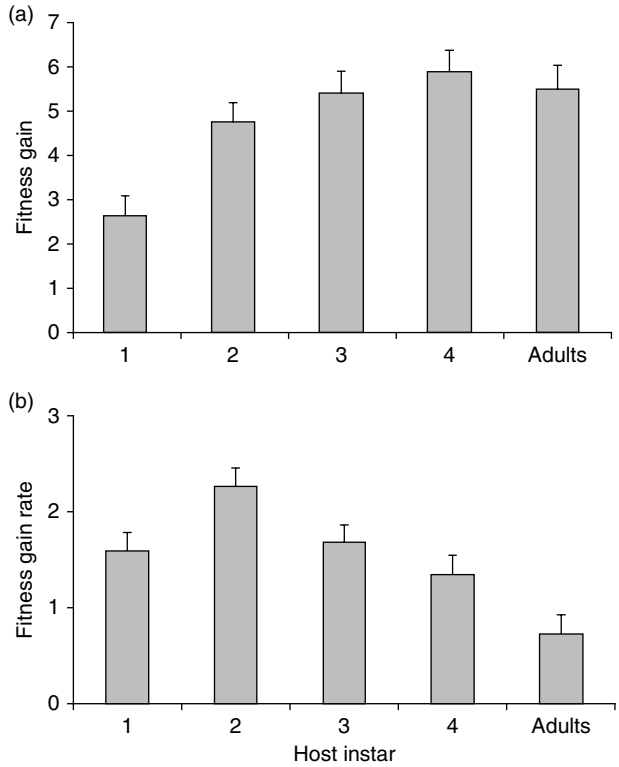

Fig. 11.8. Host profitability in function of host instar in *Aphidius colemani* parasitizing *Myzus persicae*. (a) Fitness gain per host estimated with life-history traits measurement (development time, sex ratio, potential fecundity); (b) fitness gain rate estimated with life-history traits (development time, sex ratio, potential fecundity) and handling time. (From Barrette *et al*., 2009.)

Because normally only one offspring per host survives, females generally reject already parasitized aphids when unparasitized ones are available (Mackauer, 1990). Parasitized aphids are marked with a contact pheromone (Chow and Mackauer, 1986; Hofsvang, 1988). Discrimination between self-parasitized, conspecific-parasitized and heterospecific-parasitized aphids (Völkl and Mackauer, 1990) suggests that the marking pheromones vary among parasitoid species, and possibly also among conspecific females. In addition, stinging and the injection of venom may result in subtle changes in the host's defensive behaviour and a transient paralysis. Mackauer and Chow (1990) showed that in *Aphidius smithi* and *E. californicus*, females 'preferred' pseudoparasitized pea aphids over healthy ones. In contrast, females of *Binodoxys* spp. rejected paralysed hosts, a fact indicating that paralysis might be a possible mechanism for the avoidance of self-superparasitism (Desneux *et al*., 2009).

The level of exploitation of an aphid colony is influenced by the distance between colonies (Tentelier *et al*., 2006), the presence of competitors (Le Lann *et al*., 2011), the size and quality of the colony (Barrette *et al*., 2010) and the patch experience of parasitoid females (Lanteigne *et al*., 2015).

Male foraging behaviour

Few studies have examined foraging behaviour and mate finding by males. Females of aphidiine wasps release a sex pheromone to attract males (McNeil and Brodeur, 1995; Nazzi *et al*., 1996). In contrast to females, which mate only once, males can copulate several times throughout their life (Singh and Pandey, 1997). The virtual absence of virgin females (which can produce only sons) in field populations of aphidiine wasps suggests that mate finding is very effective (Mackauer, 1976; Mackauer and Völkl, 2002; Nyabuga *et al*., 2012).

Virgin females of *Aphelinus asychis* produce a trail sex pheromone, which induces searching behaviour in males (Fauvergue *et al*., 1995).

Patterns of resource use

Aphid parasitoids show different levels of host specialization. Some species attack a few aphid species, whereas others specialize on habitat and exploit most aphid species within a given habitat (Stilmant *et al*., 2008; Desneux *et al*., 2012). Life-table studies indicate that most species of aphid parasitoids can,

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at least in theory, overwhelm their host population (e.g. Mackauer, 1983) and hence should make effective biological control agents. In practice, however, average rates of parasitism in the field are often less than 5%, which is usually insufficient for control in most cases (Hughes, 1989). A number of extrinsic and intrinsic factors account for low impact (Mackauer and Völkl, 1993; Boivin *et al*., 2012). Extrinsic factors, which include environmental conditions and the risk of female mortality (e.g. from predation or hyperparasitism), are discussed first.

Adverse weather conditions such as wind and rain reduce foraging activity, chiefly by preventing females from dispersing in search of hosts (Fink and Völkl, 1995; Weisser *et al*., 1997; Schwörer and Völkl, 2001). Although a wasp's mean residence time per patch is longer during adverse weather conditions than during optimal conditions, the total number of ovipositions declines, which could explain why many parasitoids have low reproductive success in the field despite their high potential fecundity (Fink and Völkl, 1995; Weisser *et al*., 1997). Moreover, parasitoids may change their foraging behaviour in response to perceived adult mortality risks (Rosenheim, 1998). For example, females of *Pauesia silvestris*, a parasitoid of *Cinara* species on Scots pine, foraged more thoroughly on the bark (as opposed to needles) in the absence of honeydew-collecting ants. However, in the presence of ants, which capture and kill parasitoids, females searched more intensively on needles, where they were safe from such attacks (Völkl and Kroupa, 1997). Intraguild predation (see below), ants (see below) and hyperparasitism (Sullivan and Völkl, 1999; Brodeur, 2000) can also limit the potential of parasitoids to suppress aphid populations. For example, Brodeur and McNeil (1992) found levels of hyperparasitism exceeding 65% in mummies harbouring *Aphidius nigripes* in potato fields.

Three general patterns of resource use can be distinguished: host resources are exploited well below the female's actual egg load; the degree of resource exploitation varies with the female's egg load; and the degree of resource exploitation varies with the host type. These patterns are not mutually exclusive but overlap to some degree.

Low resource utilization

Most aphidiine and *Aphelinus* species parasitize a relatively small number of aphids in each colony, regardless of colony size and egg load (Mackauer and Völkl, 1993). Females of *A. rosae* laid, on average, only 2.8 eggs in each colony of rose aphids comprising 10–40 aphids, although the ovaries of each female contained at least 200 mature eggs. Females were most successful attacking aphids in small and medium-sized colonies, while they quickly abandoned large colonies after only a few ovipositions (Mackauer and Völkl, 1993). Similarly, Ives and Settle (1996) found that *A. ervi* provided with high densities of pea aphid produced very few or zero mummies.

Resource utilization varies with ant attendance

This phenomenon is typically found in *Lysiphlebus* species. Foraging behaviour of *Lysiphlebus cardui* for *Aphis fabae cirsiiacanthoides* on C*irsium arvense* was influenced by trophobiotic ants (Völkl, 1994b). In the presence of ants, females generally remained in a discovered aphid colony for long periods, often more than one day, until they had depleted the supply of 200–300 mature eggs in their ovaries or had parasitized all available aphids. However, females laid significantly fewer eggs and dispersed earlier in aphid colonies that were not attended by ants. The aphids' defence behaviour was reduced in the presence of guarding ants, which favoured increased oviposition by the parasitoid. Average rates of parasitism in ant-attended colonies increased with season and could reach 100% due to the parasitoids' increasing colonization success (Weisser, 2000). Similar patterns of resource exploitation were observed in other *Lysiphlebus* species.

Resource utilization varies with the host type

In *P. pini*, patterns of host utilization differed markedly with the generation of its main host, *C. piceicola*, feeding on Norway spruce. Average patch times were longest, and females laid the highest number of eggs when searching for fundatrices and fundatrigeniae in early spring. Oviposition numbers were constrained only by the number of available hosts or eggs, whichever was lower (Völkl and Novak, 1997). By contrast, females laid fewer eggs (independent of colony size) when foraging for viviparous aphids or oviparae later in the season. Rates of parasitism and the number of mummies per colony were lowest during midsummer, when *P. pini* exploited alternate hosts (e.g. *Cinara pinea*) on pine. This seasonal pattern of parasitization was correlated with variation in host size. Differences

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between years were due mainly to variations in environmental conditions. Low temperatures in spring favoured *P. pini*, while high temperatures led to decreased parasitism rates; this could be explained by differences between the activity patterns of *P. pini* and worker ants (*F. polyctena*) that protected the aphids. Parasitoid females were very active at low temperatures and showed increased oviposition rates, while the activity of the worker ants was reduced drastically. A similar pattern of parasitism was observed in *Euaphidius cingulatus*, a parasitoid of aphids in the genus *Pterocomma* on willows (Völkl, 1997). Laboratory studies have also shown that the defensive behaviours of alate aphids and alatoid nymphs were more effective than those of apterae of similar size (Wyckhuys *et al*., 2008).

Aphid Pathogens (Fig. 11.9)

The most significant microbial natural enemies of aphids all belong to the Fungi, although a few RNA viruses have been recorded (van den Heuvel *et al*., 1997; Moon *et al*., 1998; van Munster *et al*., 2002). Most fungi infecting aphids are found in the Entomophthoromycota or the Ascomycota, although species that contribute most regularly to the regulation of aphid populations are from the Entomophthoromycota (Pell *et al*., 2001). At least 29 species of Entomophthoromycota are known to infect aphids (Keller, 2006). Among these, *Pandora neoaphidis*, an aphid specialist infecting >70 species, occurs most frequently, has a worldwide distribution and regularly causes epizootics (Pell *et al*., 2001; Nielsen *et al*., 2003). *Neozygites fresenii*, *Conidiobolus obscurus*, *Zoophthora radicans*, *Entomophthora planchoniana*, and occasionally other species, can also be locally abundant (Pell *et al*., 2001; Steinkraus, 2006). Our knowledge about how common particular species are is influenced both by their ecological traits and by the timing and location of research conducted on them.

Fig. 11.9. *Acyrthosiphon pisum* infected by the entomopathogenic fungus *Pandora neoaphidis*. (Photograph courtesy of Rothamsted Research, Harpenden, UK.) The insert shows the distance over which fungal spores from the cadaver are projected. (Photograph courtesy of J.K. Pell.)

Entomophthoroid species are usually obligate pathogens, while aphid-pathogenic ascomycete species can be facultative. Ascomycota infecting aphids in the field often belong to the genera *Beauveria*, *Isaria* (= *Paecilomyces*), *Lecanicillium* (= *Verticillium*) or *Metarhizium* (Steinkraus, 2006). *Lecanicillium* species from the *lecanii* species complex are the only ascomycetes that regularly cause aphid mortality in nature (Milner, 1997); occasionally they cause epizootics in aphid populations in tropical and subtropical areas (Shah and Pell, 2003).

General biology of aphid-pathogenic fungi

Conidia (spores) are responsible for infection during the season when aphids are most active. After the death of an infected aphid, fungi exit from within the cadaver, particularly through the intersegmental membranes (Butt *et al*., 1990). Many thousands of conidia are then produced externally from each aphid cadaver, with numbers depending on aphid biomass (Steinkraus *et al*., 1993).

Conidia of some species are hydrophilic, being covered with pre-formed mucous (e.g. *Lecanicillium* and entomophthoroid species), while the surfaces of *Beauveria* and *Metarhizium* conidia are hydrophobic (Boucias and Pendland, 1991). Both types of conidia adhere to host cuticle non-specifically and can germinate rapidly; penetration through the cuticle is accomplished by both enzymatic and mechanical means (Askary *et al*., 1999). If an aphid is moulting at the time of cuticular penetration, infection can be prevented because the invading fungus is shed with the cast skin (Kim and Roberts, 2012). Once the fungus has penetrated the cuticle, it grows either as wall-less protoplasts (some

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entomophthoroid species), hyphal bodies, or blastospores within the aphid. Infected aphids produce fewer progeny before death than uninfected ones (e.g. Fournier and Brodeur, 2000; Baverstock *et al*., 2006). For entomophthoroid species, host death is usually caused by physiological starvation of the host after the fungus has utilized all internal contents. For ascomycetes, dying hosts often contain only sparse vegetative growth, and fungal growth continues after the host is dead (Vega *et al*., 2012). For many aphid/fungus combinations, death occurs approximately 3–5 days after infection at 20°C, but can vary with temperature (e.g. Baverstock *et al*., 2008a) and the initial concentration of inoculum (e.g. Fournier and Brodeur, 2000; Hesketh *et al*., 2008).

Some fungal species influence the behaviour of their hosts prior to death, often to improve the likelihood of transmission (Roy *et al*., 2006; Hughes *et al*., 2012). Pea aphids responded less to alarm pheromone prior to death when infected with *P. neoaphidis*; this change in behaviour favours the fungus, as the preservation of aphids in close proximity to one another would improve transmission. Infection of pea aphids with either *P. neoaphidis* or *Beauveria bassiana* also results in higher proportions of progeny developing into alatae (Hatano *et al*., 2012); although this could have evolved to aid aphid escape from infection, it may also facilitate pathogen dispersal.

Host specificity is a highly variable biological trait among species of entomopathogenic fungi. A generalist species may infect and develop successfully in hosts of numerous taxa, while a specialist would infect only one, or a few, host species (Brodeur, 2012). The host range of entomophthoroid species is generally narrower (see below), while for ascomycete species the host range is broader. However, in recent years, molecular analyses of commonly occurring entomopathogenic ascomycetes have shown that what was previously considered as one species could, in fact, be several species. For example, *B. bassiana sensu lato* (Rehner and Buckley, 2005), *Metarhizium anisopliae sensu lato* (Bischoff *et al*., 2009) and *Lecanicillium lecanii sensu lato* (Zare and Gams, 2001) are each composed of several species. Since these taxonomic changes have been made, the host specificity of the newer species has not been entirely determined and, in many cases, the identities of isolates evaluated in older publications on host specificity are simply not known. However, it appears that what can now be identified as *B. bassiana sensu stricto* should still be considered as an opportunist capable of exploiting insects from numerous taxa (Rehner and Buckley, 2005).

Specialized biologies of entomophthoroid species

Entomophthoroid species have unique attributes that are not shared with the distantly related ascomycetes. First, conidia produced by entomophthoroid species are typically actively discharged from conidiophores on cadavers by hydrostatic pressure (Pell *et al*., 2001). Conidial discharge continues for some time; for *Pandora nouryi* emerging from *M. persicae* cadavers under high humidity, peak conidial discharge occurred 12–20 h after aphid death at >15°C (Li *et al*., 2006). After host death, cadavers are often fixed in place on the plant by fungal rhizoids that emerge through the ventral surface of the cadaver (e.g. *P. neoaphidis*, *Zoophthora* species) or through the proboscis (e.g. *C. obscurus*) (Fig. 11.10). Attachment to the substrate ensures that the fungus remains in an optimal environment (often elevated or near other hosts) to promote transmission (Roy *et al*., 2006).

If primary conidia land on non-host surfaces, they produce another conidium (a secondary conidium) that, in *P. neoaphidis*, is also actively discharged, thus increasing the ability of the fungus to reach and infect new aphid hosts. In *Zoophthora* and *Neozygites* species, higher-order conidia are not always actively discharged but are produced on fine capillaries called capilliconidiophores. The capilliconidium is borne on the top of the conidiophore some distance above the surface and remains attached until a host dislodges it. In *Zoophthora* species, both primary and secondary conidia are infective (Glare *et al*., 1985; Pell *et al*., 1993). In *N. fresenii*, only the secondary capilliconidia are infective and the primary conidia serve only as a method of dispersal (Steinkraus, 2006).

Most entomophthoroid species also form persistent double-walled resting spores that are sexually (zygospores) or asexually (azygospores) produced within cadavers as a mechanism for survival during periods when aphids are not present or are at small population densities (Bitton *et al*., 1979). Dead infected aphids containing resting spores remain on foliage and bark or fall to the ground, where the spores can remain dormant for many years. Laboratory studies with *P. nouryi* in *M. persicae*

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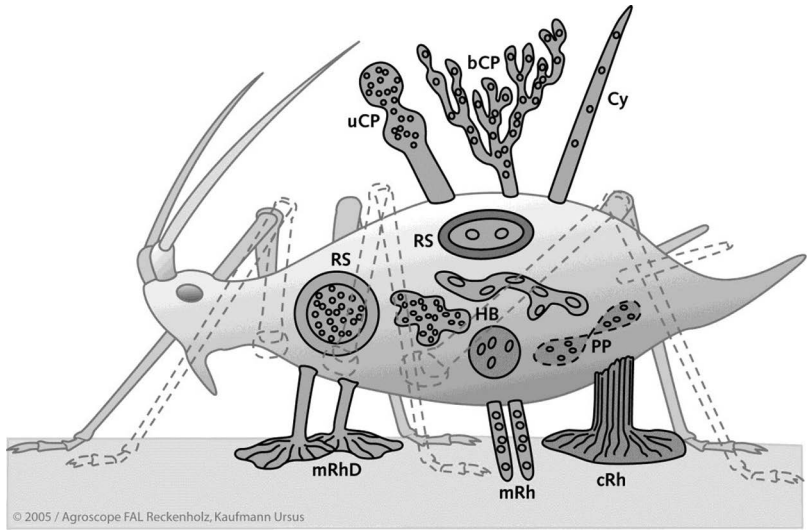

Fig. 11.10. Entomophthoralean structures present inside infected aphids and on the aphid surface. Projected conidia (asexual spores) are not shown. PP = protoplasts; HB = hyphal bodies; RS = resting spores (zygospores or azygospores); uCP = unbranched conidiophores (specialized hyphae from which conidia are produced); bCP = branched conidiophores; Cy = cystidia; mRhD = monohyphal rhizoids with disc-like (specialized) holdfast; mRh = monohyphal rhizoids without specialized holdfast; cRh = compound rhizoid. (From Keller, 2006.)

demonstrated that between 15 and 25°C, resting spore production was associated positively with inoculum level and associated secondarily with temperature and photoperiod (Zhou and Feng, 2010). However, winter field studies in the same system, when temperatures were often <10°C, found that low temperatures were the most important variable associated with resting spore formation (Zhou *et al*., 2012). Resting spores germinate by producing forcibly discharged germ conidia or capilliconidia (the latter only in *N. fresenii*), both of which are infective. Resting spores are formed by *P. neoaphidis* in Argentina (Scorsetti *et al*., 2012), although this fungal species is not known to make resting spores in the northern hemisphere. There, overwintering forms reported include dormant 'loricoconidia' in the soil (Nielsen *et al*., 2003) and specialized spherical hyphal bodies within cadavers on aboveground plant substrates where relative humidity is low (Feng *et al*., 1992). In the laboratory, cadavers can remain capable of producing infective conidia for circa 80–96 days when maintained at a constant 5°C on moist soil, although this capacity is reduced to less than 50 days under natural winter conditions (Nielsen *et al*., 2003; Baverstock *et al*., 2008a). In areas where aphids are present during winter, this ability to persist during colder periods could allow cycles of re-infection to occur during winter (Feng *et al*., 1991). Specialized persistent hyphal bodies within winter-collected aphid cadavers have also been observed for *E. planchoniana* (Keller, 1987).

Epizootiology of entomophthoroid fungi

Epizootiology is 'the study of animal disease dynamics on the basis of mass phenomena', and therefore deals with disease on a population level (Shapiro-Ilan *et al*., 2012). Although the basic fungal life cycle is relatively simple, the epizootiology of fungi within populations is complex and regulated by the host population (density, susceptibility, distribution), the fungus population (density, virulence, distribution) and the environment (temperature and humidity), all of which are linked by transmission (Steinkraus, 2006). Both aphid and fungus populations are discontinuous in the environment, so evolution of the mechanisms that encourage transmission within and between host populations is essential for fungal survival.

Abiotic conditions

Fungi cannot germinate, infect or sporulate if ambient relative humidity falls below 90–93%, making

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moisture the most important limiting factor (Millstein *et al*., 1983; Hemmati *et al*., 2001). *Pandora neoaphidis* infected cadavers produce more conidia when in direct contact with water than when in a saturated environment (Wilding, 1969). There is a positive correlation between *N. fresenii* and *E. planchoniana* induced aphid mortality and the preceding hours of leaf wetness (Ekbom and Pickering, 1990); high infection levels are also associated with rainfall (Hemmati *et al*., 2001). Ambient humidity may be essential in the initiation of an epizootic, but thereafter it becomes secondary as, during the night at least, microclimatic conditions are usually favourable (Hemmati *et al*., 2001). Both *P. neoaphidis* and *Z. radicans* have evolved an internal clock set by the time of dawn that regulates the timing of host death such that it occurs at the end of the photophase, thereby ensuring that sporulation and infection occur during the night (Milner *et al*., 1984). *Neozygites fresenii* also sporulates most profusely at night, suggesting a similar mechanism (Steinkraus *et al*., 1996, 1999).

Temperature affects the number of conidia produced by an aphid cadaver and the rate at which sporulation and infection (time to death) occur; these in turn affect the rate of epizootic establishment. Suboptimal temperatures reduce the number of conidia produced from *Z. radicans* and *P. neoaphidis* infected cadavers and extend the time to germinate, infect and kill (e.g. Leite *et al*., 1996), thereby reducing the rate of transmission and epizootic development. While many entomophthoroid species are less active as temperatures increase, *N. fresenii* is well adapted to function in hot weather (Steinkraus *et al*., 1991, 1995).

Dispersal and contact rate

Actively discharged conidia escape the boundary layer and enter the airstream, facilitating local and distant dispersal (Steinkraus, 2006). Conidia of *N. fresenii* and *P. neoaphidis* have been detected in the air above, and some distance from, crops infested with infected aphids (Steinkraus *et al*., 1996, 1999; Hemmati *et al*., 2001). This is an important mechanism for dispersal between patchily distributed hosts and is highly effective when large numbers of aphids are present. However, it relies entirely on wind direction and many conidia may be lost.

Dispersal of fungi within infected and migrating alatae is more targeted. In a series of studies in China, 19–37% of dispersing alatae from nine different species that landed on isolated, elevated sentinel plants (wheat, brassicas, lettuce) were infected with fungi from five entomophthoroid species (predominantly *P. neoaphidis*) (Feng and Chen, 2002; Huang *et al*., 2008). Furthermore, in flight mill experiments, *P. neoaphidis* infected aphids flew further than uninfected aphids and, having landed, established colonies that subsequently became infected, demonstrating the potential for dispersing alatae to establish infection in a new location (Chen and Feng, 2006).

Another targeted form of dispersal is through vectoring by co-occurring insect natural enemies, particularly predators that have been contaminated by conidia while foraging and then carry the inoculum to new aphid populations. Transmission of *P. neoaphidis* by the ladybirds, *C. septempunctata* and *Harmonia axyridis* (harlequin ladybird) has been reported (Pell *et al*., 1997; Roy *et al*., 2001; Wells *et al*., 2011).

Once an inoculum has entered an aphid population, the rate of transmission is modulated by the rate of contact with new hosts. This can be influenced by both host and inoculum density and distribution, but also by host mobility. In response to insect natural enemies, aphids move around more in order to escape, and this increases their likelihood of contacting inoculum; foraging by both predators and parasitoids increases the transmission of *P. neoaphidis* in surviving populations of several aphid species (Roy *et al*., 1998; Baverstock *et al*., 2009). Even the presence of co-occurring herbivores can encourage aphid movement as a response to crowding, thereby increasing transmission (Baverstock *et al*., 2008b). In a mesocosm-scale experiment, transmission of *P. neoaphidis* in aphid populations on patches of plants of the same species (a host of the aphid) was greater than in aphid populations on patches of plants with a mixture of species (including non-hosts of the aphid) (Baverstock *et al*., 2012). The mechanism for this was related to the mobility and resulting density of the aphids and not the plants themselves; aphids in the single plant species patch distributed themselves evenly among plants at low densities, while in the multiple plant species patches, aphids became concentrated on a limited number of suitable host plants and transmission was greater.

Although some predators also consume, or partially consume, *P. neoaphidis* infected cadavers, this reduction in overall inoculum levels is small by comparison with the large increases in transmission

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observed in the presence of foraging insect natural enemies (Pell *et al*., 1997; Roy *et al*., 1998, 2008). However, ants with a mutualistic relationship with aphids rapidly remove *P. neoaphidis* infected cadavers, and also living infected aphids, before sporulation occurs, which could reduce transmission significantly (Nielsen *et al*., 2010).

Host range, resistance and susceptibility

The host ranges of entomophthoroid fungi are relatively limited. *Pandora neoaphidis*, *E. planchoniana* and *N. fresenii* only infect aphids (Nielsen *et al*., 2001; Pell *et al*., 2001). *Zoophthora radicans* has been recorded from numerous different insect orders, although isolates are often more infective to the host species from which they were isolated than to other species (Pell *et al*., 1993). Within a taxon of insect hosts such as aphids, it can be essential for the survival of the fungus for it to be able to infect a number of different species; *P. neoaphidis* has been recorded from numerous pest and non-pest aphid species (e.g. Pell *et al*., 2001; Manfrino *et al*., 2013). Studies comparing the susceptibility of seven pest aphid species to different isolates of *P. neoaphidis* suggest that some aphid species, particularly *Rhopalosiphum padi*, are resistant (Shah *et al*., 2004), although others have recorded infection of *R. padi* in the field, and sometimes at high levels (e.g. Basky and Hopper, 2000).

The aphid species that is generally considered to be most susceptible to a wide range of *P. neoaphidis* isolates is *A. pisum* (Shah *et al*., 2004), although great variability in susceptibility has also been demonstrated between alatae and apterae (e.g. Lizen *et al*., 1985). In particular, greater resistance to *P. neoaphidis* is seen in some races of *A. pisum* specialized to particular leguminous host plants, and is associated with the presence of mutualist endosymbionts (e.g. Ferrari *et al*., 2004; Scarborough *et al*., 2005). It would seem that this relationship is highly co-evolved in relation to specialist aphid pathogens; while a symbiont confers resistance in the pea aphid to the specialist pathogen *Zoophthora occidentalis*, it provides no resistance to the generalist *B. bassiana* (Parker *et al*., 2013). Interestingly, similar relationships with endosymbionts have not been found in the soybean aphid, *Aphis glycines* (Wulff *et al*., 2013).

For a single clone of pea aphid and a single isolate of *P. neoaphidis*, susceptibility can also vary directly in response to the host plant. Aphids on pea varieties with low levels of leaf wax were more susceptible to *P. neoaphidis* than individuals on high wax varieties (Duetting *et al*., 2003), and aphids cultured on beans were more susceptible if returned to beans after inoculation than if they were returned to other leguminous species (Tkaczuk *et al*., 2007). Among isolates, there is also huge variation in virulence to any particular aphid species (Shah *et al*., 2004). The epizootiology of diseases caused by different isolates therefore depends on a number of virulence parameters associated with the fungal isolate and susceptibility parameters of the host that could interact in complex ways.

Intraguild Interactions and Mutualistic Ants

Intraguild predation and competition

Natural enemies of aphids exist in natural and managed ecosystems as a community that typically includes taxonomically and functionally different groups: predators, parasitoids and pathogens. These communities can be complex, and species can interact with one another through predation and competition. One form of omnivory is intraguild predation (IGP), where one species of natural enemy attacks another species with which it also competes for a shared prey or host species. For example, multifaceted relationships can evolve between a predator, a parasitoid and a fungus that all exploit the same aphid species. Rosenheim *et al*. (1995) concluded that intraguild interactions were widespread within communities of biological control agents of arthropod pests, and that they were likely to influence the efficacy of biological control. The literature is now filled with evidence of positive, negative, or neutral interactions between different types of biological control agents.

Aphid predators are commonly involved in IGP interactions when competing for the same aphid prey within a colony (Lucas, 2005; Hautier *et al*., 2008). Field evidence of a high prevalence of IGP among Aphidophaga species comes from the work of Gagnon *et al*. (2011a,b), who used molecular analyses of gut contents to examine the nature and incidence of IGP among four species of coccinellid predators in soybean fields: *H. axyridis*, *C. septempunctata*, *Coleomegilla maculata* (12-spot ladybird) and *Propylea quatuordecimpunctata* (14-spot ladybird). Levels of IGP were very high, with averages of 47% and 59% of all coccinellids containing

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DNA of other coccinellids in their guts in 2004 and 2005, respectively (Fig. 11.11). Moreover, 13% of the sampled predators contained two, and even three, other coccinellid species in their gut. Under laboratory conditions, Lucas *et al.* (1998) showed that interactions between the larvae of the lacewing *Chrysoperla rufilabris* and the ladybird beetle, *C. maculata*, resulted in reciprocal predation, i.e. both predators were at risk of being eaten by a competitor. Hindayana *et al.* (2001) found that larvae of the hover fly species *E. balteatus* were susceptible to predation by larvae of the lacewing *C. carnea* and the ladybird *C. septempunctata*, while *E. balteatus* pupae were consumed only by lacewing larvae. Lucas *et al.* (1998) suggested that in interactions between members of the same guild, specialist species were more likely than generalists to become prey. In contrast, competition between larvae of the predatory midge *A. aphidimyza* and other aphid predators was always asymmetrical in that gall midge larvae generally served as prey. This species is not adapted to kill prey other than aphids, due to its highly specific feeding requirements (Lucas *et al.*, 1998).

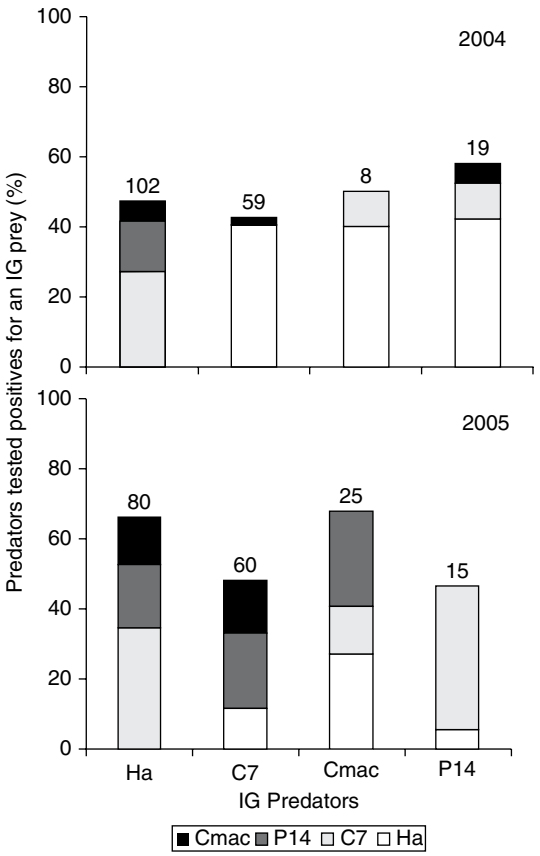

Fig. 11.11. Levels of intraguild predation among four species of ladybird beetles measured by molecular gut content analysis in soybean fields in Québec, Canada, in 2004 and 2005. Results are expressed as the proportion of each species of intraguild prey detected in the gut of intraguild predators. Ha = *Harmonia axyridis*; C7 = *Coccinella septempunctata*; Cmac = *Coleomegilla maculata*; P14 = *Propylea quatuordecimpunctata*. Numbers above histogram bars represent the number of individuals tested. (From Gagnon *et al.*, 2011a.)

The nature, intensity and outcome of intraguild predation among aphidophagous predators are influenced by, for example, climatic conditions (Sentis *et al.*, 2014), identity and age structure of intraguild predators (Lucas *et al.*, 1997; Lucas, 2005), distribution and density of the aphid prey (Lucas and Rosenheim, 2011; Sentis *et al.*, 2013, 2014; Gagnon and Brodeur, 2014) and host-plant architecture (Lucas and Brodeur, 1999).

Aphid parasitoids also experience mortality due to intraguild predation (Brodeur and Rosenheim, 2000). Brodeur and McNeil (1992) showed that predation of *A. nigripes* mummies on potato accounted for 15% of total parasitoid mortality. Working in cotton, Colfer and Rosenheim (2000) demonstrated that adult coccinellids consumed numerous aphid mummies, although they preferred living aphids as prey. Similarly, *B. communis* in *A. glycines* (soybean aphid) mummies on soybean are at risk of predation, and IGP tends to increase over the season as aphid density increases and more predators are attracted to aphid aggregations (Heimpel *et al.*, 2010). Some species of aphid parasitoid have evolved mechanisms to reduce IGP. For example, *A. ervi* females avoided leaves visited by the larvae and adults of *C. septempunctata* during the previous 24 h, but not if the interval was greater (Nakashima *et al.*, 2004). In contrast, avoidance behaviour was not observed in *L. fabarum* foraging in aphid colonies in which adult *C. septempunctata* and larvae of *E. balteatus* were present (Meyhöfer and Klug, 2002).

Fungal pathogens with a broad host range can also be involved in intraguild interactions. This applies in particular to some mitosporic fungi developed as mycoinsecticides for use against aphids. For example, *B. bassiana*, *Paecilomyces fumosoroseus* and *Lecanicillium* spp. can infect aphid predators and parasitoids, but often only at high doses and/or

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under laboratory conditions favouring the fungus and/or stressing the host (Lacey *et al*., 1997; Askary and Brodeur, 1999; Pell and Vandenberg, 2002). Physiological susceptibility under laboratory conditions often represents the 'worst case scenario' for infection of beneficial insects, which may differ from ecological susceptibility in the field. Beneficial arthropods and mitosporic mycoinsecticides can, therefore, coexist even when the potential of some isolates and species for infecting beneficial organisms has been demonstrated in the laboratory (James *et al*., 1998).

Within the guild of aphid natural enemies, arthropod predators can be intraguild predators of fungi, and also affect fungal dispersal and transmission (Roy and Pell, 2000). For example, the ladybird, *C. septempunctata*, and the carabid beetle, *Pterostichus madidus*, both feed on aphid cadavers sporulating with *P. neoaphidis*, in contrast to larvae of the lacewing, *C. carnea*, and the hover fly, *E. balteatus*, which do not consume *P. neoaphidis* infected aphids (Roy *et al*., 2001). In this study, *P. neoaphidis* infected aphid cadavers were less palatable to *C. septempunctata* larvae than uninfected ones. Hungry larvae did attempt to consume cadavers, but never consumed them entirely. Rates of transmission were increased significantly in the presence of foraging ladybirds (Roy *et al*., 2001), which suggests that predators may, in fact, enhance the transmission and dispersal of entomopathogenic fungi rather than having a negative impact as intraguild predators (Roy *et al*., 2001; Pell and Vandenberg, 2002).

Interactions between parasitoids and pathogens are generally asymmetrical in favour of the pathogen. The pathogen invariably kills the host faster than the parasitoid can complete its development, although the final outcome of such competitive interactions is dependent on the relative timing of parasitism and infection (Kim *et al*., 2005). Development of the parasitoid *A. nigripes* was impeded by the fungus *Lecanicillium* sp., but many parasitoids still emerged from aphids infected 4 days after parasitization (Askary and Brodeur, 1999). Interactions between pathogens and parasitoids are also affected by plant resistance. Fuentes-Contreras *et al*. (1998) reported that aphids and parasitoids developed more slowly on aphid-resistant wheat cultivars, but the time required for an aphid to be killed by a fungus remained the same. Some parasitoids avoid infected hosts (Brobyn *et al*., 1988). There is some evidence that the combination of parasitoids and fungal pathogens can have an additive effect with respect to aphid control (Hagen and van den Bosch, 1968); that is, that parasitoids are not affected negatively by entomopathogenic fungi. This is supported by field experiments. For example, recent evidence indicates that aphid control can be enhanced by the combination of different natural enemies. For instance, the combination of the parasitoid *A. asychis* and the fungus *P. fumosoroseus* resulted in better control of *D. noxia* than did the application of a single antagonist; percentage parasitism and parasitoid emergence were not affected by the fungus (Mesquita *et al*., 1997).

The effect of mutualistic interactions with ants on predation and parasitism

Many aphid species have evolved mutualistic relationships with honeydew-collecting ants (Buckley, 1987). Both partners derive benefits from this association; the ants gain access to nutrients and, by attacking intruders into an aphid colony (potential competitors for the carbohydrate source), act as effective guards against the aphids' natural enemies. The adults and larvae of coccinellid species were more abundant in areas where ants were naturally absent or experimentally excluded (Sloggett and Majerus, 2000b; Majerus *et al*., 2007). There is less information about the influence of ants on the density of other predatory species, especially syrphid and chrysopid larvae. Müller and Godfray (1999) and Fischer *et al*. (2001) demonstrated a general decrease in predator density in ant-attended colonies, which in turn persisted longer. On tansy, the predacious bug *A. nemorum* was significantly less abundant in ant-attended colonies of *Metopeurum fuscoviride* than in unattended ones, where the presence of predators significantly reduced colony persistence (Fischer *et al*., 2001).

Ant-attendance also reduces the risk of parasitism. Völkl (1997) reported that in central Europe, 14 of 40 parasitoid species attacking ant-attended aphids, when approaching an aphid colony, were generally treated aggressively by honeydew-collecting ant workers. Therefore, resource utilization by these parasitoid species was widely restricted to unattended aphid colonies. Foraging parasitoids were more effective when ant-tended aphid colonies were feeding on plants with a high structural diversity (e.g. leaves and flowers of *Chenopodium* spp.) than on plants with a low structural diversity (e.g. stems of the thistle *C. arvense*; Mackauer and Völkl, 1993; Völkl, 1997). A number of predator and

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parasitoid species have evolved morphological, chemical and/or behavioural adaptations to gain access to ant-attended resources (e.g. Eisner *et al*., 1978; Liepert and Dettner, 1993; Völkl and Mackauer, 1993; Sloggett *et al*., 1998).

Ant-parasitoid and ant-predator interactions can affect the outcome of biological control. An example of this is the release of the polyphagous parasitoid *A. colemani* in the South Pacific for biological control of *Pentalonia nigronervosa* (banana aphid) (Völkl *et al*., 1990). Small aphid colonies occur mainly in concealed areas of the banana plant, such as the space between pseudostems and leaf sheaths. *Aphidius colemani* females foraged intensively in these areas, but were ineffective as control agents because they were heavily attacked by honeydew-collecting ants (Stechmann *et al*., 1996). Moreover, the abundance of predators was also reduced by ant attendance (Stechmann and Völkl, 1990).

The role of defensive aphid endosymbionts

Not all aphids are equally susceptible to parasitism and infection. Even within the same aphid species, considerable variation can exist for resistance to a specific parasitoid (Henter and Via, 1995). Aphids harbour several bacterial endosymbionts. These include the primary (obligate) bacterium *Buchnera aphidicola*, as well as a number of secondary symbionts that are facultative and thus not needed for aphid survival (Douglas, 1998; Oliver *et al*., 2010). Among the secondary endosymbionts, bacteria have been identified that have a variety of effects on their aphid hosts, including thermal tolerance, efficiency of host-plant use and defence against fungal pathogens and parasitoids (Oliver *et al*., 2010).

Symbiont-mediated defence has been identified against both parasitoids and pathogens (Oliver *et al*., 2014). The best-studied symbiont–host–enemy system in this context is *Candidatus* Hamiltonella defensa protecting the pea aphid, *A. pisum*, from the aphidiine parasitoid *A. ervi* (Oliver *et al*., 2010). This protection (though usually not complete) is mediated by a bacteriophage ('APSE') that encodes a toxin acting on parasitoid eggs and/or larvae (Oliver *et al*., 2010). *Candidatus* H. defensa also protects the black bean aphid, *A. fabae*, against the aphidiine *L. fabarum*, and here variation in defensive performance suggests a co-evolutionary arms race between the symbiont (and/or its phage) and the parasitoid (Schmid *et al*., 2012; Rouchet and Vorburger, 2014). Last, *Ca.* H. defensa has been found to protect the cowpea aphid, *Aphis craccivora*, against successful parasitism by two species of *Binodoxys* but not against *Lysiphlebus orientalis* or *A. colemani* (Asplen *et al*., 2014). This study indicates that the effect of *Ca.* H. defensa and/or its phage may be host-genus specific. However, Hopper *et al*. (unpublished) found that *A. craccivora* was not protected by *Ca.* H. defensa against parasitism by two species of *Aphelinus*. Some endosymbionts other than *Ca.* H. defensa may also confer resistance to aphids, including *Candidatus* Regiella insecticola (Vorburger *et al*., 2010) and *Spiroplasma symbiotica* (Oliver *et al*., 2003). Even when effective against some parasitoids, defensive symbionts in aphids are not ubiquitous in aphid populations and frequently occur at intermediate frequencies (Oliver *et al*., 2014). This is likely to be due to costs of infection and incomplete vertical transmission of the symbionts (Dykstra *et al*., 2014; Oliver *et al*., 2014).

Endosymbiont-mediated protection against fungal pathogens has not been studied as well as protection against parasitoids. Bacterial symbionts in the genera *Regiella*, *Rickettsia*, *Rickettsiella* and *Spiroplasma*, which are all distantly related to each other, all protect pea aphids against *P. neoaphidis* by increasing resistance and lowering transmission (Scarborough *et al*., 2005; Lukasik *et al*., 2013). In contrast, the secondary bacterial endosymbiont in soybean aphids, *Arsenophonus*, did not influence infection by *P. neoaphidis* (Wulff *et al*., 2013).

Conclusion

Aphids are attacked by a wide range of natural enemies, many of which are highly fecund and, at least in theory, should be capable of reducing aphid populations below economic thresholds. However, Aphidophaga often fail to achieve their expected potential in the field. Many predators are not very effective in locating aphid prey, and specific habitat requirements (such as the availability of a pollen or nectar supply as food for adults) additionally reduce their activity in the vicinity of aphid colonies. Although parasitoids apparently are very successful foragers within their habitat, species-specific oviposition strategies may cause their departure before all available hosts in a colony are exploited. Similarly, aphid-pathogenic fungi have effective transmission and dispersal mechanisms but can be limited by their requirement for high humidity. Intraguild predation additionally may lower the impact of Aphidophaga.

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Biological control of aphid pests has achieved notable successes (Chapter 20, this volume), although the results have remained difficult to predict. We suggest that the practice of biological control currently does not reflect all the available information on predators, parasitoids and pathogens. Such information not only is critically important in the selection of the most appropriate control strategy but also it may explain why control is only partially successful in some situations or in only part of the pest's range.

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12 Population Dynamics: Cycles and Patterns

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Introduction

The aim of the study of population dynamics is to identify the causes of numerical change in a population and explain how the interaction between these causes results in the observed changes. Figure 13.1, this volume, illustrates many of the components involved. These components have been allocated separate chapters in this volume, and the next chapter takes one important crop pest species, *Sitobion avenae* (English grain aphid), and uses a modelling approach to illustrate how the components integrate to describe its population dynamics over different spatial scales.

This chapter looks at the abundance on crops of several aphid species and what explanations for the patterns observed can be proposed from field-derived evidence.

Analyses based on age-specific life tables and key-factor analysis, which are well-established techniques for many other insects (Southwood, 1966), are not available in their normal format to aphidologists. Such analyses require a census of the different life stages of the insect over several generations; this is impossible when generations largely overlap, as they rapidly do with aphids following initial establishment. Also, the polyphenism of aphids, with high numbers of a local population being dispersing alatae, can result in subpopulations on widely differing host plants. Some of these may be crops, and others wild plants; up to now, this has severely limited our understanding of the population dynamics of the regional population of an aphid species.

Given the complexities when subpopulations occur on a succession of hosts, long-term studies of aphid population dynamics have focused on monoecious aphids on long-lived plants such as trees. It is then possible to census a resident aphid population over an extended period. The best-known example is probably the work of Dixon and his co-workers over many years on the sycamore aphid, *Drepanosiphum platanoidis* (Kindlmann *et al*., 2007).

Overwintering Populations

Most aphids that are crop pests are of primary interest on an ephemeral crop plant, but also utilize other plants at other times. Until now, the emphasis on studying their population dynamics has been on the population cycle on the crop, which only on a regional and not on a field scale is likely to be relevant to the long-term population dynamics of a species.

The annual nature/management of most crops means that the aphids often need to disperse to other hosts for overwintering, though in mild winters in the UK some aphids can overwinter on autumn-sown or perennial crops; this then leads to an earlier build-up of the population in spring (Oakley and Walters, 2008). Overwintering populations of *Rhopalosiphum padi* (bird cherry–oat aphid) can often be found on autumn-sown cereal crops, and Morgan (2008) theorized from a simulation model with barley that decreasing the mortality rates of apterous nymphs by as little as 5% over the

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autumn and winter amplified summer peak densities by as much as 60-fold.

Most crop pest aphid species are able to reproduce sexually, and in temperate regions this typically occurs in autumn (Dixon, 1973). After mating, oviparous females produce eggs that overwinter. Aphids may overwinter as eggs or in the mobile stages. Some species adopt one or the other strategy exclusively, but some have different options in different clones (Chapter 4, this volume). Aphid population dynamics over winter are dependent primarily on temperature and predation. The impact of these factors determines levels of mortality and can be direct, interactive or mediated through their effect on plant condition.

Only a small proportion of the alatae leaving crops will find a suitable host for overwintering (Ward *et al*., 1998). Where species overwinter on wild herbaceous plants (e.g. *Myzus persicae* – Davis and Radcliffe, 2008) or grasses scattered over large areas, sampling populations is nigh on impossible. Much of our knowledge on winter mortality in the field (where there are a variety of mortality factors) therefore comes from species that overwinter on trees, and particularly in the egg stage. However, much laboratory work has been done on the cold-hardiness of many aphid species feeding on crops (reviewed by Bale, 1999), which has shown the ability of eggs to survive temperatures as low as –40°C, although nymphs and adults start to die at temperatures as high as –5°C. Winter temperatures in southern England thus do not generally affect eggs, but can lead to mortality of newly hatched nymphs (Way and Banks, 1964). Harrington and Taylor (1990) followed field populations of *M. persicae* through the winter on brassicas and found that a major cause of mortality was low temperature inhibiting movement to suitable new feeding sites within a plant.

Correlations between *Diuraphis noxia* abundance and remote-sensed imagery have allowed the development of models using vegetation indices to be used as proxies for overwintering aphid abundance. Soil and topography are important factors, possibly due to desiccation increasing aphid mortality rates (Merrill *et al*., 2009). Mortality of overwintering *D. noxia* nymphs and adults correlates strongly with the accumulated hours below 0°C (Armstrong and Peairs, 1996). Havelka *et al*. (2014) found that >87 day degrees below –5°C led to complete mortality of anholocyclic *D. noxia* populations.

Temperature and predation can interact by affecting the development and activity of predator populations. Favourable temperature conditions for overwintering active aphids are also suitable for parasitoids, which may then effectively control aphid populations, whereas in the absence of parasitoids, aphid populations increase rapidly (Legrand *et al*., 2004). With some species such as *M. persicae*, however, higher populations are found in winters with higher temperatures, regardless of the presence of several predator groups, which do not appear to affect winter survival (Harrington and Cheng, 1984).

Table 12.1. Overwintering mortality of eggs of six aphid species in the field. (Modified from Leather, 1993, which includes the full references.)

Aphid species	Mortality (%)
Acyrthosiphon pisum	67.0–70.0
	83.0
	72.0
Aphis fabae	40.0
Metopolophium dirhodum	66.0
	59.0–62.0
Myzus persicae	30.0–60.0
Rhopalosiphum padi	70.0
	70.0
	80.0
	48.1–87.5
Sitobion avenae	50.0–99.0
	23.0–62.0

Leather (1993) gives data from 13 sources on the egg mortality over winter of six aphid species (Table 12.1). Mortality ranged from 23 to 99%, and included eight instances of 70% or over. Such high mortalities would be largely due to predation. *Aphis fabae* (black bean aphid) eggs on spindle trees (*Euonymus europaeus*) suffer mortality between 18 and 73%, with evidence of predation by birds and anthocorid bugs, although some eggs fail to hatch despite developing fully, even when predators are absent (Way and Banks, 1964). Eggs of *Aphis glycines* show similar high levels of mortality (~70%; Welsman *et al*., 2007). The impact of predators may be affected by temperature (see above).

Spring Populations

Few data seem available on the effect of abiotic factors on the development of populations in spring at the overwintering sites, but the positive effects of temperature on aphid development time

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and fecundity are well established (Chapter 5, this volume). Higher spring temperatures increase numbers and rainfall decreases populations of *M. persicae* (Cocu *et al*., 2005).

Predation probably has a limited impact on aphid populations in the spring. Although many predators were found on bird cherry in the spring, a high proportion of the *R. padi* population was winged by the time predator numbers peaked, suggesting that emigration to grasses explained the population decline on the winter host rather than predation (Leather and Lethi, 1982). A similar situation occurs for *A. fabae*, where fundatrices hatch 3–6 weeks before natural enemies become common, suggesting a time lag between aphid and predator populations and that predation does not affect aphid populations significantly at this time (Way and Banks, 1968).

Onset of Dispersal to Crops

The dispersal of aphids to crops is usually a consequence of a switch from the production of wingless to winged offspring. In host-alternating aphids, the number of wingless generations that occur following egg hatch on the woody winter host before winged emigrants appear is usually determined genetically. In aphids passing the winter in the mobile stages, the proportion of alatae usually increases as the population becomes crowded, and as the young spring growth of the winter host plant becomes mature and less suitable for the aphids (Chapter 4, this volume).

Intraspecific competition as population density increases leads to an increase in the proportion of winged aphids and a slowdown in the reproductive rate of wingless adults (Way and Banks, 1968). If high numbers of aphids overwinter, there will be fewer parthenogenetic generations than at lower densities before winged forms are produced (Wiktelius, 1984). However, some host-alternating aphids can persist on their primary hosts under certain conditions. The rose aphid (*Macrosiphum rosae*), for example, can continue to produce sexual morphs on roses; these aphids then join in the sexual phase with those returning in the autumn from secondary hosts (Blackman and Eastop, 2006).

Arrival on Crops

The timing of immigration will be affected by differences in temperature conditions between years, and climate change is obviously highly relevant here. In general, higher spring temperatures advance the onset of migration and rainfall delays it (Cocu *et al*., 2005).

A point often ignored is that insect and plant phenologies often have different drivers. The timing of aphid dispersal to crops is largely dependent on temperature, whereas many aspects of the development of plants are to a great extent governed by photoperiod, which remains consistent from year to year. Since under a climate change scenario photoperiod remains constant, it is likely to have a considerable impact on the interaction between aphids and their host plants.

Some areas that suffer from aphid pests do not host overwintering populations. In Minnesota, USA, *M. persicae* migrates from the south to colonize herbaceous plants before moving on to potato crops (Davis and Radcliffe, 2008).

In a survey of a large agricultural region, Macfadyen *et al*. (2015) found that the timing of emigration by aphid crop pests overwintering in the mobile stages close to the crop occurred shortly after crop emergence. By contrast, host-alternating aphids such as *A. glycines* tend to have a delayed arrival in relation to the phenology of the crop (Hodgson *et al*., 2005). Indeed, Ragsdale *et al*. (2004) report a lengthy gap between the production of alatae on *Rhamnus* spp. in the spring and the arrival of the aphid on soybean. This suggests that a third host plant is involved. Aphids that initially colonize crops can be from transient migrant populations as well as local overwintering populations from adjacent hedgerows and natural vegetation. Using genetic profiling of aphids caught in suction traps, Vialatte *et al*. (2007) showed that *S. avenae* tended to come mainly from local overwintering sites in years with a major aphid outbreak on wheat crops.

The prediction of the likely size of aphid populations arriving on crops is discussed in Chapter 16, this volume.

The Population Cycle on Crops

Methodology

Most aphids that are crop pests are of primary interest on an ephemeral crop plant, and they utilize other plants at other times. Until now, the emphasis on studying their population dynamics has been on the population cycle on the crop.

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This is unlikely to be relevant to the long-term population dynamics of a species (see earlier); a population explosion or crash there will have little or no impact on the dynamics of the regional population (Mackauer and Way, 1976). Thus, Onstad *et al*. (2005) found little similarity among 14 soybean fields in Illinois, USA, in three summers, either in the number of *A. glycines* or synchrony in their population dynamics.

Speculation as to the reasons for the changes of aphid numbers on a crop have often been based on nothing more than the numbers of apterous aphids and alatoid nymphs counted in a sequence of visual inspections of the crop, coupled with counts of predators, mummies and diseased aphids noticed at the same time. Smith (1966) sought to identify the relative importance of the different factors involved in population changes between successive samples of *Acyrthosiphon pisum* subsp. *spartii* on *Cytisus scoparius* (broom) by calculating aphid increase rates from laboratory data and working out predation from the number of predators seen multiplied by the voracity of the different predator taxa in the laboratory. Unfortunately, aphid increase and predator voracity calculated at constant temperature does not reflect what happens in the field, where the temperature fluctuates. For aphids, fecundity is very different between fluctuating and constant temperatures, though the direction of difference varies between studies (Chapter 5, this volume). For natural enemies, Hodek (1957) showed that *Coccinella septempunctata* larvae doubled their food consumption at naturally fluctuating temperatures in comparison with their voracity at constant temperature equivalent to the mean of the fluctuating temperature. Moreover, plants grown under controlled and usually artificially lit conditions are of quite different and often poorer quality as hosts for aphids. Furthermore, predator voracities in the laboratory ignore the time spent searching in the field, but perhaps more importantly, predator numbers encountered while sampling aphids are likely to be serious underestimates (see later). As a result, Smith (1966) overestimated aphid increase rates and underestimated predation by insect taxa to the extent that he had a huge gap of unexplained mortality, for which he invoked predation by birds.

Others have attempted to measure mortality factors and emigration directly in the field. van Emden (1963), working with *Brevicoryne brassicae* on Brussels sprouts, marked 120 leaves with colonies and visited them every 4 days to look for non-emerged mummies, cast skins of departed alatae, signs of activity of predators, such as moist smears and sucked aphids, new mummies formed, etc. When no more aphids were left on a leaf, a substitute was marked on a nearby plant. No attempt was made to measure aphid increase rate in the field, but counts of the aphid population on the crop at the same sampling intervals were made.

van den Berg *et al*. (1997) and Mills and Latham (2009) made direct observations of aphid colonies for standardized time windows to assess predation; however, much predation happens at night. van den Berg *et al*. (1997) used clip cages to try to measure aphid increase rate in the absence of predators.

In the end, data on changes in aphid reproductive rate will have to be included in a population dynamics exercise, and at present we do not have a satisfactory numerical approach for such an analysis conducted on a crop. The principal barrier is that changes in aphid reproductive rate are crucial; they are continually affected by temperature and other weather variables and also by host substrate condition, which also varies continually with weather and as leaves mature and then age (van Emden, 1965; van Emden and Bashford, 1969). Perhaps not surprisingly, therefore, Tenhumberg *et al*. (2009) found a large discrepancy between the mean *Acyrthosiphon pisum* (pea aphid) population derived from a single adult when modelled on the basis of temperature (531) and the empirical population (2394). However, Hughes (1962; full methodology details are given by Hughes, 1976) explored the possibilities of developing a time-specific rather than an age-specific form of population analysis of a crop aphid. His life table was based on the concept of an 'instar period', taken as a constant if measured on the physiological timescale of day degrees above the threshold temperature for development. His analysis was based on 'twin samples' taken one instar period apart (Fig. 12.1). On the first sampling occasion, leaves were collected and the aphids in the different instars counted. A second batch of leaves was taken with predators, mummies and diseased aphids removed and kept in the laboratory, so that the number of new mummies and diseased aphids appearing in one instar period was known. The potential rate of increase (new first-instar aphids) during the instar period was calculated from the relative number of aphids in the first, second and third instars, on the assumption that these formed a geometric series

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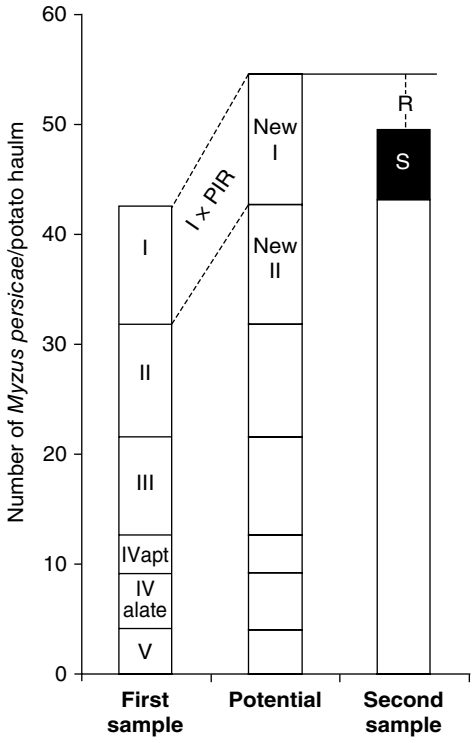

Fig. 12.1. Example of a time-specific age analysis from twin-sample data for *Myzus persicae* in potatoes from the International Biological Programme (see text). I–V = aphid instars; apt = apterous; PIR = potential increase rate calculated from proportions of aphids in the first three instars; R = residual mortality; S = measurable subtractive processes. (Modified from Mackauer and Way, 1976.)

(tested by chi-square). Thus, the actual population in the second sample could be compared with an 'expected' population assuming no mortality. Once the measured subtractive factors had been taken into account, any gap remaining ('residual mortality') was regarded as the maximum mortality attributable to predation. The technique has been criticized by Carter *et al.* (1978) on the basis that stable geometric series of the first three instars will rarely occur in the field. It is also true that, since chi-square is scale dependent, the instar series will need to be based on large numbers to give the test adequate discrimination.

Hughes's method has not been widely used, but probably more because of the labour involved in instar identification than for statistical reservations. The concept that an increasing proportion of younger aphids in a population indicates a high potential increase rate is reasonable, and Hughes's calculation is one approach. The evidence is that it gives estimates of residual mortality that are within the range of predation impact that can be expected, certainly in contrast with residual mortalities obtained when laboratory data are applied to the field. During the International Biological Programme of 1964–1974, the biological control of *M. persicae* on potatoes was studied in ten countries in 1970/71 (Mackauer and Way, 1976). The Hughes technique was used by eight workers in five countries, producing 34 twin-sample data. Only four produced measurable negative residual mortalities, and in every case these data were taken at very low population levels. Even then, chi-square showed a significant deviation of numbers in instars I–III from a geometric series. Aalbersberg *et al.* (1988) found the technique worked well for *D. noxia* except during the population crash at the end of the season, when negative residual mortalities could be found.

Factors causing numerical change

Initial reproductive rates vary considerably between species. Aphid pests of perennial crops such as *Aphis spiraecola* (green citrus aphid) on citrus have a rapid population increase in the spring, originating from the initial immigrant alates then supplemented by alates from other host plants nearby (Zehavi and Rosen, 1987; Lebbal and Laamari, 2015). On annual crops, aphid populations are characterized by a typical logistic curve (Chapter 13, this volume), with initially low levels of reproduction. Infestations of *D. noxia* that disappear early in wheat (before the appearance of the first node) do not cause any economic yield loss (Kriel *et al.*, 1986). Predators may follow aphid pests from adjacent native vegetation into the crop rapidly (Macfadyen *et al.*, 2015), but at the start of the infestation, predation rates are typically insufficiently high to counter new aphid immigrants, and populations inevitably begin to rise (Costamagna *et al.*, 2013a).

Abiotic factors

Changes in aphid populations are affected by weather, with temperature and rainfall the most important factors. Developmental time, reproductive capacity, longevity and mean generation time

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are all correlated positively with increasing temperature, up to a threshold level that differs from species to species (Slosser *et al.*, 1989; Chapter 13, this volume). Up to 90% of variation in population change of *D. noxia* is explained by accumulated 'heat units' and rainfall (Legg and Brewer, 1995). High temperatures become detrimental; for example, temperatures above 25°C are detrimental to *A. pisum* population growth (Campbell and Mackauer, 1977). In the summer of 1976, temperatures in southern England caused a collapse of cereal aphid populations, and adult syrphids and coccinellids searching for food became highly apparent to the public; there were many reports of coccinellids biting people (H.F. van Emden, unpublished).

Increasing temperature (up to an optimum) of course increases the rate of reproduction of predators as well as that of aphids, and different rates of such change with temperature in predators and aphids have the potential for improving the impact of predators at different, especially lower, temperatures (van Emden, 1966 – using data of Dunn, 1952). Low temperatures can be beneficial to aphid populations in delaying the colonization of the crop by natural enemies (Nakata, 1994).

Bouts of heavy rainfall can knock aphids off plants, resulting in sudden, and sometimes dramatic, reductions in aphid populations, especially when in combination with high winds (Walker *et al.*, 1984; Atsebeha *et al.*, 2009). Some aphids, for example *S. avenae* in the crevices between the ear kernels (Watt, 1979), have behaviour that renders them less susceptible to being knocked off the plant. High levels of rainfall can create suitable conditions for fungal infection of aphids, although aphids that are found in more humid microhabitats (e.g. *Metopolophium dirhodum* (rose–grain aphid) and *D. noxia* as contrasted with *S. avenae*) are less affected (Feng *et al.*, 1991).

Humidity can also be important for some aphid species. *Aphis spiraecola* requires high levels of humidity (~40% RH) for population growth, with humidity lower than this leading to population decline (Dubey and Singh, 2011).

Natural enemies

Other chapters in this volume (Chapters 11 and 20, respectively) review the natural enemies of aphids and their practical use in the biological control of aphids. Here, we limit ourselves to natural enemies already present in the environment as drivers of population change in the field.

Natural enemies have variable impacts on aphid populations on the crop. Different predator groups respond differently to aphid presence and population levels. Whether natural enemies can control aphid pests seems to vary with the species of aphid, and often with year for the same aphid species. Much predation of aphids in winter wheat occurs at night and involves ground-dwelling staphylinids (Holmes, 1984) and spiders, which are not included in estimates of predator numbers made during the hours of daylight. When plant conditions are favourable (see later), predators or parasitoids rarely have a major impact at the early logarithmic phase of aphid population growth (Tomanović *et al.*, 2008; Lozzia *et al.*, 2013; Ullah *et al.*, 2014). However, when crops are grown in structurally complex landscapes, they are colonized earlier by natural enemies, which may result in more effective control of aphids during this phase of population growth (Raymond *et al.*, 2015). Specialist predators such as coccinellids often track population changes in aphid crop pests closely, so that the highest predator densities are found at the aphid peak in the crop (Hutchinson and Hogg, 1985; Idris and Roff, 2002; Soni *et al.*, 2013). Thus, densities of syrphids also track changes in *A. pisum* populations throughout the season, as do rates of parasitization (Nakashima and Akashi, 2005). Such correlations are indicative of a positive density-dependent numerical response, and there is often no impact on the aphid population. This indicates that, in contrast to the numerical response, functional responses are often negatively density dependent; that is, in the exponential phase of aphid population growth, the time taken by predators to find and consume prey is too long for them to be able to keep up with the increase rate of their prey (Costamagna *et al.*, 2013a). On soybean, however, the aphids located on the upper nodes have the highest reproductive potential and, because the predators concentrate there, *A. glycines* is controlled effectively (Costamagna *et al.*, 2013b). The peak of predator abundance is usually later than the aphid peak, again indicating that effective control by natural enemies is not occurring. For example, both *M. persicae* and *Aphis gossypii* (melon or cotton aphid) peaked on vegetable crops 3 weeks before the predator; the aphids were not controlled effectively in these crops (Vuong *et al.*, 2001).

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The impact of parasitoids is often increasingly reduced after the first generation by hyperparasitoids (Summy and Gilstrap, 1983; Walker *et al*., 1984); hyperparasitization not infrequently approaches 100% by the end of the season. Only when parasitization levels surpass 30% do *A. gossypii* populations start to decline (Slosser *et al*., 1989), and aphid populations in wheat collapse when parasitization rates reach 50% (Abdel-Rahman *et al*., 2000). Parasitization rates quoted are usually much lower than this; the <9% recorded by Hutchinson and Hogg (1985) is perhaps more typical. However, estimates of parasitization based on mummies are probably considerable underestimates, since many parasitized aphids leave the plant to mummify on the ground (Gowling and van Emden, 1994). Summy and Gilstrap (1983) regard the removal of numbers of immature primary parasites in alate *Schizaphis graminum* (greenbug) as significant. Estimates of both parasitization and predation usually ignore such 'non-consumptive' mortality; the activity of natural enemies causes a significant proportion of aphids to be lost after falling off the plant (Fig. 23.4 – Gowling and van Emden, 1994). On the other hand, there may also be some overestimation of parasitization, particularly when aphid numbers are declining, since unemerged mummies have greater 'longevity' on the crop than unparasitized aphids.

Aphid pathogens rarely seem to cause significant reductions in aphid numbers during the season, though Deguine *et al*. (2007) regarded them as primarily responsible for a mid-season decline in the population of *A. gossypii* in cotton (see later). However, pathogens can be important mortality factors in the end-of-season decline from peak numbers; Plantegenest *et al*. (2008) attributed 75% of the decline in *S. avenae* numbers in winter wheat to this cause.

Host-plant condition

Plant growth stage has a strong influence on aphid population changes, as this will often determine the soluble nitrogen concentration of the phloem sap, which for aphids is frequently the limiting factor on reproductive rate (Dixon, 1973). Young, growing crop plants where nitrogen is being mobilized in the phloem are often where aphid population growth is most rapid. Within-year changes in aphid numbers on trees regularly show spring and autumn peaks, with a long intervening period of lower populations; Kindlmann *et al*. (2007) attributed this pattern to changes in host-plant quality, with amino acids being translocated to the young leaves in the spring and being exported from senescing leaves in the autumn.

Variation in tissue condition within plants can have large effects, with younger leaves being more attractive to aphids, supporting higher rates of population increase (van Emden and Bashford, 1969; Costamagna *et al*., 2013b). Some aphid species, for example *B. brassicae* (van Emden, 1965) and *A. glycines* in soybeans (Tilmon *et al*., 2011) largely remain on the leaves they colonize, and so the amino acid status of their substrate changes as the season progresses. *Sitobion avenae* and *M. dirhodum* are both common cereal pests but respond differently to plant condition, mainly due to their preference for different parts of the plant. The reproductive rate of *S. avenae* on young cereal ears is far higher than on leaves, whereas that for *M. dirhodum* is highest on the leaves and the aphid is rarely found on the ear (Watt, 1979).

As pointed out earlier, photoperiod is an important driver of plant phenology, and therefore plant condition. Since the arrival of aphids on a crop is related more to abiotic factors such as temperature, the amino acid status of the crop when the aphids colonize will not be predictable. *Aphis spiraecola* and *Macrosiphoniella millefolii* populations increase rapidly when photoperiod reaches 14 h, because this triggers stem elongation of commercial yarrow (*Achillea collina*) (Lozzia *et al*., 2013) and *A. gossypii* populations on cotton begin to increase shortly after the onset of the bloom (O'Brien *et al*., 1993), which is a photoperiod timed event with major increases in amino acid transport.

Variation in the condition of plant tissues can have large effects, with younger leaves most attractive to aphids and supporting the highest rates of population increase. Both *M. persicae* and *A. fabae* have higher rates of increase on younger flowering soybean plants than when these are at or past the full pod stage, with most aphids and the highest rate of increase on the young upper nodes (Costamagna *et al*., 2013b). Early in the season, *A. glycines* is found on newly expanding trifoliate soybean leaves. As the season progresses, it is found lower in the canopy, further from the terminal bud. This reflects changes in the distribution of nitrogen in the plant phloem (Tilmon *et al*., 2011).

Declines in aphid populations can also be attributed in part to changes in the nutritional status of

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plant tissues. *Macrosiphum euphorbiae* (potato aphid) populations feeding on potato plants consistently decline once potato tubers have started filling (Parker *et al*., 2000); fecundity then drops by 25–45% as the amino acid composition in the phloem of the potato plants changes (Karley *et al*., 2003). In most crops, maturation is important in reducing the reproductive rates of aphids, but mycoses and natural enemies have rated as important in driving the decline (Feng *et al*., 1991; Soni *et al*., 2013). However, the decline is probably due primarily to plant condition, with natural enemies merely accelerating its rate.

The importance of crop plant condition for aphid population development is reflected in the approaches to reducing levels of crop damage by using aphid-resistant crop varieties (Chapter 22, this volume) and cultural measures (Chapter 21, this volume).

Emigration

The departure of alatae from the crop represents a local loss of individuals. Since it is triggered primarily by crowding and maturation/deterioration of the host plant, its main effect on population size is at the end of the season, and is discussed later.

The development of populations on crops

Numerical changes in aphid populations on crops follow a relatively consistent pattern in different aphid species and crops, although patterns may change unpredictably from year to year because of the importance of photoperiod on the amino acid status of the crop when the aphids colonize (see earlier). The main phase of population growth often follows a sigmoidal pattern (e.g. Fig. 12.2 and Chapter 13, this volume), with a rapid initial increase followed by a slowdown leading up to a peak in population before a rapid decline (often called the 'crash'). Of course, there is variation in the amplitude and phase of the rate of increase and the size of the peak population. A sigmoidal rise to a peak, though found at some time during the season in most species, does not always start with the arrival of aphids on the crop.

van Emden's (1965) study of *B. brassicae* on marked cabbage leaves showed a small initial peak of reproduction following immigration, until predation became a significant factor, but as leaves started to senesce from late August onwards, the aphid population rocketed in spite of greatly increased mortality from aphid predators.

This pattern could be illustrated three-dimensionally (van Emden, 1966) by plotting the number of aphids on different sample dates and the number of predators in the sample (as a kind of 'predator index') on the two horizontal axes and the per cent predation in the revisited colonies on the vertical axis (Fig. 12.3). This shows a double-peak pattern of aphid density, with the numbers kept low for most of July by increasing predation. However, even increased predatory pressure in August failed to prevent an explosion of aphid numbers into the autumn. The double-peaked pattern reported for aphids on woodland trees (Kindlmann *et al*., 2007) and citrus (Lebbal and Laamari, 2015) (Fig. 12.4), and attributed by Kindlmann *et al*. to changes in amino acid status, was therefore also seen with the brassica crop, and the autumn peak dramatically shows that the increase in amino acids later in the season accelerates aphid reproduction beyond the control capacity of the mortality factors. Similarly, Hutchinson and Hogg (1985) recorded that mortality of *A. pisum* attributable to predation on lucerne ranged from zero to about 30%, but that even at the highest predator densities, *A. pisum* populations increased exponentially.

Predation, however, clearly does determine the duration and level of the trough in aphid density between the two peaks. Parajulee *et al*. (1997) successfully increased predator numbers in cotton by relay-intercropping it in strips with a variety of spring and summer crops, and found that this not only reduced *A. gossypii* numbers but also caused the population to show two peaks in contrast to the single peak in non-intercropped cotton (Fig. 12.5). The pattern of a trough between two peaks, caused by unfavourable plant condition but with its depth determined by natural enemy activity, is frequently found in annual crops (e.g. in *Therioaphis trifolii maculata* (spotted alfalfa aphid) on lucerne (Tambe and Kadam, 2015); Fig. 27.2 in the IPM Case Histories, this volume, and Fig. 12.6). An increase in the movement of amino acids in the phloem also occurs during the development of inflorescences. This often precedes autumn leaf and/or plant senescence in annual crops, but in crops such as brassicas that flower in the following year if not harvested, dense aphid colonies appear on the flowering stems. This would result in a third population peak after the depression of the population during the winter.

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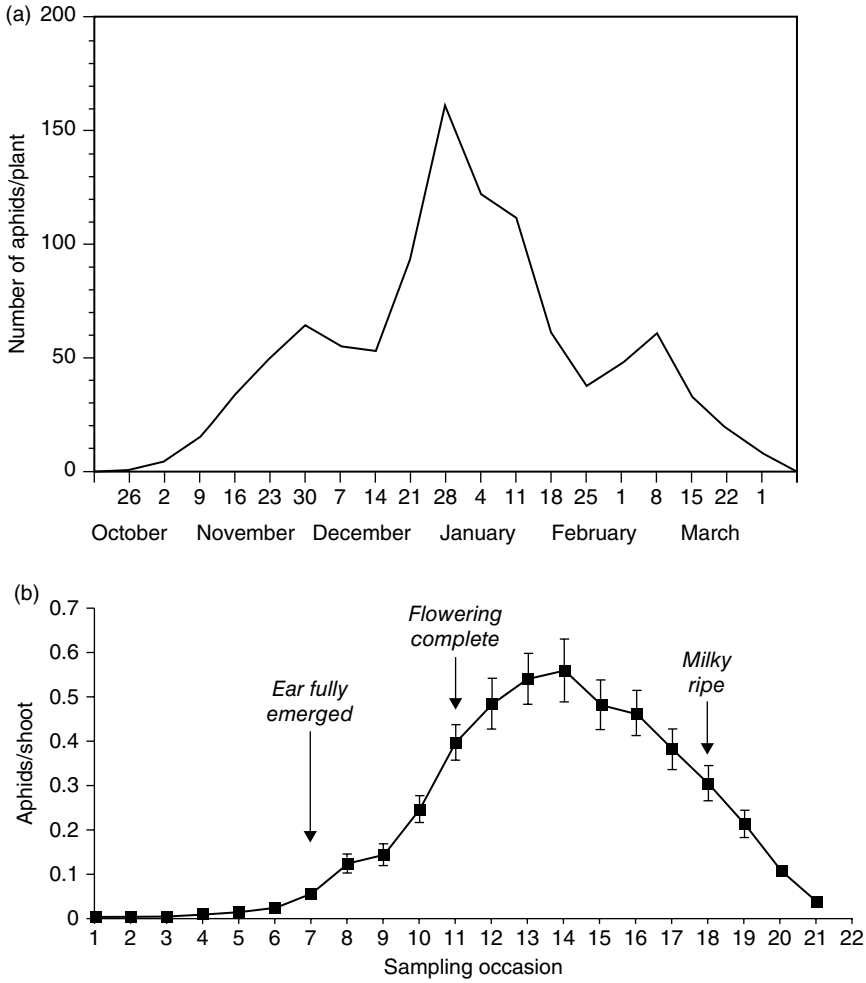

Fig. 12.2. (a) Seasonal population build-up of *Aphis spiraecola* on *Cosmos bipinnatus* during 2006. (Simplified from Dubey and Singh, 2011.) (b) Population growth of *Sitobion avenae* (aphids/shoot) on wheat in 2002. (From Winder *et al*., 2014, with permission.)

At the other extreme, aphids such as *S. avenae* show an exponential rise to a single peak, followed by a crash in the population as the plants mature and senesce. However, this exponential rise is delayed for some time after aphids have arrived on the crop (Fig. 12.2b). The general importance of amino acid status suggests that the trigger for the rise is the switch from vegetative to reproductive growth.

Quite commonly with cereal aphids, there is a brief 'hiccup' in the exponential phase (Fig. 12.7). This can even take the form of a very temporary reduction in the size of the population on the plant, with sample points otherwise strictly on an exponential curve changing to the one below and the next above; the exponential rise to the peak is then continued. Such 'hiccups' are often ignored in drawing the curve; that this phenomenon occurs later for *S. avenae* than for *M. dirhodum*, which feeds lower down on wheat (Fig. 12.7), suggests a host plant change is probably again involved. Similar 'hiccups' are seen with *A. spiraecola* and *S. avenae* in Fig. 12.2 and with *Rhopalosiphum maidis* in Fig. 12.6a.

Although aphid reproductive rate and temperature are closely correlated in the laboratory, the

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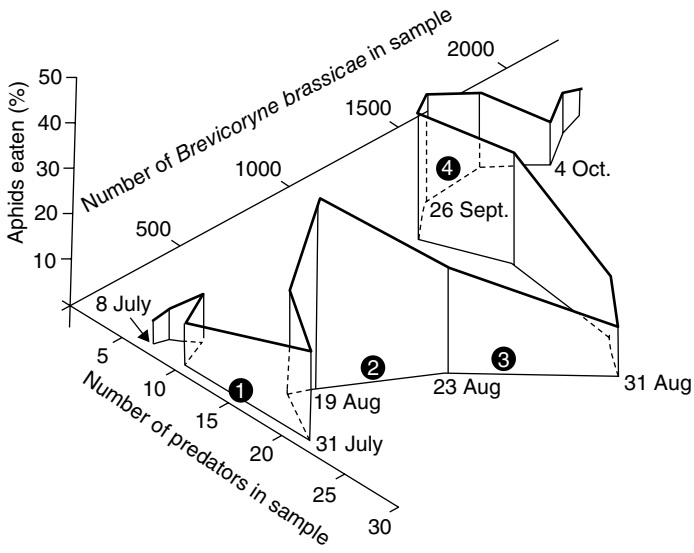

Fig. 12.3. A graphical representation of the effectiveness of aphid predators, showing good control of *Brevicoryne brassicae* on cabbages early in the season. (From van Emden, 1966.) For symbols ❶–❹, see text.

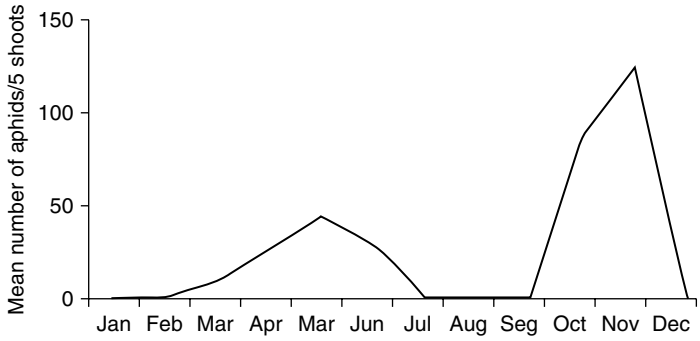

Fig. 12.4. Monthly fluctuations of the mean number of aphids/5 shoots on clementine in a citrus orchard in 2012. (Simplified from Lebbal and Laamari, 2015.)

overriding importance of host-plant quality is clearly shown in Fig. 12.3 by reference to the four periods and the contemporaneous predatory activity. In period 1, with a negligible increase in the aphid population, mean daily temperature was 16.5°C (range 14.0–17.0). When aphid numbers increased sharply between 19 and 23 August, mean temperature was a little lower in period 2 at 16°C (range 13.5–17.0), and even lower in period 3 (mean 13.5°C, range 12.50–14.50). At the time of a later surge in aphid numbers (period 4), mean temperature was down to 10.5°C (range 7.0–12.0). *Diuraphis noxia* populations in Orange Free State, South Africa, show a striking double peak (Fig. 12.8) that appears quite unrelated to weather conditions (Kriel *et al.*, 1986).

Many of the phenomena described above reflect the main conclusions from the international study of *M. persicae* on potatoes (Mackauer and Way, 1976 – see earlier):

1. Parasitoids, even in the absence of hyperparasitoids, had little impact on the aphid population.
2. Fungal attack was only sporadic, and there were no signs early in the season, even where humidity conditions were favourable.
3. Predation (residual mortality) was heavy surprisingly often, but even so, only induced a decline in the *M. persicae* population after the crash or at other times when aphids were increasing at well below their maximum rate, even on a relatively poor host (potato). As an example, a twin sample in Italy (where the potential increase rate (PIR) was only 1.24) can be contrasted with one in Scotland (where PIR was 1.99). At the former site, 17.6% predation was accompanied by an 8.6% aphid

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population decline, whereas at the latter, an 8.8% increase in the population occurred although predation was much higher (43.7%).

4. There was a low and steady rate of emigration, and natural enemies were removing potential migrants even well after the population peak.

Emigration at the End of the Season

Crop maturation (see above), crowding and plant deterioration due to aphid damage as well as unfavourable weather cause a crash in the aphid populations at the end of the crop season. This crash can be very rapid; Basky (1993) found that a peak *D. noxia* population of nearly 4000/wheat plant on 3 July had completely vanished by 20 July. As mentioned above, part of this crash is a consequence of host-plant condition reducing aphid reproductive rate (Karley *et al*., 2003), accelerated by natural enemies including pathogens (Plantegenest *et al*., 2008). Feng *et al*. (1991) considered that parasitoids and pathogens were more important than crop maturation in causing the post-peak decline of cereal aphids. This is in contrast to most other studies; for example, Karley *et al*. (2003) were consistently able to associate the crash in aphid numbers on potato with changes in the phloem amino acid composition of the potato leaves. However, another aspect of the crash is the effect of plant deterioration in switching reproduction from apterae to alatae (Wiktelius, 1984; Parker *et al*., 2000; Chapter 4, this volume), which emigrate from the crop to alternative habitats (usually trees or wild herbaceous plants). This phenomenon does not appear to be triggered in response to predation but by the impacts of crowding (Costamagna *et al*., 2013b).

Models have estimated that emigrants suffer high levels of mortality as autumn approaches, with less than 5% of alate emigrants surviving more than 10 days after landing on a new host (Fabre *et al*., 2010). In the end, only 0.6% of *R. padi* successfully find their winter host (Ward *et al*., 1998). Variability in alata production and emigrant survival, as well as predation of emigrants on their off-season hosts, are probably the reasons why autumn egg numbers change dramatically from one year to the next on the same overwintering sites (Welsman *et al*., 2007).

Longer-term Regulation of Aphid Populations

At the start of this chapter, we pointed out that aphids were unsuitable subjects for building age-specific life tables as a basis for understanding their population dynamics. Nevertheless, Mackauer and Way (1976) carried out the first age-specific

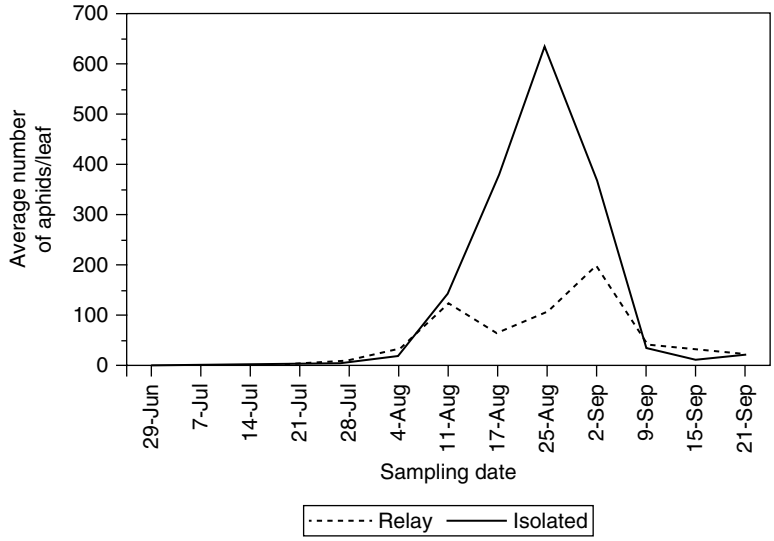

Fig. 12.5. Abundance of cotton aphids in strip-intercropped (------) and isolated (——) cotton, averaged over 3 years. (From Parajulee *et al*., 1997, with permission.)

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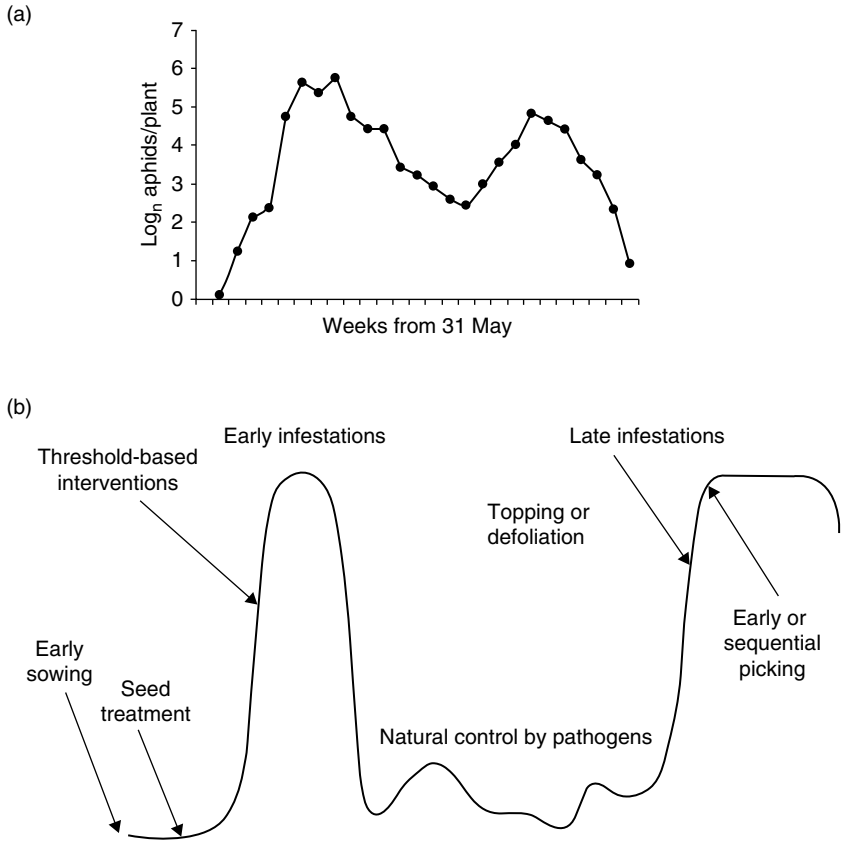

Fig. 12.6. (a) Abundance of *Rhopalosiphum maidis* on grain sorghum in 1989. (Modified from Michels and Burd, 2007.) (b) Stylized representation of the dynamics of *Aphis gossypii* on cotton. (From Deguine *et al*., 2007.)

analysis made with field data of aphids (*M. persicae*). They got round the problems aphids presented by using a whole year as their age-specific time division; in this way, their census datum (the 'population index' published by Broadbent and Heathcote (1961) from trapping records in potato fields for the years 1942–1959) could be used as the 'one discrete generation' in their analysis. When the logarithmic difference from the previous year is plotted against the population index and the points are joined in chronological order, a clockwise spiral results (Fig. 12.9). This is characteristic of an efficient mechanism of population stability, but one in which the density dependence is delayed and which overcompensates for large deviations from the equilibrium (Varley and Gradwell, 1968). The most likely mechanisms suggested were aphids leaving the summer hosts when moving to and between weed hosts, and predation by natural enemies in the spring. Davis *et al*. (2014) used a 17-year time series of three cereal aphid species (*R. padi*, *M. dirhodum* and *D. noxia*) compiled from a trapping network spanning the north-western USA, and found that the abundances of all three species were consistent with the operation of delayed density dependence. Alyokhin *et al*. (2005) used a graphical method, similar to that used by Mackauer and Way (1976), with peak numbers of *Aphis nasturtii* (buckthorn aphid), *M. euphorbiae* and *M. persicae* on potato from 1949 to 2003. They found strong evidence of direct density-dependent regulation of the populations of all three species. There was also evidence of delayed density dependence for *M. euphorbiae*. The periodicity of population fluctuations for *A. nasturtii* and *M. persicae* was 6.1 years and 3.9 years, respectively. The effects of density-independent weather factors were relatively minor compared to density-dependent regulation. Thacker

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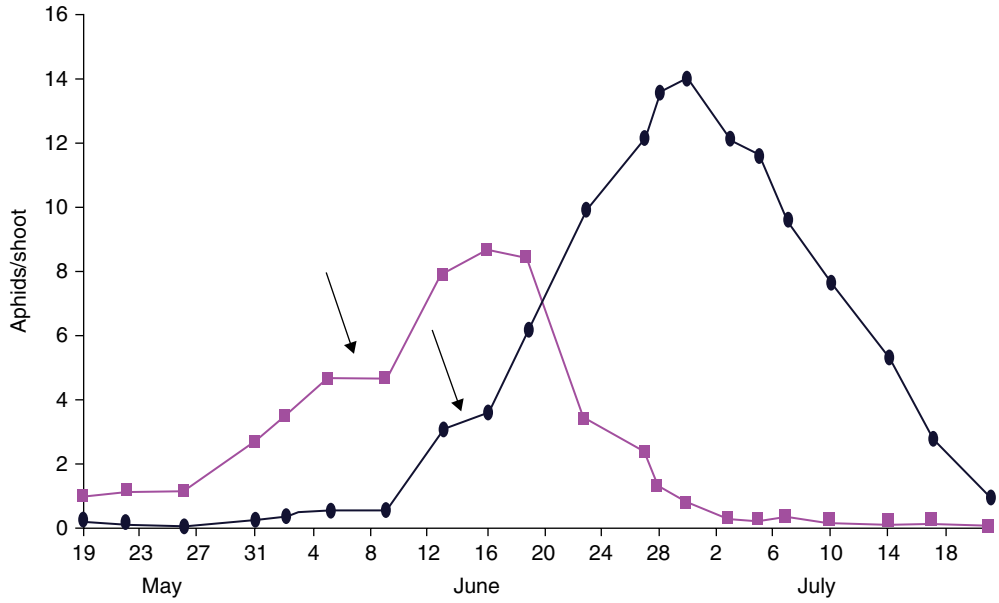

Fig. 12.7. Abundance of *Sitobion avenae* (black line and diamonds) and *Metopolophium dirhodum* (purple line and squares) on wheat. Arrows indicate the 'hiccups' mentioned in the text. (Data courtesy of J.M. Holland.)

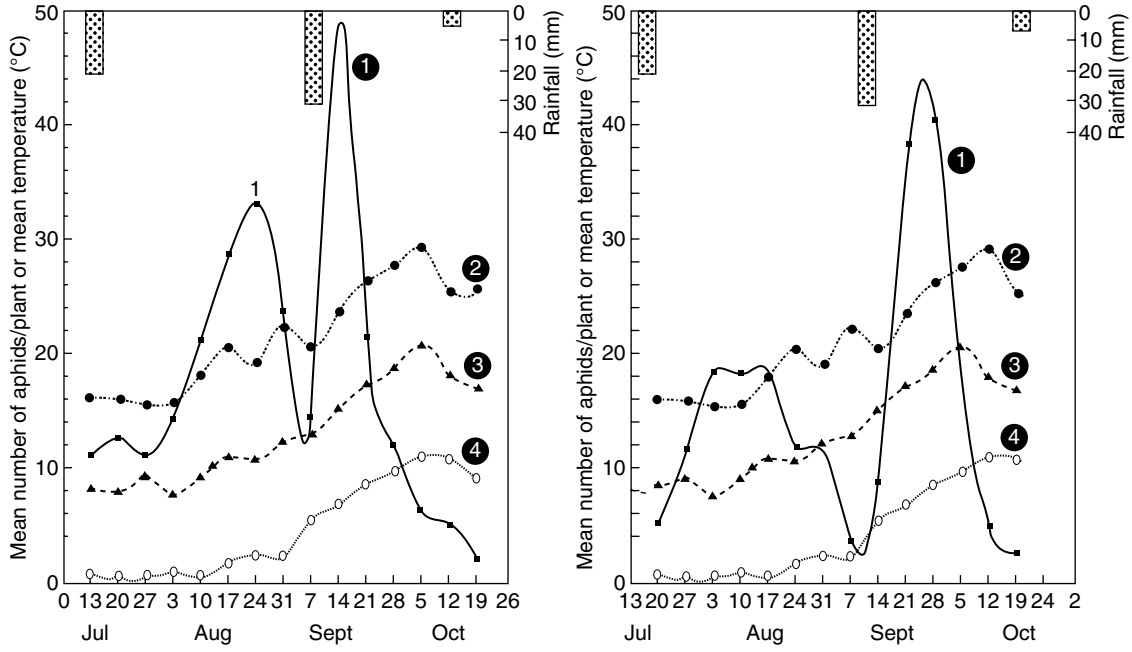

Fig. 12.8. Abundance of *Diuraphis noxia* in relation to climatic conditions and wheat growth stage at two sites in 1982. ❶, mean number of aphids/plant; ❷, mean maximum temperature; ❸, mean temperature; ❹, mean minimum temperature. (Redrawn from Kriel *et al*., 1986.) Note that the first peak was already in steady decline before the heavy rain in early September.

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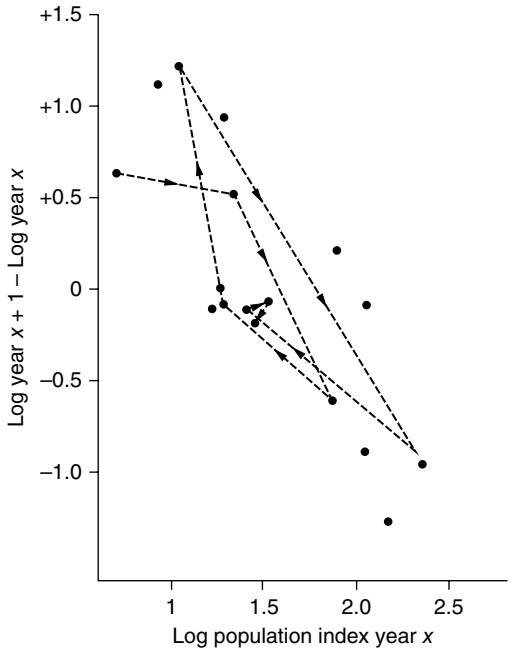

Fig. 12.9. Changes in *Myzus persicae* abundance from year to year plotted against abundance in the earlier year. The population data have been taken from Broadbent and Heathcote's (1961) trapping data for 1942–1959. (From Mackauer and Way, 1976.) Points for 1942–1950 have been joined in sequence as an example of a clockwise spiral pattern (see text).

et al. (1997) found apparent delayed density dependence in *A. fabae* egg counts between 1980 and 1992 at Rostock, Germany. They concluded that this was an artefact of unusual cyclical weather in this 12-year period; however, it seems unlikely that such unusual weather cycles could be the explanation for the density dependence shown for aphids by the other authors cited above. Way and Banks (1968) had previously pointed to the frequent alternation of high and low years of *A. fabae* on bean crops. They suggested that immigration was affected by predation on spindle trees in a biennial pattern since, after high aphid numbers in the summer, many predators would overwinter and reduce the population the following year. The resulting low *A. fabae* summer population would produce a low overwintering predator population; thus, a high number of aphids would arrive on crops the following spring. A similar mechanism leading to a biennial pattern was recorded for *A. pisum* in Serbia (Tomanović *et al.*, 1996). High autumn parasitization leads to more parasitoids emerging in the spring, leading to a reduction in the aphid population, and therefore low parasitoid numbers in the autumn.

In suction-trap catches, *D. platanoidis* also has a 2-year cycle of abundance. The total number of *D. platanoidis* on a tree is relatively constant from year to year, in spite of this cycle. This paradox results from what Kindlmann and Dixon (1992) refer to as the 'seesaw effect', describing an inverse relationship between the spring peak and the increase in numbers in autumn culminating in long-distance migration. Again, the changes are density dependent; strongly increasing numbers at low densities but more weakly at high densities (Jarošík and Dixon, 1999). The stronger density-dependent changes at low densities relate to the reduced intraspecific competition for space that then prevails, since the unexploited carrying capacity of the tree is high.

Conclusion

Although attempts over the years to understand the causes of population change of aphids on crops from field-collected data have provided good evidence for what underlies the one-, two- or three-peak cycles, all the methodologies can be criticized, and validation of the interpretations by experiment has proved difficult or impossible. The time-specific life-table approach has emerged as the best way to analyse population change, and it should perhaps now be revisited.

Hutchinson and Hogg (1985) sought to improve Hughes's (1962) method in their studies with *A. pisum*, replacing the calculation of 'potential increase rate' based on instar frequencies with the intrinsic rate of increase (r_m) estimated on a day-degree scale under field conditions in clip cages (i.e. in the absence of natural enemies). They found this gave a reliable estimate of the potential population growth rate.

One of the most important innovations of Hughes's method was to analyse population changes in 'instar period' units. The power of computers to model changes almost continuously (by small fractions of an instar period) is a substantial step forward, at least to the point where the likely 'what if?' outcomes of possible pest management interventions can be predicted reliably. This approach is explored in the chapter that follows.

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13 Aphid Population Dynamics: From Fields to Landscapes

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Introduction

There are close to 5000 aphid species in the world, of which about 200 are crop pests. For these pests, never before have decision support systems been in so much demand (Chapter 17, this volume) both to help reduce pesticide use and also to prevent damaging outbreaks. However, for only a handful of these species is there a sufficient level of ecological and biological understanding to merit undertaking a population dynamics approach. Unsurprisingly, the emphasis has been on aphids that cause the most serious crop damage (Table 13.1), and these are firmly our focus. The majority of aphid pest population studies are concentrated within agriculture, particularly on a small number of aphids that use cereals as their host. Rice, wheat and maize provide 60% of the world's food energy intake, so it is perhaps not surprising that aphids feature heavily as biological threats, particularly in rice and wheat (FAO, 2016). There are considerable amounts of data concerning the ecology of these aphids, and consequently there have been repeated modelling attempts, statistical or otherwise, that have sought to capture and predict their population dynamics. These cereal aphid studies form the backbone of this chapter and will be discussed at length, but we shall also occasionally discuss the dynamics of aphids that use other annual crops and trees as their host.

Our overall purpose is to outline the components of an aphid population that determine its dynamics, then discuss how to frame a process-based model and review some of the important issues and decisions that arise as a result. We first introduce the main characteristics of aphid populations and then move on to the concept of forcing (driving) variables, processes and their functions that will be of general applicability to all crop aphids, but often referring to our model species, *Sitobion avenae*.

Here, we define a process-based model to be a mechanistic model that incorporates processes using difference, differential or rule-based equations. Statistical or phenomenological models that have previously been reviewed by Kindlmann *et al*. (2007) are now the subject of Harrington and Hullé (Chapter 16, this volume). Our chapter does not aim to provide an in-depth mathematical critique of previous methods used, nor does it seek to offer a discussion on insights gained from aphid populations as a result of using process-based models. Instead, we hope that this chapter will reach a broad audience that may not otherwise have the mathematical skills required to read many of the citations used herein. When mathematical details are useful, we have enclosed them in a box to be consulted by the reader if they wish. Finally, we conclude with an overview of the challenges that face modellers in their quest to predict aphid population dynamics.

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Table 13.1. Examples of demographic and crop loss data for some of the most damaging and widespread aphid species in the world. The table provides data from individual time series that are summarized by the minimum and maximum values over that period for peak numbers of aphids and percentage yield loss in tonnes respectively.

Aphid species	Crop	Country	Period	Annual numbers of aphids/plant at peak infestation (min year–max year)	Annual percentage crop yield loss in tonnes (%) (min year–max year)	Source
Sitobion avenae	Winter wheat	England	1976–1980	0.2–90	Unknown	Carter *et al*. (1982)
		The Netherlands	1976–1977	0–40	0–9.5	Vereijken (1979)
		France (W)	1975–2005	0.1–120	0–20	Dedryver *et al*. (2009)
		Belgium	1972–1989	0.8–22	0–10	Latteur and Oger (1991)
Aphis fabae	Beans	England	1975–1978	340–15,000	0–80	Wilding (1981)
		France (E)	1972–1976	48–15,000	0–85	Bouchery (1977); Bouchery and Jacky (1977)
		France (W)	1969–1975	0–3000	0–20	Robert *et al*. (1975)
Aphis gossypii	Cotton	Cameroon	1988–1994	30–1500	0–23	Deguine (1995)
Aphis glycines	Soybean	USA	2005–2008	30–3000	0–40	Ragsdale *et al*. (2007); Rhainds *et al*. (2010)
Schizaphis graminum	Winter wheat	USA	1993–1998	0–100	0–35	Kindler *et al*. (2002)
Dysaphis plantaginea	Apple trees	France (S)	2008–2009	80–200 (per shoot)	30–80	Dib *et al*. (2010)
Rhopalosiphum padi	Maize	France (W)	1985–1987	50–1500	n/a	Henry and Dedryver (1989)
		France (W)	1997–1998	300–600	0–1	Haack *et al*. (1999)
		France (Paris area)	1984–1985	1000–50,000	n/a	Chansigaud and Vaillant (1987)
		USA	1981–1985	Mean: 3200	n/a	Blackmer and Bishop (1991)

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The Aphid System: An Overview

A graphical overview of the complex network of abiotic and biotic factors that governs aphid population dynamics is shown in Fig. 13.1. All animals linked to aphids, apart from birds, are ectothermic and respond favourably to climate, particularly temperature, but not necessarily at the same rate. Importantly, climate may be experienced by aphids

Fig. 13.1. Graphical model indicating the components of an aphid population that are relevant to a process-based model. From bottom to top, on the right stem a parthenogenetic female gives birth to live young and the telescoping of generations within the mother is just visible (birth process). The process of regulation, symbolized by a ladybird foraging for aphids, a parasitoid injecting an aphid with an egg and an aphid corpse killed by an Entomophthorales disease that is ejecting conidia, all signal 'death'. Generalist natural enemies, such as spiders, carabid and staphylinid beetles, have been omitted for simplicity, but these would occur near to or on the ground foraging for aphids that have fallen off the plant. At the base of the wheat stems, dead aphids show natural mortality. Different ages are shown by a range of instars apparent on the plants, with adults visible as either apterae or alate morphs, indicating the processes of growth, emigration and immigration. Above, the sun is a reminder that climate drives the whole system, affecting the performance of plants, aphids and their regulators.

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directly (e.g. different temperatures can produce dramatic effects on development, reproduction and movement (Dean, 1974)) or indirectly (e.g. high ambient relative humidity promotes conidia formation, dispersal and germination of fungal pathogens (Hesketh *et al*., 2010)). The activity of natural enemies like specialist ladybirds, syrphids, chrysopids, cecidomyids, parasitoids and generalist predators including carabids, staphylinids, earwigs, spiders and even birds may also all have their individual impacts on aphid growth rates.

Essential Life-cycle Issues that Modellers Need to Understand: Parthenogenesis, Viviparity and Polyphenism

Most aphids, but particularly crop aphids, are fundamentally *r* strategists: their reproductive rate is generally very high and their generation time short, compared to most other insect groups. That said, galling aphids present an intermediate strategy between *r* and K because they display a level of maternal care. The high reproductive rate of crop aphids is due mainly to the multiplicative effect of three original biological characteristics: parthenogenesis, viviparity and polyphenism – for a full biological explanation, see Chapters 4 and 5, this volume.

Parthenogenesis combined with viviparity produce female young that themselves can commence reproduction within 7–10 days after birth (Dixon, 1998). The effect is that both parthenogenetic and viviparous females drastically shorten generation times. The implication for modelling is that very high intrinsic rates of increase must be parameterized. A simple example of this is provided by Blackman (1974), who showed that during a given period, from one aphid embryo, 318,750,000 descendants could theoretically be produced within six generations (Fig. 13.2). In stark contrast, when compared to a sexually reproducing insect (e.g. moth) over the same overall time, only 1250 descendants would be born within three generations.

Moreover, aphid populations contain a mixture of forms that are morphologically different but could be genetically identical if they belonged to the same clonal lineage. This phenomenon is as a result of polyphenism, the production of distinct morphs with different biological functions by the same genotype in response to an environmental cue. In cyclical parthenogenetic (holocyclic) aphid lineages, polyphenism can explain the production of sexual morphs quite simply, in that shorter day lengths give rise to mating females and males (see Chapter 4, this volume).

Polyphenisms also arise when aphids interact, due to competition for space and/or for food. When aphids experience crowding through physical contact, winged morphs are produced. These winged aphids emigrate, producing the crash phase common in aphids of annual crops (see Chapter 4, this volume). Generally, the consequences of polyphenism are that aphids are transitory, appearing as seasonal colonizers. Further, due to their small size, winged aphid migration constitutes a 'black box' that modellers will have to overcome creatively in the absence of experimental data. This black box remains an important issue given the simple terms of Malthusian population growth (i.e. birth, death, immigration, emigration) that are the basics of any model. The availability of historical seasonal catches in the suction-trap databases, however, gives useful insights into migration dynamics (Fabre *et al*., 2010).

In summary, Williams and Dixon (2007) state that the biological features that are likely to determine pest status are the prolific rates of increase and the migration potential of aphids. Both of these factors are closely linked to abundance. Williams and Dixon (2007) dismiss host alternation (heteroecy) as a trait that promotes pest status, although Bell

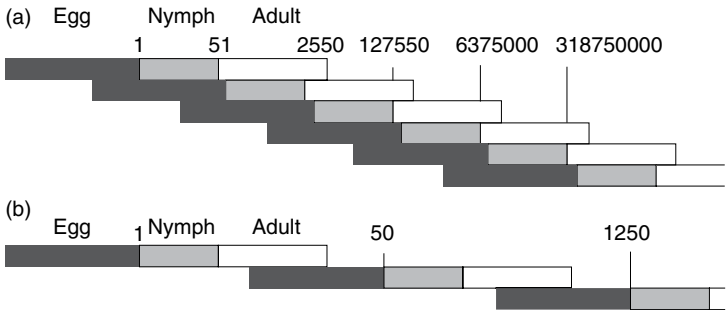

Fig. 13.2. Potential number of descendants in successive generations from a single female during the same period – (a), for anholocyclic aphids; (b) for sexually reproducing insects. (From Blackman, 1974.)

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et al. (2015) show that this trait is likely to produce a larger number of migrants when compared to monoecy. A global meta-analysis of pest status is needed to rank the importance of aphid traits that promote persistence, spread and damage.

Processes Related to Aphid Population Dynamics

The graphical model (Fig. 13.1) can be used to partition components into processes that are encapsulated within a set of individual submodels. Each process will be discussed individually in this chapter, but for completeness, they are also pictured below in a simplified diagram (Fig. 13.3). The black-lined box includes within it all those biological/demographic processes (ageing, moulting, death, reproduction and migration) that are strictly biological. Of note is the fact that the process of ageing is strongly determined by forcing variables, principally biotic (plant quality and the phenological stage of the plant) and abiotic (temperature) factors. The birth and death components are relatively easy to model compared to the extrinsic mortality linked to natural enemies, which introduces a high level of complexity. All the processes we describe occur at a point in time and can be expressed in the form of the 'relative growth rate' of the population, which is a useful short cut to describe the population dynamics (Grechi *et al*., 2010; Ciss *et al*., 2014a). A species-specific detailed graphical interpretation of a process-based model can be found in Grechi *et al*. (2010), who analysed *Myzus persicae* (peach–potato aphid) and its parasitoids on peach trees.

Extrinsic Forcing Variables

Extrinsic forcing variables are those that independently drive the population dynamics of aphids and include plant quality, abiotics and the regular community made up of a range of natural enemies (Fig. 13.3). There can be feedback mechanisms between aphids and some forcing variables that suggest interdependence and the need for a more relaxed definition under certain conditions. Migration is a biological process that removes or adds individuals from the population and is discussed later in biological and demographic processes.

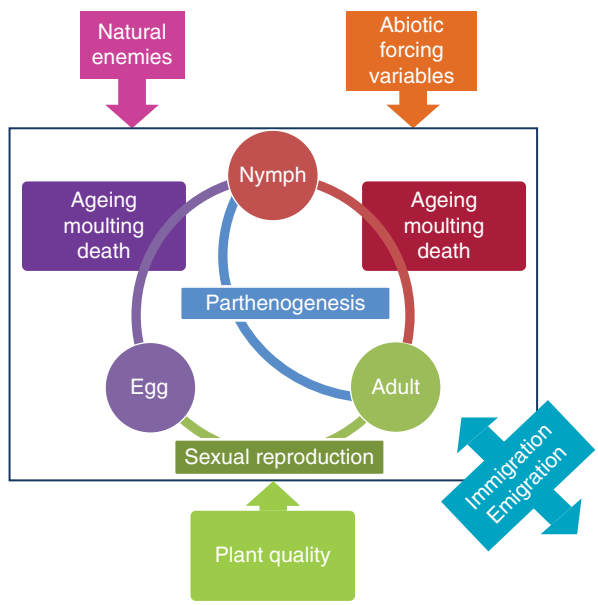

Fig. 13.3. A simplified diagram illustrating the main processes for consideration during model construction. The life of the aphid is encapsulated within the black-lined box and the variables that determine the success of those aphids are extrinsic forcing variables. These variables include host-plant quality, natural enemies and abiotic forcing variables, of which perhaps the most important is temperature. Aphids are prolific migrants and those arriving or leaving need to be known and parameterized, indicated by the immigration/emigration box.

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Abiotic forcing variables: climate

Insects do not regulate their metabolism, and so the vital stages in their life cycles depend heavily and almost instantaneously on ambient temperature. Temperature has been cited as the principal mechanism that drives the developmental 'clock' for pest aphids at all scales and most environments (Dean, 1974; Bale, 2002). Long-term modelling studies of climate effects show that temperature and precipitation are key drivers, but that CO_2 has an ambiguous relationship with population change in aphids (Pritchard *et al*., 2007; Soussana *et al*., 2010). In the fifth Intergovernmental Panel on Climate Change report (IPCC, 2014), it is acknowledged that interactions between CO_2, fertilization, temperature, soil nutrients, ozone, pests and weeds are not well understood. Further, the effect of temperature is not felt consistently across all trophic levels, and thus could lead to a mismatch between the host aphids and their regulators (Jeffs and Lewis, 2013). For climate projections, Soussana *et al*. (2010) argue that modellers will need to combine an ensemble of greenhouse gas emission scenarios with both regional climate models and crop and pasture models. Further, for added realism, Soussana *et al*. (2010) state that this already complex ensemble should also include adaptation options concerning both management practices and species/varieties if accurate estimates of pest numbers are to be produced. Understandably, most crop models do not include all these effects, but it is clear from this short review that temperature is a critical extrinsic forcing variable and one we consider in detail.

Modelling the effect of temperature

Aphids, as well as the species that interact with them (host plant, fungal pathogens, insect predators and parasites), are all driven by temperature. However, the clearest effect of temperature on aphids is on their development rate. Development rate is a major component of biotic potential and fitness. The effect of temperature has been modelled several times for the English grain aphid, *S. avenae* (Carter *et al*., 1982; Carter, 1985; Zhou *et al*., 1989; Plantegenest *et al*., 1996). In most cases, the biological data used were those of Dean (1974), obtained at constant temperatures in a controlled climatic chamber. The development parameters for *S. avenae* have also been estimated under naturally fluctuating temperatures, and these have been shown to agree better with field data (Pierre, 1991; Jeffs and Leather, 2014). Using constant temperature data in models is useful but, due to climate change, long-term projections ought to consider also the effects of extreme or fluctuating temperatures. Some parameters are now known for *S. avenae* (Jeffs and Leather, 2014).

Temperature typically enters a model via a link to development rate that determines both physiological age and physiological time. This simply recognizes that ageing is slow at low temperatures and fast at high temperatures, and that above or below an optimal threshold, ageing is slower. Of course, death of an individual may be incurred if the temperatures are extreme and long lasting. From a modelling point of view, the physiological age includes both estimates for the proportion of the total development elapsed, the actual time and the temperature experienced at each point in time. Approaches have varied for *S. avenae*, but the most success has come from non-linear models as shown in Box 13.1.

Biotic forcing variables: plants

Host plants influence aphid population dynamics in several ways. The presence/absence and synchrony of the host in space or time (e.g. 'green bridges') and the host plant's physiological state, genotype and biochemistry are linked to aphid performance (e.g. rate of increase or/and percentage of winged individuals in the population). Thus, host plants are of intrinsic importance in modelling the aphid niche (Dedryver and Harrington, 2004; Vialatte *et al*., 2006). Bell *et al*. (2012) showed for 170 species of migrating aphid that their abundance was resource controlled by plants, particularly for aphids that had a winter host. This is supported by work in France at a similar scale, showing that the average annual abundance of *S. avenae* caught by suction traps is correlated with the proportion of wheat within a radius of approximately 70 km around those traps (Fig. 13.4).

Depending on the type of chemical or physical defences used by a plant, the ingestion of phloem may promote or reduce aphid growth, development, survival and fecundity (Smith and Chuang, 2014). Ma and Bechinski (2009) modelled Russian wheat aphids (*Diuraphis noxia*) and showed that younger plant growth stages resulted in higher reproductive rates. Clearly, there are also specific and intraspecific effects to consider when modelling aphid performance, especially as there may be a change of host races below the species level (Vialatte *et al*., 2006). For example, in a large-scale study of over 500 genotypes of hexa-, tetra- and diploid

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Box 13.1. Modelling development under the effects of temperature

Aphids respond to temperature non-linearly. As a consequence, models typically comprise a period of exponential growth (i.e. indicating increasing performance with increasing temperature), an inflexion point (i.e. thermal maximum) and an x intercept (i.e. thermal death point). Here, we give an example of a combined exponential model originally described by Logan *et al*. (1976), known as the Logan I model, and of an inverse quadratic model suggested by Dean (1974) and modified slightly by Plantegenest *et al*. (2001) to fit Dean's cereal aphid data (Fig. 1a,b). The inverse quadratic model, a reciprocal regression equation, takes the form:

$$R(\theta) = \frac{1}{a(\theta - b)^2 + c} \qquad (13.1)$$

where $R(\theta)$ is the rate (or speed) of development at temperature θ and b is the optimum temperature. Parameters a and c are fitted to the data as part of the regression modelling process and are not known a priori. The inverse quadratic model has only three parameters, while Logan's model has four (not shown).

Figure 1b shows quite clearly that Eqn 13.1 behaves well at low temperatures but poorly at and after the inflexion point. There are a plethora of other models and the most popular are detailed in a review by Malaquias *et al*. (2015).

Now that the simple effect of temperature on aphid development is understood, there is a need to compute the physiological age of an individual as a function of temperature, given by

$$x = \int_0^t R(\theta(u))\,du \qquad (13.2)$$

where x is the age, expressed as the proportion of the total development time elapsed from the entry in the stage of interest, t is the actual time, $\theta(u)$ is the temperature experienced at each instant u between 0 and t. Equation 13.2 is equivalent to a description of a car travelling at time t through sections of a road. The speed within each section of the road is known and the distance travelled is the sum (or integral) of the speed over time.

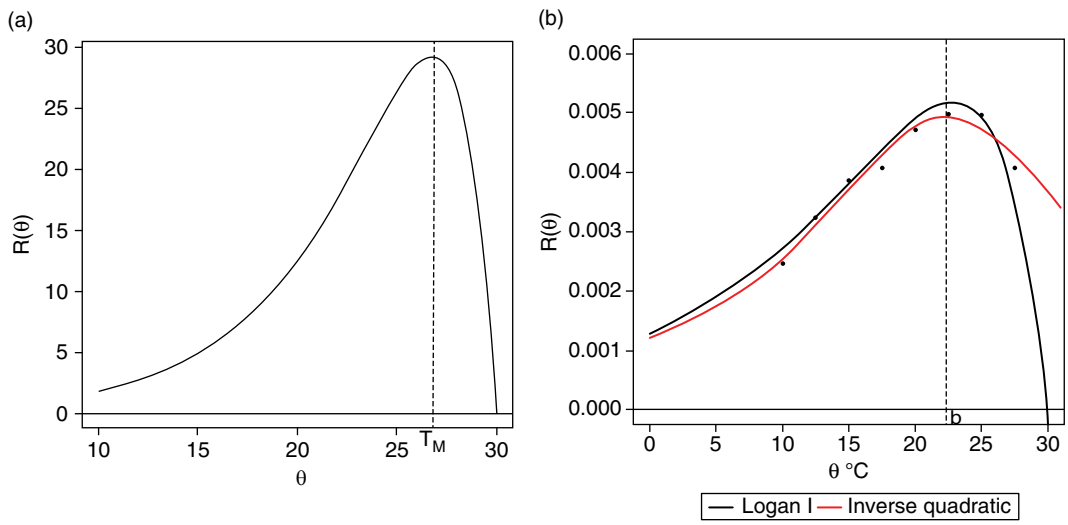

Fig. 1. Logan I development rate model for *Sitobion avenae*. (a) General shape where T_M (dotted line) indicates optimal development temperature. (b) Fitting the Logan I model (black line) to Dean's (1974) data (black dots) and, in red, the inverse quadratic model (Eqn 13.1). The vertical dotted red line and letter b indicates the optimum temperature of the inverse quadratic model.

wheat varieties assessed for resistance to cereal aphids (*Rhopalosiphum padi* and *S. avenae*), the main sources for resistance, and thus the greatest impact on aphid performance, were found in the ancestral diploid lines of wheat (i.e. *Triticum monococcum*, *Aegilops tauschii* and *Aegilops speltoides*) (G. Arradotirr, unpublished). Moreover, in another study of *S. avenae* performances on 67 different

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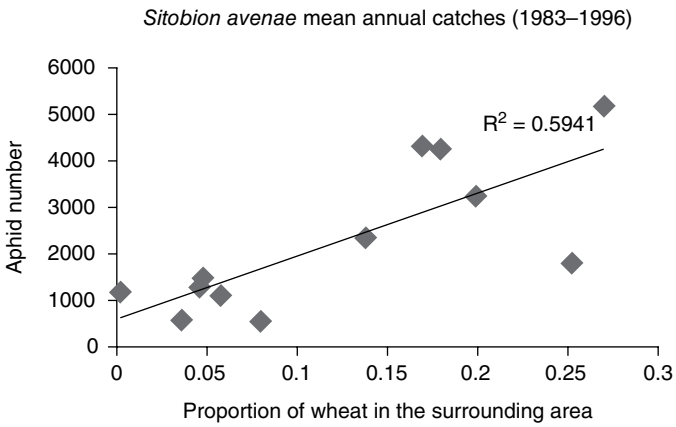

Fig. 13.4. Relationship between the mean cumulated annual numbers of *Sitobion avenae* in 12 suction traps of the French suction-trap network (Agraphid) and the proportion of wheat in the cropping area surrounding the traps within a 70 km radius. (From C.-A. Dedryver, unpublished.)

T. monococcum lines, very different levels of resistance were found (Di Pietro *et al*., 1998).

Modelling the effect of host plants

Process-based models that include a host-plant effect are scarce because of the lack of plant data (Carter *et al*., 1982; Plantegenest *et al*., 1996, 2001; Ciss *et al*., 2014a). There are several issues to consider when incorporating host plants into a model, principally: the direct effect on an aphid's ageing and fecundity due to sap quality; the joint effect of plant maturation and aphid crowding on wing formation and emigration; and last, how temperature is used to drive both plant and aphid growth. Caillaud *et al*. (1995) showed that the potential rate of increase *r* of *S. avenae* was on average two times lower on resistant than on susceptible *T. monococcum* lines in the same environmental conditions, and that for the same *T. monococcum* line, *r* values differed with the aphid clone used. Plantegenest *et al*. (1996, 2001) attributed an effect of the growth stage of the plant after milky ripening to both aphid mortality and fecundity. In their study on aphids, Ciss *et al*. (2014a) used a bivariate ad hoc equation to fit the relative growth rate of the apterae of *S. avenae* at a given growth plant stage and a given temperature (Fig. 13.5). The residual noise around the model (red dots) is a product of sampling error, use of daily mean temperatures, other causes of mortality than pure ageing and immigration and emigration. The response is detectable, however, and the residuals are unbiased. Ma and Bechinski (2009) addressed individual variability in reproduction rates on barley using 'same-shape' distribution models to quantify performance under field variable temperatures and plant growth stages. They produced similar surface plots to those in Fig. 13.5 but for *D. noxia*.

Biotic forcing variables: regulation by natural enemies

Aphids are regulated by predators, parasitoids and pathogens, but whether they alone can reduce aphids below the economic threshold is subject to much debate (Welch *et al*., 2012; Chapter 11, this volume). Here, modelling can play a key role in revealing the apparent unpredictability in the response of the natural enemy community (Hoover and Newman, 2004; Piñol *et al*., 2009; Hesketh *et al*., 2010; Mills and Kean, 2010; Bahlai *et al*., 2013). Models are likely to require both consumption/infection rate estimates as well as aspects of natural enemy behaviour. For model 'realism', the expectation is that trophic interactions are now measured in the field as opposed to the laboratory, facilitated through PCR and next-generation sequencing (Traugott *et al*., 2013; Wirta *et al*., 2014). Currently, molecular methods struggle to reveal numbers consumed per individual per day because it is not possible to determine the digestion time for samples collected in the field (Traugott *et al*., 2013). This methodological artefact may ultimately limit a model's potential in predicting dynamics, although what these molecular methods lack in quantification, they make up in providing detailed food web and spatial information. Sourcing laboratory data to populate some of the natural enemy parameter space may be required for some time yet.

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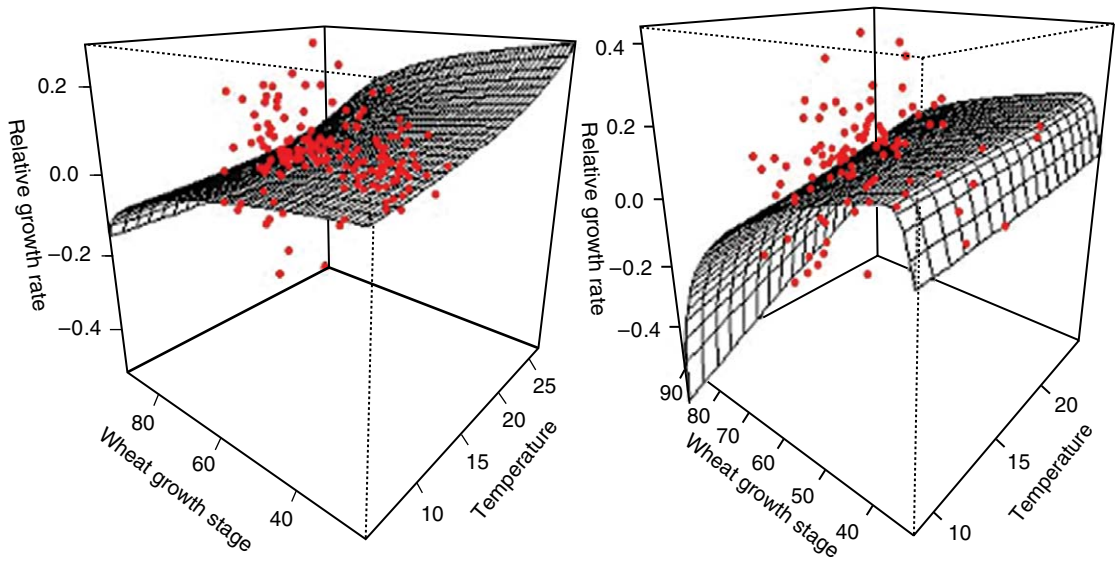

Fig. 13.5. The relationship between wheat growth stage and *Sitobion avenae* relative growth rate obtained from field data in the Rennes area (left) and in the Basin of Paris (right). The temperature scale is in °C. (From Ciss *et al*., 2014a.)

Incorporating predators and parasitoids into models

Models with one or two predators or parasitoids rarely apply to most field situations, for which a multitude of species that interact tend to be the norm (Hemptinne *et al*., 2012; Jeffs and Lewis, 2013), although agroforestry may be a special case (Piñol *et al*., 2009). For example, Western European populations of the grain aphid *S. avenae* have 9 species of primary parasitoids and over 50 species of polyphagous predators directly associated with it (Sunderland *et al*., 1987; Traugott *et al*., 2008). The size and breadth of the natural enemy community presents a challenge for any modelling framework because it has dynamic and unpredictable properties (Schellhorn *et al*., 2014), although solutions are forthcoming including non-linear methods (Ameixa *et al*., 2013).

While models by Carter (1985), Skirvin *et al*. (1997) and Kindlmann and Dixon (2010) struggled to deal with the breadth of the natural enemy community, the issue has received a little more attention recently (Caron-Lormier *et al*., 2011; Bahlai *et al*., 2013). In their simulation model, Bahlai *et al*. (2013) condensed predator and parasitoids into a 'Natural Enemy Unit', which was defined as the numbers of individuals that could kill 100 aphids in 24 h. Piyaratne *et al*. (2013) used relative predator units to avoid the confounding effect of using the total number of predators that was argued would not capture the variability in consumption rates between species and within life stages. The natural enemy communities featured in these models were still small by field standards, and they did not necessarily overcome the problem of natural enemy behaviour and life cycles that must also be parameterized (Bahlai *et al*., 2013). The use of functional and performance traits (e.g. body size/mass; vertical stratification; growth rate) can increase significantly our understanding of the mechanisms that may drive communities and generalize behaviour parameters to a wide range of organisms. These traits are starting to be used in models in which aphids feature. For example, Caron-Lormier *et al*. (2011) used 14 invertebrate functional types in their model of a wheat system, demonstrating the potential to simulate biodiverse communities of which aphids were a part. Recently, fuzzy logic has been used to capture the behaviour of predator–prey relationships in a spatially heterogeneous system. Leal-Ramírez *et al*. (2015) chose to study the ladybird *Cycloneda sanguinea* and its prey, the tropical citrus aphid, *Aphis* (*Toxoptera) citricidus*. While this model is simplistic because it is unlikely that the ladybird can develop solely on a diet of the brown citrus aphid (Morales and Burandt, 1985), it does demonstrate that differential equations and

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their coefficients can be replaced by fuzzy rules. In doing so, Leal-Ramírez *et al*. (2015) were able to make a model that was more intuitive and less complex mathematically.

Incorporating diseases into models

Fungal pathogens that regulate aphids in the field are drawn almost exclusively from the Entomophthorales (Entomophthoramycotina: Zygomycetes) that comprise six common aphid pathogenic species worldwide (Chapter 11, this volume). Ascomycete species, such as *Lecanicillium lecanii* and *Beauveria bassiana* that also infect aphids, do not occur at high densities naturally and are not considered further. After killing their aphid host, Entomophthorales produce infective conidia that are ejected mechanically around the cadaver, which makes them very efficient in propagating the disease among aphid colonies (Plantegenest *et al*., 2001). Hesketh *et al*. (2010) provide a useful summary of the attributes of this group (e.g. reproductive output, sporulation rate, life-cycle length, etc.) that will be of considerable utility for modellers. The weak point of Entomophthorales is their strong dependence on a high ambient relative humidity (RH): indeed, RH above 90% is a requirement of Entomophthorales because it promotes conidia formation, dispersal and germination (Hesketh *et al*., 2010). Wilding and Perry (1980) and Dedryver (1981) described epizootics occurring naturally in aphid populations and showed that several species of Entomophthorales, and especially *Pandora neoaphidis*, were very effective in naturally controlling crop aphids outdoors (*Aphis fabae*, *S. avenae*, *Metopolophium dirhodum*) in oceanic areas like the west of France, where 8–10 hours at 90% RH/day were common at the end of spring. Conversely, Gutierrez and Ponti (2013) predicted that *P. neoaphidis* would give poor control of the spotted alfalfa aphid, *Therioaphis trifolii maculate*, under the dry climate of California and Arizona.

While there have been a large number of statistical models that have sought to understand the optimal conditions of Entomophthorales population growth and infection rate (Pierre and Dedryver, 1984), there is a dearth of mathematical models in this area, in spite of their apparently greater simplicity compared to prey–parasite or prey–predator models. However, Schmitz *et al*. (1993) estimated the rate of increase of aphids infected by *P. neoaphidis* at different times after birth and compared it with that of healthy aphids. Following Oduor *et al*. (1997), who described a SIR model (susceptible, infected and recovered) for *Neozygites floridana* on mites, Ardisson *et al*. (1997) described a complete SIR epizootiological model for an *P. neoaphidis* infection of *S. avenae* and estimated its parameters. Fungal models require an assessment of the likely transmission rate of the disease, which is highly dependent on aphid population density (Fig. 13.6) and on relative humidity. However, Plantegenest *et al*. (2001) were able to demonstrate that fungal pathogens could be modelled without incorporating precipitation or humidity and still achieve acceptable population estimates. Further, because of the significant role of infected alates in dispersing these pathogens, host migration parameters are also likely to be of considerable importance (Chen and Feng, 2006).

Biological and Demographic Processes: Modelling Birth, Ageing, Moulting, Reproduction, Migration and Death

In the blacked-lined box of Fig. 13.3, the life cycle of the aphid takes place. There is, of course, immigration into and emigration out of the population, and this we shall address shortly. Beyond that, the remaining processes of ageing, moulting, death and reproduction (sexual/parthenogenic) are common submodel components in most published frameworks. However, approaches vary (e.g. discrete and continuous models), and the nomenclature used (i.e. birth, death, etc.) is not consistent between studies.

As mentioned previously, temperature has a profound effect on the rates of reproduction and birth and on ageing processes, but there are obviously other forcing variables to consider, like the predisposition of young to become infected by a disease or eaten compared to adults; this may be important under certain conditions.

Modelling birth through fecundity

Our focus is to model the fecundity of parthenogenetic morphs. Indeed, the sexual phase tends to affect the winter survival and hatching success of eggs in spring; these are highly variable and cannot be assessed easily. Winged and wingless parthenogenetic adults often have different fecundity curves that produce slightly different rates of increase (Simon *et al*., 1991). However, it is not a requirement that this polyphenism must be expressed in

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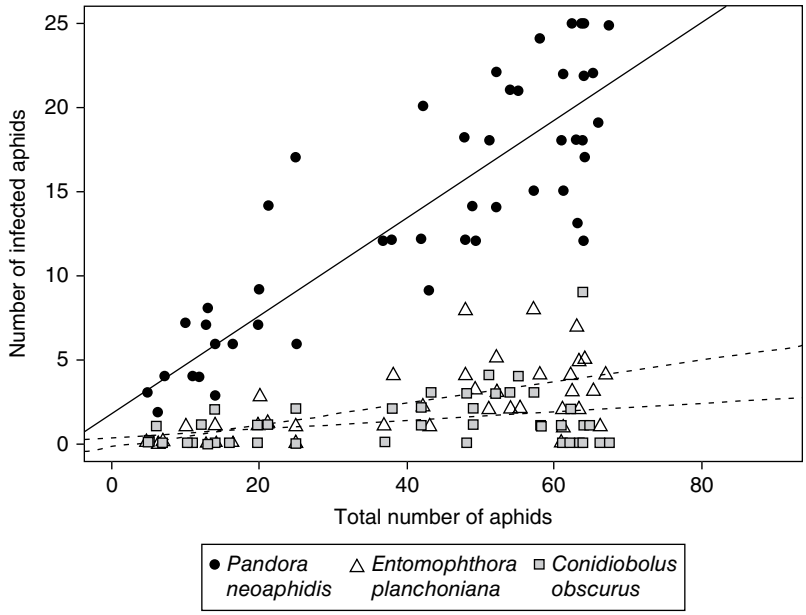

Fig. 13.6. Different density-dependence effects of three aphid-pathogenic Entomophthorales species (*Pandora neoaphidis*, *Entomophthora planchoniana*, *Conidiobolus obscurus*) in cereal aphid populations in western France. (From Dedryver *et al*., 2010.)

the model formulation. Instead, fecundity curves are often applied more generally. For example, the growth rates of *S. avenae* are known at various temperatures (Watt, 1979; Kieckhefer and Gellner, 1988). Its evolution with age after the moult to adult is shown in Fig. 13.7, which demonstrates how fecundity decays differently as a function of temperature. To summarize, when modelling the aphid birth process, one can split the effect of temperature in two parts: one that accelerates/decelerates the rate at which embryos are produced by adults, and another that scales the total potential fecundity, a measure of the reproductive potential, and determines what the range of potential fecundity values will be according to host-plant quality. Potential fecundity is a useful measure of aphid performance (Chapter 5, this volume). Box 13.2 explains in detail a way of building a thermo-dependent birth model in *S. avenae*. The procedure is taken from Plantegenest *et al*. (2001).

Modelling age and moulting

Ageing keeps time in the model and it is necessary to divide time somehow, either using days or physiological units. Let us consider the biology of the aphid *S. avenae* very briefly. In this and many other aphid species, four larval stages and an adult instar are apparent. At the third larval stage, larvae develop with wing pads, called pterothecae, while others do not, leading to a split in the model where these two morphs must be tracked individually. The consequences are that, in some species of aphid, the winged adults have lower fecundities and seem to respond differently in experimental treatments (Dixon, 1998; Chapter 5, this volume). If models merely tracked time by instars, they would miss quite a lot of detail and so the instar must be divided by time. For example, the different stages in development may not respond equally to a forcing variable such as temperature, and a high-resolution model may be required to capture this facet.

Early models used the QUIP (QUarter Instar Period), the time necessary to achieve a quarter of an instar, but this has fallen out of favour. Nowadays, large computing power has allowed modellers the luxury of dividing models into infinitesimally small time steps, although this has to be matched by high-quality data to model. A moulting rate term can be added to the model if it is felt that during the process of the moult the aphid is more vulnerable to attack, for example. It must be stressed at this point that there are some models in which age structuring is

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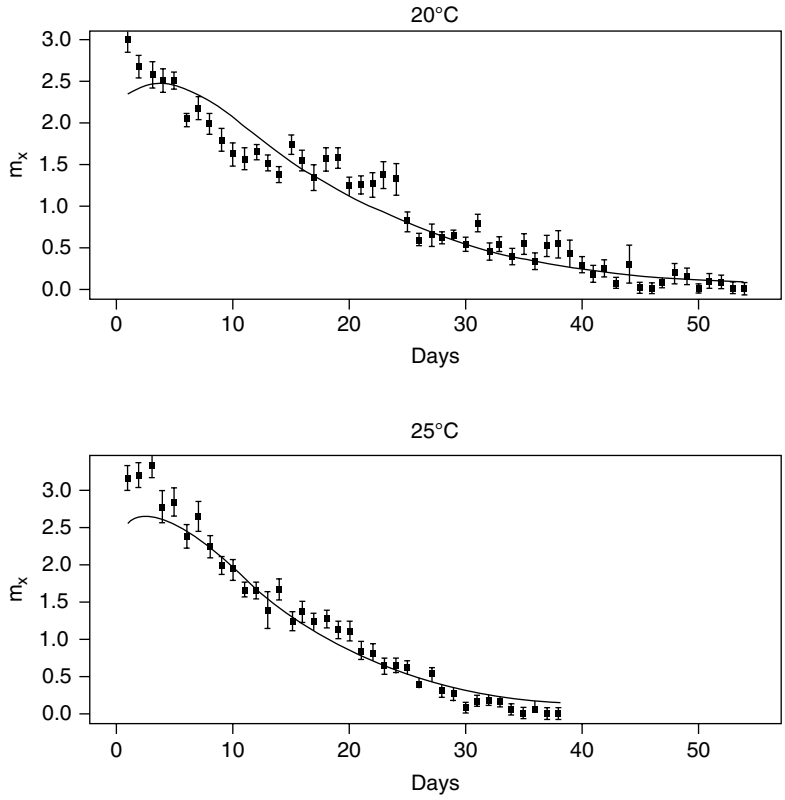

Fig. 13.7. Observed mean points with confidence interval and fitted regression model on the daily fecundity of *Sitobion avenae* females at 20°C and 25°C, where m_x is the age-specific birth rate. The plots show how fecundity as a function of time keeps its shape of decay at two different temperatures. However, the lower asymptote will be reached in a much shorter time at higher temperatures. (From Plantegenest *et al.*, 2001.)

absent, which leads to a simpler framework (Grechi *et al.*, 2010; Ciss *et al.*, 2014b). The relevance of such simplified models is good when the age structure is smooth and changes slowly. In that case, the intrinsic rate of increase responds almost instantaneously to the forcing variables. The simplification is also useful when the amount of calculation required is huge, as in spatio-temporal models (Ciss *et al.*, 2014b). Age-structured models have their benefits, though because some mortality factors act preferentially on some specific stages, the age structure of the population can sometimes be far from stable.

Modelling the migration process

Aphid migration is fundamental to understanding population growth rates and has been reviewed recently by Reynolds *et al.* (2006) and Irwin *et al.* (2007). Parry (2013) provides a conceptual process-type model of cereal aphid flight, which is helpful when integrating aphid migration into a modelling framework. Parry *et al.* (2015) summarizes existing dispersion models for a wide range of pests, including aphids, citing 'Silam' and 'Hysplit' as useful model frameworks.

While there are some detailed behaviours (e.g. the effect of crowding on alate production; direct effects of host plant phenology) that may be more challenging to represent, a few thresholds and principles exist that provide some important but simple model parameters. First, although not the same for all species nor necessarily the same for all alate morphs within a species (e.g. exules, gynoparae), the minimum temperature take-off threshold in field situations is 13°C, typically much higher 16–18°C, and the upper threshold when migration is said to cease is 31°C (Johnson, 1969; Walters and Dixon, 1984; Irwin *et al.*, 2007). An upper wind speed

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Box 13.2. Modelling fecundity with temperature using *Sitobion avenae*

As shown previously, aphid fecundity is key to explaining why aphids become pests. However, the primary factor determining its rate is temperature. Specifically, the physiological age for reproductive adults is defined by Eqn 13.3, where the median fecundity time D_{50} depends on the ambient temperature $\theta(.)$

$$X = \int_0^t \frac{1}{D_{50}(\theta(u))} du \qquad (13.3)$$

An extra multiplicative-scale effect (Fig. 1) is applied

$$U(\theta, S) = KF_{pT}(\theta, S) \qquad (13.4)$$

where F_{pT} is the potential total fecundity at temperature θ and plant phenological growth stage S and K a scaling parameter. This can then be incorporated in the fecundity equation

$$m(x) = KF_{pT}(\theta, S)\ln(x + b)e^{-Kx} \qquad (13.5)$$

where m(x) is the fecundity at age x. The number of births at time t is obtained by integrating over all possible ages:

$$B(t) = \int_0^\infty m(x, t)dx \qquad (13.6)$$

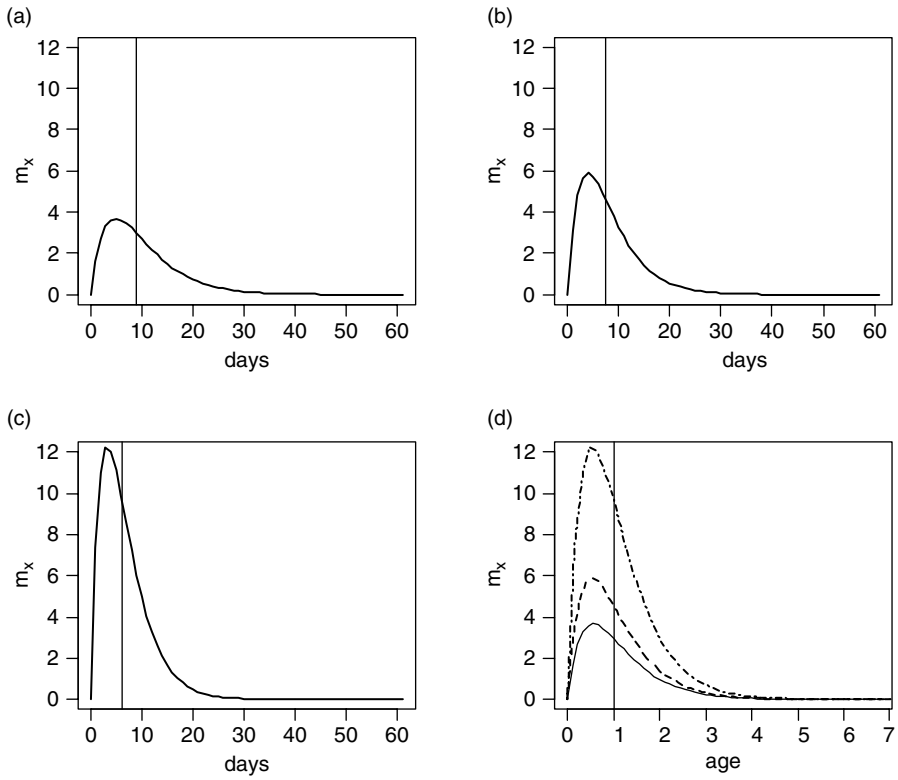

Fig. 1. Effects of temperature on the age-specific birth rate of aphids. The first three graphs (a,b,c) show that both the birth rate and the total amount of offspring vary with ambient temperature $\theta(.)$. For subplot (a) the temperature was θ_1, for (b) θ_2 and for (c) θ_3, where $\theta_1<\theta_2<\theta_3$. The vertical line marks the point at which 50% of the offspring are born. In (d), which has been rescaled by fixing the physiological age to arbitrary units, the total number of offspring can be derived by multiplying by a coefficient that takes account of temperature. The vertical line marks age 1, conventionally the age where 50% of the offspring are born. For a more detailed mathematical understanding, see Plantegenest *et al*. (2001) and references therein.

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threshold exists for take-off (3 m/sec), which agrees well with the wind threshold for natural enemies of aphids and of a similar size (Johnson, 1969; Walters and Dixon, 1984; Langer *et al*., 2004). Once airborne, the density of aphids diminishes with height, summarized by the coefficient *b* that characterizes the vertical density profile (Johnson, 1969; Walters and Dixon, 1984; Reynolds and Reynolds, 2009). Generally, the density of insects at high altitude increases with increasing temperature and decreasing wind speed, and the distances travelled are highly dependent on those atmospherics (Johnson, 1969; Bell *et al*., 2013; Parry *et al*., 2015). The period of migration is limited to the daylight hours, as is the case for a great many insects (Nottingham *et al*., 1991; Bell *et al*., 2013).

Reynolds and Reynolds (2009) showed that after 1 h of migration, aphids were predicted to have travelled between 6 and 30km downwind, dependent on whether the atmosphere was convective or neutrally stable, respectively. Further, Reynolds and Reynolds (2009) showed that aphids were actively migrating, exhibiting behaviours that caused them to produce lift and become neutrally buoyant in updrafts. Ciss *et al*. (2013, 2014b) studied the invasion and landing rates of aphids through simulation modelling and were able to reproduce field density estimates at large spatial scales, acknowledging that the proportion of wheat crops and how they were arranged in the landscape was of critical importance. It should be noted that on 'real landscapes', the spatial pattern of the aphid landing was found by Ciss *et al*. (2013) to be sensitive to aphid behaviour. Why aphids terminate their flights where they do is not yet clearly understood, hence model uncertainties.

Modelling death

It is straightforward to record aphid mortality, but when examined through the lens of survival analysis, more parameters can be derived (i.e. age-specific survival rate, shape and scale) that are useful to modellers. It should be recognized that death rate can be expressed equally as a survival rate, and hereafter will be referred to as either 'survival rate' or 'survival threshold'.

Survival rate

Survival rate is the probability that an individual's lifetime is equal or greater than that at a given point in time (Selhorst *et al*., 1995). One approach is to model survival in days and allow it to increase when temperature decreases between some limits (10–25°C), a relationship which is known for *S. avenae* (Williams and Wratten, 1987). Importantly, there will also be a level natural mortality for those aphids that reach the maximal age; this will be a function of temperature, indicated by a lower asymptote (Fig. 13.8). Ma and Bechinski (2008) modelled the survival of the Russian wheat aphid across the entire life cycle using covariates for temperature and plant-growth stage within a proportional hazards model. Alternatively, in the absence of survival data, theoretical survival rates have been used (Morgan, 2000).

Survival thresholds

Both cold shocks and heat stress reduce aphid survival (Jeffs and Leather, 2014). However, threshold temperatures vary between species and place of geographical origin, and care should be taken to avoid casually adopting minimum and maximum threshold temperatures.

MINIMUM SURVIVAL TEMPERATURE THRESHOLD. For many aphid pests, winter is a determining factor because their overwintering success determines their abundance the following spring. When aphid eggs

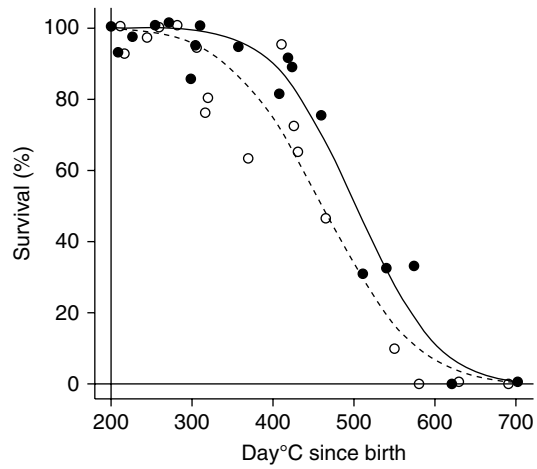

Fig. 13.8. Relationships between age of adult aptera (•—) and alatae (○– – –) and the proportion surviving as determined by probit analysis. The analysis determined that the survival of adult *Sitobion avenae* in the field during winter fitted a reverse sigmoid curve that gave median lifespans of 511 day degrees for apterae and 451 for alatae. (Redrawn from Williams and Wratten, 1987.)

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are strongly cold-hardy (Knight and Bale, 1986; Leather, 1992), parthenogenetic morphs that survive on crops during winter in temperate, oceanic and Mediterranean countries are freeze susceptible. To summarize numerous (and sometimes contradictory) results, the middle-term survival rate of parthenogenetic individuals of most aphid species in fields decreases significantly between –3°C and –7°C, and is generally poor below –10°C. However, frost susceptibility of parthenogenetic morphs is stage, species and clone specific, and also depends strongly on environmental conditions like the presence of snow and habituation to frost (Williams and Wratten, 1987; Vorburger, 2004). Consequently, including an accurate, single minimum threshold may be challenging because of the diversity of responses below the species level. It might be the case that a measure of central tendency is used to generalize across all types, but this may ultimately be unsatisfactory.

MAXIMUM SURVIVAL TEMPERATURE THRESHOLD. Most authors agree a survival threshold around 30°C for temperate aphids. Dean (1974) found that the larval mortality of *M. dirhodum*, *S. avenae* and *R. padi* was 100% at a constant temperature of 30°C. A comparable threshold of 31°C was found for *Aulacorthum solani* (De Conti *et al.*, 2010), for example. Tropical clones of *Aphis gossypii* seem, however, to survive quite well up to 36°C (Lu *et al.*, 2010). Walgenbach *et al.* (1988) did not observe significant differences between *Schizaphis graminum* (greenbug) survival and development at constant and fluctuating temperature regimes up to 28°C, at which point the aphids died.

Comprehensive Model

The components described in the preceding paragraphs can be conveniently incorporated in a set of Von Foerster–McKendrick equations that are given in Box 13.3. Figure 13.9 gives an insight on the whole process, by enlarging an infinitesimal slice of age.

Scaling up from Fields to Landscapes: Demographic Considerations

Modeller's headache: three issues to scaling up

The title of this chapter alludes to a spatial scaling issue of modelling field populations and then generalizing the processes found in those fields to landscapes scales. Upscaling addresses the challenge that ecologists are trying to deliver: broad but accurate representations that will inform policy whether it be for a district, state, nation, or even a continent. However, many problems need to be overcome to produce accurate landscape-level models, and although the list is seemingly endless, the main issues are data quality, response functions and the likelihood of extreme events.

First, models are invariably produced in the absence of high-quality landscape data that would otherwise set the parameters (e.g. migration distance, predation rate) at appropriate levels. It would be a mistake to take the average and simply scale up using this method.

This then leads on to the second issue related to scaling up and the response functions. When a response function (i.e. functional responses to prey; reaction norms to abiotic forcing variables, etc.) has been validated and the mechanism understood, only then can modellers reliably extrapolate accurately beyond measured conditions. While validation remains a problem (Kindlmann *et al.*, 2007; Kindlmann and Dixon, 2010), Parry *et al.* (2006) and Ciss *et al.* (2013) have both explicitly modelled landscape effects and confronted the problem of scaling up using individual-based models and a combination of mathematically explicit equations and cellular automata, respectively. For example, Ciss *et al.* (2013) demonstrated how a micro-scale model could lead to the provision of an equation for a macro-scale model: they mimicked the processes of take-off and landing of winged aphids as a 'behavioural reaction' to landscape at the scale of small square plots (0.25 × 0.25 km). These plots were the units of cellular automata used to upscale to the global response at the scale of 5 × 5 km pixels provided by a geographical information system (GIS).

Demographic characteristics of aphid populations that should be implicit within models

Variation seems to be the *raison d'être* of aphids. Not only are the life-history characteristics variable but so too are populations in space and time. There are, however, some generalizations that need to be understood, which are discussed below.

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Box 13.3. Building a comprehensive model continuous in age and time

Once development and reproduction are understood (Boxes 13.1 and 13.2), the final stage is to build a comprehensive life-cycle model of an aphid. However, we have only included the essential equations, and for a more detailed understanding see Plantegenest *et al*. (2001).

Ageing and death

Equation 13.7 expresses the decay of all age classes, except newborns. Just after birth, the only vulnerabilities are ageing or dying. So, let $\mu(x)$ be the death rate at age x, thus:

$$dn(x,t) = -\mu(x)n(x,t)dx \qquad (13.7)$$

where $dn(x,t)dx$ denotes the total differential of the number of aphids aged x at time t when time increases by dt and age by dx.

The rules of differential calculus lead to the following form, known as the Von Foerster–McKendrick equation:

$$\frac{\partial n(x,t)}{\partial x} + R\frac{\partial n(x,t)}{\partial t} = -\mu(x)n(x,t) \qquad (13.8)$$

R is the ageing speed or ageing rate, and denotes the partial derivatives. Although rather complex, this equation is highly tractable, both theoretically and numerically. It also has the following advantages:

1. The effects of all the factors that modify the speed of ageing are embedded in the single term R (.,.).
2. The variable $\mu(x)$, as stated above, is the age-specific mortality rate and encompasses all causes of mortality (e.g. natural death, predation, parasitization, diseases, insecticides, etc.). Moulting can be added to the same term by a moulting rate term, g(x).

Fecundity

A partial derivative equation (Eqn 13.8) requires initial and boundary conditions to define its particular solutions. The initial condition is the population age structure at time zero. A sample of the population and an evaluation of its age structure are required to initialize the model. The right boundary condition is not defined but, over time, both survival and fecundity tend to reach a value of zero. The left boundary condition defines the appearance of newborns at age zero. The basic concept is that aphids of every age contribute to the birth of new aphids with the age-specific birth rate $m(\theta, x)$, defined previously in Box 13.2 'Modelling fecundity with temperature using *Sitobion avenae*'. The process is that at each new age of the adult population, newborns contribute to that generation and, if this accepted, then

$$n(0,t) = \int_0^\infty m(\theta(t), x)n(x,t)dx \qquad (13.9)$$

becomes the second Von Foerster's equation, termed the birth (or recruitment) equation. Equations 13.8 and 13.9 constitute the core of the model. Practically, they are replicated for each larval instar. For all instars except the first, the birth equation is replaced by a moulting equation. For all instars apart from adults, the mortality rate is indirectly computed by a moulting rate. To implement the whole model, these equations need to be solved numerically (see Plantegenest *et al*., 2001).

Variation in time

Variability in time is key to understanding the levels of uncertainty apparent within a model, and therefore how reliable predictions are for any location. As seen in Table 13.1, populations vary between years, sometimes by several orders of magnitude, and this has implications for crop losses that range from non-existent to large. Data in Table 13.1 are an example of variation in time that requires the consideration of both between- and within-year variation.

BETWEEN YEARS. Kindlmann and Dixon (2010) argue that regular 2-year cycles should be predicted by models, but their model is only relevant to tree aphids. For example, the volatility in Table 13.1 illustrates that crop aphids are rarely subject to temporal autocorrelation between years.

WITHIN YEARS. Crop aphids have a strong seasonal component to their life cycle in temperate countries, although aphids do exhibit low within-year fluctuations in the Mediterranean. Exogenous and endogenous processes produce a common characteristic of within-year aphid population dynamics – the 'mid-season crash'. The crash is primarily the result of alate emigration in response to crowding, as well as a function of the reproductive rate (Paulson *et al*., 2009). The size of the crash is very much dependent on the species, because of the differences in reproductive rate. A further point is that the within-year peak in aphid numbers

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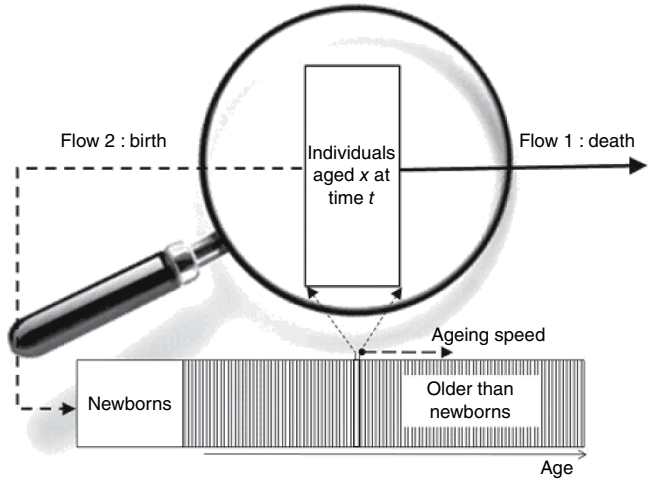

Fig. 13.9. The basic structure of a population dynamics model continuous in both age and time. The vertical bars in the lower box show that the whole population can be divided into infinitesimal slices of age. One of them is enlarged in the magnifier. This compartment shifts on to the right at a speed R (speed of ageing) depending, at least, on current temperature. In the left end of the lower box are newborn aphids, produced by almost all the slices with its own age-specific contribution *m(x)*.

can be uni-, bi- or multimodal. Most crop aphids are anholocyclic and so respond very quickly to changes in meteorology. Thus, temperature can have a radical effect on the population, which may dampen or exacerbate the previous weekly trends. However, there are patterns to the within-year dynamics that resonate with most crop aphids. Notably, the larger the size of the initial aphid population, the larger and earlier the peak (Kindlmann and Dixon, 2010).

Variation in space

Spatial synchrony refers to the spatial autocorrelation in time and is a special class of spatial autocorrelation that is quite different to simple spatial clustering. When detected, the norm is for the autocorrelation to decay with distance. It is very apparent in aphid populations, for two reasons: aphid migration is so effective at redistributing individuals that a level of synchrony is inevitable, and further, anholocyclic aphids in the world's crops respond quickly to changing temperatures and crop stages and are likely to be synchronized with these extrinsic forcing variables, which leads to the Moran effect (Sheppard *et al*., 2016). Synchrony can be tested using bootstrapped correlograms and wavelets, but why should a phenomenological model be given such importance in process-based modelling? Simply, spatial synchrony can help define a model's resolution (i.e. grain) over which modellers can generalize a process over space. The model must still be validated, however convincing the statistics.

While early work by Hanski and Woiwod (1993) provided a broad overview of synchrony in aphid populations, since that time models have become more comprehensive. It can be shown using a nonlinear spline correlogram that the annual counts of *S. avenae* across the UK have a correlation length of 320 km (J. Bell, unpublished) and a large element of spatial synchrony. For example, wavelets show that approximately 80% of the spatial synchrony of long timescale fluctuations in UK aphid first-flight phenologies can be explained by the influence of winter climate fluctuations (Sheppard *et al*., 2016), a well-known relationship (Harrington *et al*., 2007; Bell *et al*., 2015).

Very little, if any, work has been done at the field level on spatial synchrony, although there are plenty of studies using clustering methods to detect patterns that confirm that these clusters are short-lived (e.g. Winder *et al*., 1999). For illustrative purposes, Fig. 13.10 shows the variation in *S. avenae* populations in six fields across France during the same year. It is clear to see that, unlike the suction-trap caught aphids (Fig. 13.10), the spatial coherence of

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S. avenae is low, with a tendency for high aphid populations with prominent peaks on wheat in the north and in the west, compared to low numbers with flattened peaks in the south and in the east. The conclusion that can be drawn as a result is that spatial assumptions drawn from one process (e.g. migration synchrony) cannot be generalized to others (synchrony in within-field population growth).

Conclusions

Process-based models are useful tools for unravelling complex dynamics, and help to erect new hypotheses and guide management decisions based on their results. Parry (2013) highlights the need to overcome the problem of 'scaling up' models to explore multiple hypotheses and scenarios. Scenarios are often needed by policy makers who have a demand for knowledge at larger spatial scales or who require the impacts on wider processes to be estimated. Mechanistic, process-based modelling can deliver what is beyond even the largest experiment, thus elucidating underlying processes that drive aphid populations.

We all must recognize that data are not perfect and data sets never include all the information that is needed. Thus, the role of the modeller is to translate the data to a more meaningful understanding and delimit the range of forecasting that can be provided, given the partial information that is at

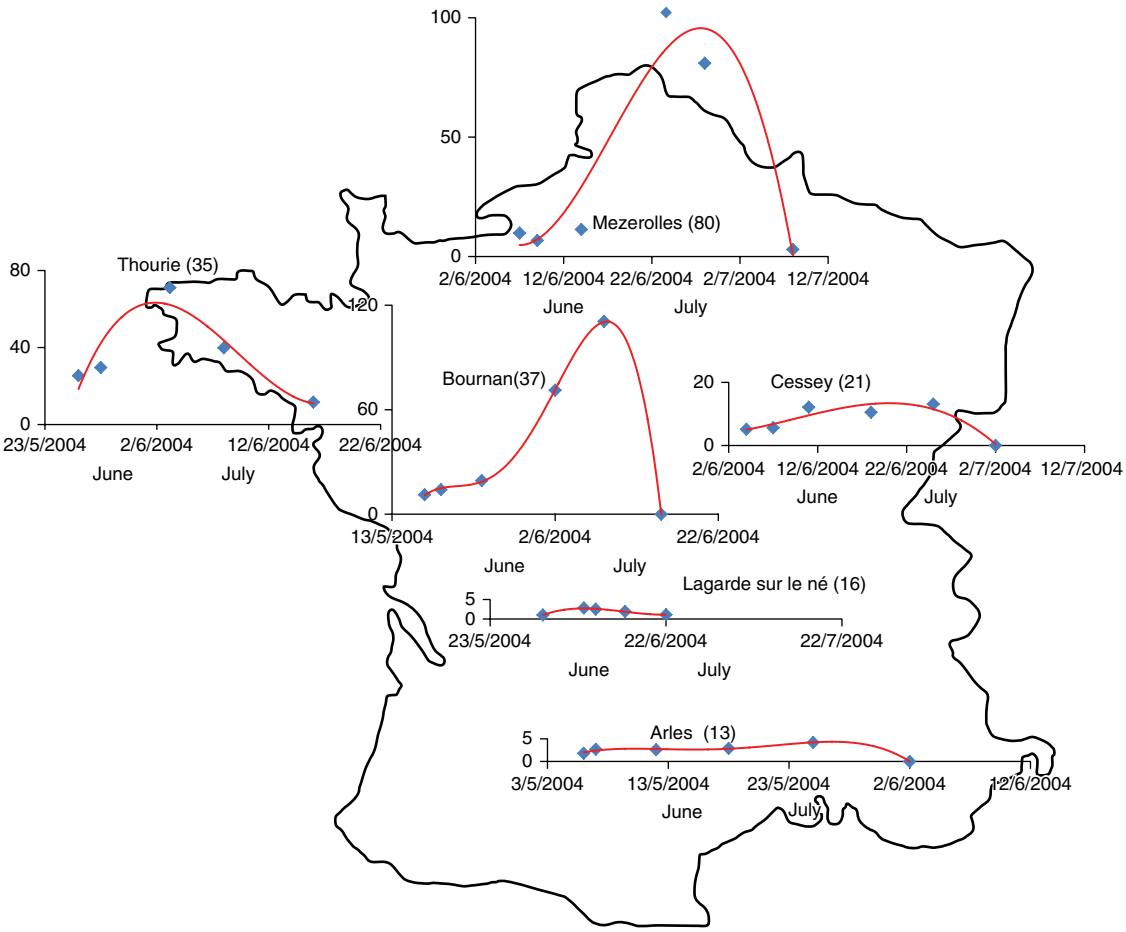

Fig. 13.10. An example of regional differences in *Sitobion avenae* populations (mean numbers of aphid per ear) on winter wheat in France for 2004. Each curve represents one field in one site. (C.-A. Dedryver, unpublished.)

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their disposal. This process explains the success of Bayesian inference and models that aim to determine how the information gathered restricts the field of possible outcomes (Fabre *et al*., 2006). The balance between data and their acquisition cost is of paramount importance to consider in the future.

Modelling is becoming easier and more accessible to all, and arguably the rise of individual- or agent-based models is a signal that not all models have to be programmed by mathematicians. Indeed, efforts are now made to provide mathematical models to biologists with the core maths having been pre-coded. The movement was initiated in the 1980s by the development of the program Stella (Stella 10.0, isee systems inc, New Hampshire, USA). More recently, insect modellers (e.g. Bahlai *et al*., 2013) have turned to DYMEX (Dymex 3.0, Hearne Scientific Software Pty Ltd, Australia), one of the most comprehensive programs available. These platforms avoid the tedious task of writing computer code in low-level languages and of spending time in implementing numerical schemes. Unfortunately, only the differential and difference equations are easy to include in such generic systems. Partial differential equations, used for instance in spatially explicit models, are not yet available in such software, as each equation, and each type of boundary conditions, requires a different discretization (a process by which a continuous variable is split into discrete components) scheme.

The initial conditions of a model are founded on the quality of data and its spatial and temporal extent. Of course, aerial populations of winged aphids have been sampled by the Rothamsted suction traps since the 1960s and modelled (Bell *et al*., 2015). While links have been made between suction-trapped and field-caught aphids (Fabre *et al*., 2010), these data are part of one process, migration. Large-scale field data are rare, especially ones that are of any spatial or temporal extent. The French decision support system named 'COLIBRI' is arguably unique, because it was created to monitor grain aphids in wheat fields. The investment was considerable, requiring 4 years to develop and a further 5 more years to be validated (Plantegenest *et al*., 1999). These types of investment are needed to answer the big questions in agriculture, like food security under reduced inputs and insecticide resistance, for example. Models may seem like an academic pursuit but they give a new perspective on agriculture, allowing us to 'win on average' for the benefit of farmers, farming and the users of the landscape.

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14 Feeding Injury

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Introduction

The sternorrychan superfamily Aphidoidea includes aphids (Aphididae), adelgids (Adelgidae) and phylloxera (Phylloxeridae), and all three of these families pose a serious problem in the production of food and fibre crops. In fact, all of the world's major crops are attacked by at least one species of Aphidoidea, although some plants suffer greater injury than others (Blackman and Eastop, 1994, 2006). The importance of crop losses caused by aphids and other insect herbivores has been described in these terms: 'The shift of energy from plants to insects rivals in scale mankind's own demands on the photosynthesizing world' (Southwood, 1997). Moreover, aphids and other sap-sucking arthropods can extract more energy per unit area than grazers and browsers, and they do so without consuming any of the plant structural tissues (Dixon, 1985). Several well-known introduced pests illustrate the ability of the Aphidoidea to limit crop yields and to have profound ecological and sociological impacts. The Russian wheat aphid (*Diuraphis noxia*) was first found in the USA in 1986, and by 1993 was estimated to have caused US$893 million in losses to US cereal crops (Morrison and Peairs, 1998). While cereal cultivars with Russian wheat aphid resistance are now widely deployed, the rapid emergence of new biotypes continues to challenge breeders (Botha *et al*., 2005). The soybean aphid (*Aphis glycines*) was first discovered in North America in 2000 and has since become the most important arthropod pest of soybean, in some cases causing up to 40% reductions in yield (Ragsdale *et al*., 2011). During a 2001 outbreak, densities of this aphid were so high that they actually posed a windborne nuisance in Toronto and Detroit and delayed a baseball game at the Toronto SkyDome (DiFonzo, 2009). Other pests in the Aphidoidea with high-profile social impacts are grape phylloxera (*Daktulosphaira vitifoliae*) and the balsam woolly adelgid (*Adelges (Dreyfusia) piceae*). Grape phylloxera was introduced from the USA to Europe in the mid-19th century, and remains a costly limitation on the production of European wine grapes worldwide (Granett *et al*., 2001). Likewise, the balsam woolly adelgid, which was introduced into the USA from Europe around 1900, has changed the face of North American forests (Pimentel *et al*., 1999). This pest has caused severe injury to the natural ecosystem of balsam fir (*Abies balsamea*) throughout the southern Appalachians, where it has destroyed 95% of the Fraser firs (*Abies fraseri*) (Alsop and Laughlin, 1991). As a result of adelgid-mediated Fraser fir death, Alsop and Laughlin (1991) reported the loss of two native bird species and the invasion of three other bird species in the region, illustrating the wider ecological impacts of the Aphidoidea.

Aphidoidea can affect crop yield and quality adversely through direct and indirect damage. Direct damage can be caused by aphids alone, whereas indirect damage includes pathogen transmission and predisposition to other stresses. A common example of predisposition is the way in which the copious excreta of Aphidoidea supports the growth of sooty mould fungi (e.g. *Capnodium citri* and other filamentous ascomycetes), which in turn cause cosmetic damage and reduce the plant's photosynthetic capacity (Reynolds, 1999). Aphids have an even greater economic impact as vectors of plant

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viruses (a topic discussed in Chapter 15, this volume). This chapter, however, will focus on direct damage by aphids and other Aphidoidea. We will describe the diversity of symptoms caused by this group of insects, and discuss the current state of knowledge of the biochemical and physiological mechanisms leading to damage. Additionally, we will discuss the ramifications of studying aphid injury in relation to crop improvement, and highlight current research frontiers in this area.

The Causes, Signs and Outcomes of Infestation: Injury, Symptoms and Damage

Terminology

In discussing the impacts of the Aphidoidea on crops, it is useful first to define the terminology used to describe the effects of herbivory on plants (Fig. 14.1). As defined by Peterson and Higley (2001), the term 'injury' refers to 'a stimulus producing an abnormal change in a physiological process', whereas 'damage' refers to 'a measurable reduction in plant growth, development, or reproduction (including yield) as a result of injury'. Last, as defined in this chapter, 'symptoms' are 'the subjective evidence of disease or physical disturbance', or 'something that indicates the presence of bodily disorder' (Merriam-Webster, 2014). In the field of plant protection, the term 'symptom' is typically reserved for traits that can be discriminated easily with the naked eye, such as necrotic spots or leaf rolling, and that can be useful in diagnosing the source of injury. It is important to note, though, that injury and damage can occur even in the absence of obvious symptoms; for example, infestation by *Rhopalosiphum padi* (bird cherry–oat aphid) on wheat (*Triticum aestivum*) can lead to yield losses (Voss *et al*., 1997), despite the lack of diagnostic symptoms (Fig. 14.2).

Common symptoms of infestation

Infestation by Aphidoidea may cause extensive apparent symptoms, or the host plant may be entirely

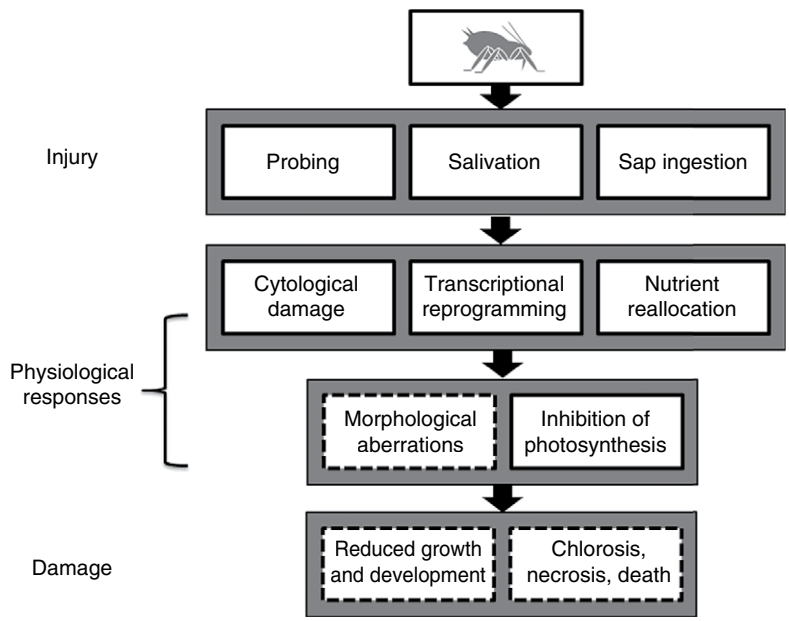

Fig. 14.1. Impact of Aphidoidea on host plants. Insect feeding (i.e. injury) causes perturbations in the physiology of the host plant that can, in turn, cause damage to the plant (i.e. reductions in growth, development and survival). In some cases, Aphidoidea may cause symptoms (outlined with dashed lines) that can serve as diagnostic indicators of physiological dysfunction. However, it is possible for yield losses and other damage to occur even in the absence of obvious symptoms. Each process outlined in the diagram can contribute to the development of all subsequent steps in the disease progression.

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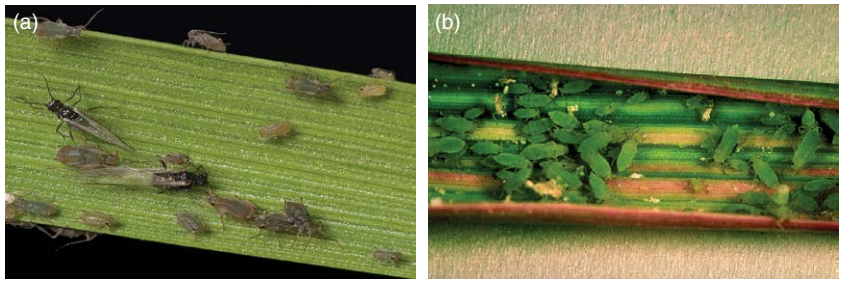

Fig. 14.2. Asymptomatic and symptomatic aphid infestations. Host plants may lack obvious outward signs of damage, as in the case of (a), wheat leaves challenged with *Rhopalosiphum padi* (bird cherry–oat aphid). (Photograph courtesy of Dr Stewart Gray.) Alternatively, Aphidoidea may cause a diverse range of symptoms, including (b) leaf rolling and longitudinal chlorotic and necrotic streaks on wheat caused by *Diuraphis noxia*. (Photograph courtesy of Dr Frank Peairs. Panel (b) is reprinted from Goggin, 2007, with permission.)

asymptomatic (i.e. free of obvious morphological aberrations, as in the case of wheat infested with bird cherry–oat aphid). The nature and magnitude of symptoms will vary depending on which combination of insect and host species we examine (Table 14.1), as well as on the density of the infestation and the stage of plant development at which it occurs. Symptoms elicited on plants by Aphidoidea range from the inhibition of growth and the hastening of senescence (termed 'desistance') to the deformation of new growth and the proliferation of plant tissues into abnormal structures (ie. neoplasms). Desistance includes chlorosis, necrosis (Figs 14.2b and 14.3), and stunting, while common forms of deformation include leaf curling (Fig. 14.2b) and misshapen fruit, and neoplasms include galls on roots, leaves, or other plant parts (Fig. 14.4). In some cases, the sympoms of aphid infestation are severe enough to kill the plant. For example, heavy infestations of *Sipha flava* (yellow sugar cane aphid) can kill sorghum (*Sorghum bicolor*) (Breen and Teetes, 1990), and the Russian wheat aphid can lead to the necrosis and death of susceptible wheat seedlings (Burd *et al*., 1998). Symptoms may be limited to the site of infestation, as in the case of necrosis caused by *Macrosiphum euphorbiae* (potato aphid) on tomato (*Solanum lycopersicum*) (Fig. 14.3a), or it may spread systemically to uninfested parts of the plant, as in the case of the vein-clearing symptoms induced in new growth of lucerne (*Medicago sativa*) by *Therioaphis trifolii maculata* (spotted alfalfa aphid; Fig. 14.3b). Some of the deformations induced in host plants by Aphidoidea appear to be adaptive to the insects that cause them. In particular, gall formation and pseudogalling such as leaf rolling provide the insects with protection from weather and natural enemies, including grazing herbivores, and modifications in plant development, such as proliferation of vascular tissue in galls, may help channel nutrients to the insect feeding site (Price *et al*., 1987; Stone and Schönrogge, 2003; Rostás *et al*., 2013).

Detection and quantification of symptoms induced by Aphidoidea

Although the symptoms elicited by aphids and their relatives have been recognized for a long time, the precise measurement of these symptoms still lags behind comparable work in other disciplines like plant pathology and plant physiology. To fill this gap, imaging techniques that were developed to study other phenotypic changes in plants (Chaerle and van der Straeten, 2001) can be applied to detect and quantify symptoms of Aphidoidea infestation at a range of different spatial scales.

At the landscape level, multispectral and hyperspectral imaging can identify changes in the appearance of plant canopies that are useful indicators of infestation. Spectral data can be collected with sensors at ground level, on crop dusters or other aerial devices, or even on satellites (Reisig and Godfrey, 2006), and this approach has been used to detect grape phylloxera infestations in vineyards (Benheim *et al*., 2012), hemlock woolly adelgids in forests (Pontius *et al*., 2005) and multiple aphid species on cereals, row crops and forest trees (e.g. Scotford and Miller, 2005; Reisig and Godfrey, 2006; Pena and Altmann, 2009). In some systems, remote sensing can discriminate accurately among multiple potential sources of plant stress. In wheat,

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Table 14.1. Examples of the diversity of symptoms caused on crops by Aphidoidea.

Injury type	Aphid	Crop	Reference
Asymptomatic injury	*Rhopalosiphum padi*	Cereals	Riedell and Kieckhefer (1995)
	Acyrthosiphon pisum	Legumes	Hill (1997)
	Rhopalosiphum maidis	Cereals	Bing *et al*. (1991)
Symptomatic injury			
Desistance			
Stunting	*Aphis (Toxoptera) citricidus*	Citrus	Blackman and Eastop (1994)
	Diuraphis (Holcaphis) tritici	Cereals	Kindler and Hammon (1996)
	Diuraphis noxia	Cereals	Burd *et al*. (1993)
Chlorosis	*Diuraphis noxia*	Cereals	Burd *et al*. (1993)
	Therioaphis trifolii maculata	Lucerne	Jiang and Miles (1993)
	Pemphigus betae	Sugar beet	Donahue *et al*. (1998)
	Macrosiphum euphorbiae	Tomato	Hebert *et al*. (2007)
Necrosis	*Schizaphis graminum*	Cereals	Ryan *et al*. (1990)
	Tinocallis caryaefoliae	Pecan	Wood and Reilly (1998)
	Macrosiphum euphorbiae	Potato, tomato	Miles (1990); Hebert *et al*. (2007)
	Sipha flava	Sorghum	Breen and Teetes (1990)
Deformation			
Misshapen fruits	*Dysaphis plantaginea*	Apple	Varn and Pfeiffer (1989)
	Diuraphis noxia	Cereals	Peairs (2001)
Pseudogalling	*Diuraphis noxia*	Cereals	Burd *et al*. (1993)
	Myzus persicae	Peach	Miles (1990)
	Aphis gossypii	Cotton, melon	Miles (1990)
	Acyrthosiphon kondoi	Legumes	Miles (1990)
	Brevicoryne brassicae	Crucifers	Boyd and Lentz (1994)
	Lipaphis pseudobrassicae	Crucifers	Boyd and Lentz (1994)
	Macrosiphum euphorbiae	Tomato	Walgenbach (1997)
	Dysaphis plantaginea	Apple	Varn and Pfeiffer (1989)
	Aphis pomi	Apple	Blackman and Eastop (1994)
	Aphis spiraecola	Apple	Blackman and Eastop (1994)
	Aphis craccivora	Legumes	Drees and Jackman (1998)
Neoplasm			
Leaf	*Daktulosphaira vitifoliae*	Grape	Granett *et al*. (2001)
	Phylloxera notabilis	Pecan	Drees and Jackman (1998)
	Phylloxera caryaecaulis	Hickory	Blackman and Eastop (1994)
	Pemphigus spp.	Poplar	Hill (1997)
	Eriosoma lanigerum	Apple	Brown *et al*. (1995)
	Aphis glycines	Soybean	
Shoot	*Adelges (Sacchiphantes) abietis*	Spruce	Johnson and Lyon (1988)
	Adelges (Gilletteella) cooleyi	Spruce	Johnson and Lyon (1988)
	Phylloxera caryaecaulis	Hickory	Blackman and Eastop (1994)
	Phylloxera devastatrix	Pecan	Drees and Jackman (1998)
Root	*Daktulosphaira vitifoliae*	Grape	Granett *et al*. (2001)
	Eriosoma lanigerum	Apple	Brown *et al*. (1995)

for example, Russian wheat aphid infestation can be distinguished from drought or unfavourable agronomic conditions with 98% accuracy (Backoulou *et al*., 2011). This technology has great promise to reduce growers' scouting costs, facilitate highly targeted pesticide applications and enable area-wide management of invasive species and other important insect pests.

At the level of individual plants or plant organs, techniques to quantify the symptoms of Aphidoidea

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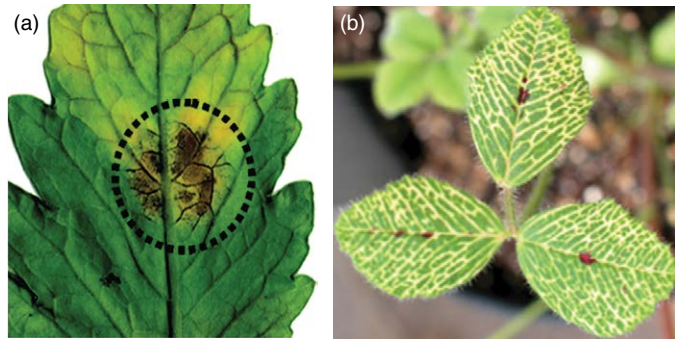

Fig. 14.3. Desistance: chlorosis and necrosis. Examples of desistance caused by Aphidoidea include: (a) chlorosis and necrosis on tomato in response to *Macrosiphum euphorbiae*. The dotted line represents the position of the cage to which aphids are confined. Necrosis is limited to the aphid feeding site, while chlorotic symptoms can extend beyond the point of infestation (Hebert *et al*., 2007); (b) systemic veinal chlorosis on a newly formed, uninfested lucerne leaf that is orthostichous to a mature leaf infested with *Therioaphis trifolii maculata*. (Photograph in (b) courtesy of Dr John Klingler; (a) is reprinted from Goggin, 2007, with permission from Elsevier.)

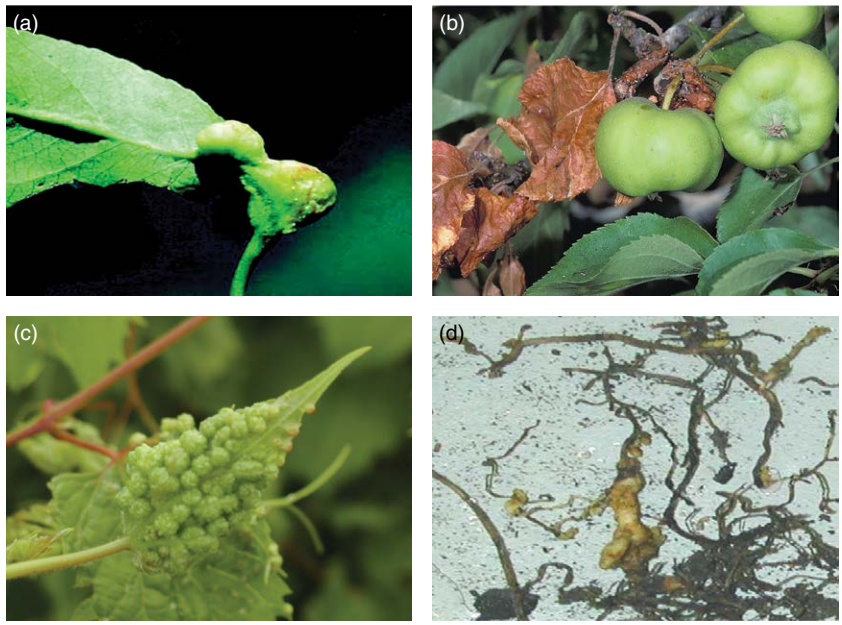

Fig. 14.4. Deformation: galls induced by Aphidoidea. (a) Foliar galls on the narrowleaf cottonwood (*Populus angustifolia*) induced by *Pemphigus betae* (sugar beet root aphid). (Photograph courtesy of Dr Thomas Whitham.) (b) Misshapen apple fruit caused by *Dysaphis plantaginea* (rosy apple aphid). (Photograph courtesy of Jack Kelly Clark.) Leaf (c) and root (d) galls elicited by *Daktulosphaira vitifoliae* (grape phylloxera). (Original photographs courtesy of R. Isaacs and Kevin S. Powell; (a) is reprinted from Goggin, 2007, with permission.)

infestation can also enable breeding programmes to select for less susceptible cultivars. Symptoms of infestation such as chlorosis are often less labour-intensive measures of plant susceptibility than is insect population growth, and can offer an efficient means of detecting tolerance, a phenomenon that cannot be identified on the basis of insect numbers alone (Chapter 22, this volume). In sorghum, for example,

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measuring chlorophyll loss *in vivo* with a Soil Plant Analysis Development (SPAD) spectrophotometer offers a rapid, non-destructive method for screening large numbers of accessions for *Schizaphis graminum* (greenbug) tolerance (Girma *et al*., 1998). New approaches in plant imaging and high-throughput phenotyping also have tremendous potential applications for quantifying herbivore damage to assess plant tolerance or resistance (Goggin *et al*., 2015). For example, automated high-throughput phenotyping (HTP) systems that use robotics to image plants in multiple spectra within and beyond the visible range can increase the population sizes that breeders can screen and enable the measurement of complex or subtle phenotypic variation that is not readily measured manually (Yang *et al*., 2013). For instance, while manual estimates of growth are typically limited to one or a small number of measurements, such as plant height that can be measured with a ruler, HTP systems can capture more detailed and accurate estimates of leaf area and compactness (Arvidsson *et al*., 2011). Moreover, HTP systems that can image fluorescence or the near-infrared reflectance of plants can estimate traits that are not measurable by the human eye, such as chlorophyll fluorescence, photosynthetic efficiency or plant water status (Yang *et al*., 2013). In short, HTP has the potential to detect differences in plant responses to infestation that would easily be missed by manual phenotyping.

Last, new techniques for imaging plant cells and ultrastructure have the potential to advance our understanding of the physiological and molecular bases of plant symptom development in response to feeding by Aphidoidea. For example, optical imaging of fluorescent and luminescent probes in live plant cells could be used to study the effects of insect infestation on cell wall structure, cytoskeletal dynamics and sugar transport (Shaw and Ehrhardt, 2013), all of which are likely to be perturbed by aphids and their relatives. These cytological approaches, together with whole-plant and landscape-level imaging of plant symptoms, could help pinpoint the physiological perturbations that result in crop damage by Aphidoidea and identify means of protecting plants from these dysfunctions.

Modes of Injury by Aphidoidea

Plant penetration and mechanical injury

Members of the Aphidoidea feed on a fluid diet extracted through slender piercing and sucking mouthparts (stylets), and saliva is injected through the maxillae into the plant to facilitate the feeding process. Injury to the plant may result from penetration by the stylets, injection of saliva and/or withdrawal of nutrients (Fig. 14.1), and the nature and extent of plant symptoms varies with the insect's mode of penetration and preferred feeding site. The stylets of the Aphidoidea can pierce the plant epidermis by passing between cells (intercellular route), through cells (intracellular route), or through stomata, and most aphids appear to use a combination of these routes on different host plants (Pollard, 1973). Once past the epidermis, the stylets of most aphids traverse an intercellular path to their feeding site in a phloem sieve element, briefly penetrating cells along the stylet path to sample cell contents (Tjallingii and Esch, 1993; Hewer *et al*., 2011). However, some aphids appear at times to take an intracellular route to the phloem (Pollard, 1973). For example, histological observation of the feeding sites of the Russian wheat aphid on wheat showed both inter- and intracellular stylet paths (Saheed *et al*., 2007a). Moreover, some tree-feeding aphids, as well as adelgids and phylloxera, use an intracellular route to access feeding sites in the parenchyma rather than in the phloem sieve elements (Pollard, 1973; Pointeau *et al*., 2012). In general, intracellelar penetration causes more ultrastructural damage to plant tissues than does intercellular penetration. However, it is important to note that even aphids that use a primarily intercellular stylet path could generate important wound signals while penetrating the epidermis or sampling cells along the stylet path. Moreover, certain phloem-feeding aphids are also able to induce galls (Wool, 2004), though gall formation is found primarily among parenchyma-feeding Aphidoidea (Miles, 1989). Also, the ability of both phloem-feeding and parenchyma-feeding Aphidoidea to injure host tissues probably depends not just on mechanical damage by the stylets but also on the effectors in the insects' oral secretions.

Aetiological agents in Aphidoidea oral secretions

Our knowledge of the saliva of the Aphidoidea is based primarily on analysis of the enzyme activities and protein composition of aphid oral secretions collected from artificial diets, and on molecular characterization of the transcripts that are expressed in aphid salivary glands (reviewed in Elzinga and

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Jander, 2013; Rodriguez and Bos, 2013; Will *et al*., 2013). Aphids and other Sternorryncha produce a gelling saliva that lines the stylet path and a watery saliva that is injected both inter- and intracellularly, particularly during cell sampling and ingestion (Will *et al*., 2013). Radiolabelling has shown that the secretions aphids inject into their feeding sites can move systemically into uninfested leaves and roots, both above and below the aphid feeding site (Madhusudhan and Miles, 1998; Burd, 2002). This injection of saliva has long been proposed as a cause of the phytotoxic symptoms induced by certain aphid species, including the Russian wheat aphid, the yellow sugar cane aphid (*S. flava*), the greenbug and the spotted alfalfa aphid. In support of this hypothesis, Lapitan *et al*. (2007) have reported that treating wheat seedlings with Russian wheat aphid oral secretions collected from artificial diets can induce similar leaf rolling and discoloration as aphid feeding itself. However, it has yet to be determined how aphids' secretions cause this damage. Saheed *et al*. (2007a,b) have proposed that the saliva of the Russian wheat aphid may impede translocation in the plant by mechanically plugging the xylem. In electron micrographs of aphid feeding sites on susceptible wheat and barley plants, they observed a smooth, electron-dense coating of saliva encasing the inner walls of affected xylem elements. However, the majority of other studies on aphid saliva are based on the premise that it alters host physiology through its chemical and molecular activities rather than through its physical properties.

Early studies on enzymatic activities in aphid oral secretions reported the presence of pectinases and cellulases, which could contribute to ultrastructural damage at the feeding site by degrading components of the plant cell wall and initiating programmed senescence (reviewed by Miles, 1999). More recent analyses of aphid saliva collected from artificial diets also suggest the presence of proteases that can degrade plant proteins (Furch *et al*., 2015), and calcium-binding proteins that could potentially interfere with signalling and defence in the host plant (Will *et al*., 2007). Both enzymatic assays and proteomic studies also point to the presence of oxidoreductases in aphid secretions. Some authors propose that these enzymes contribute to symptom development by disrupting the redox balance of plant tissues (Jiang and Miles, 1993; Miles and Oertli, 1993; Ni *et al*., 2000), while others argue that they are involved in the elicitation or detoxification of plant defences (Urbanska *et al*., 1998; Ma *et al*., 2010; Nicholson and Puterka, 2014). Analysis of the transcripts expressed in aphid salivary glands has also identified several putative effectors from *Acyrthosiphon pisum* (pea aphid), *Myzus persicae* (green peach aphid) and *M. euphorbiae* that modulate plant defence responses when expressed in plants (Elzinga *et al*., 2014; Rodriguez *et al*., 2014; Naessens *et al*., 2015; Wang *et al*., 2015; and studies reviewed in Elzinga and Jander, 2013; Rodriguez and Bos, 2013; and Furch *et al*., 2015). Interestingly, one of these effectors is homologous to pro-inflammatory cytokines utilized by ticks, nematodes and protozoans in the parasitism of vertebrate hosts (Naessens *et al*., 2015). While these studies have primarily measured the influence of salivary effectors on aphid population growth and on the expression of selected defence responses such as the oxidative burst in host plants, some of these aphid effectors are also likely to modify symptom development in susceptible plants. In addition to impeding plant defences against pathogens, the Mp10 effector protein from the green peach aphid induces chlorosis when expressed in one of its host plants, *Nicotiana benthamiana* (Bos *et al*., 2010). In a phloem-feeding Auchenorrynchan, the brown planthopper (*Nilaparvata lugens*), salivary gland extracts have also been shown to trigger transcriptional programmes in rice (*Oryza sativa*) that are associated with senescence and nutrient mobilization (Petrova and Smith, 2015).

Further studies are needed to determine the impacts of aphid effector proteins on host-plant physiology and symptom development using markers of physiological perturbation in the host. This approach should help us understand the mechanisms of how aphids damage their hosts, and could also shed light on whether aspects of this damage enhance the host's suitability for aphid infestation. Moreoever, further work is needed to characterize components of the aphids' oral secretions that originate from sites other than the salivary glands. GroEL, for example, is a bacterially-derived effector protein present in aphid saliva that is synthesized outside the salivary glands (Chaudhary *et al*., 2014), and Rao *et al*. (2013) also detected glucose dehydrogenases in aphid saliva that they could not detect in extracts of the salivary glands. These results suggest that to understand the full effects of aphids' oral secretions on host plants, it will be necessary to consider components of these secretions that originate from outside the salivary glands, including components encoded by primary

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or secondary symbionts. The identification of insect secretions that facilitate insect infestation of plants and trigger symptom development has significant applications for crop protection. It has recently been demonstrated that transgenic plants can be used to knock down the expression of specific aphid genes by RNA interference (Coleman *et al*., 2014, 2015), and this approach could generate insect-resistant crops that silence key effectors from Aphidoidea.

The Physiological Bases for Symptom Development and Damage

Whether or not Aphidoidea cause clear and characteristic symptoms such as those displayed in Figs 14.2–14.4, these insects can cause reductions in biomass, vigour and yield. Both symptomatic and asymptomatic damage result from perturbations in the host plant's physiology. The perturbations that have been characterized most extensively to date can be grouped into morphological changes, cytological damage, disruption of resource allocation and transport, and perturbation of photosynthesis.

Morphological modifications

Approximately 10–20% of aphid species, as well as certain adelgids and phylloxera, induce galls or pseudogalls on their hosts (Àlvarez *et al*., 2013), and these deformations represent the most dramatic and extensive structural changes induced by Aphidoidea. Galls, which are formed from young, developing host tissues in leaves, stems or roots, result from abnormal increases in cell proliferation (hyperplasia) and cell expansion (hypertrophy) (Shorthouse and Rohfritsch, 1992). Extensive and abnormal proliferation of the vascular tissues is common. Galls typically contain abundant phloem close to the interior walls of the gall, and the woolly apple aphid, *Eriosoma lanigerum*, induces such extensive proliferation of anomalous non-functional xylem that it reduces water flow through the galled root tissue, consequently reducing the growth of the apple trees (Brown *et al*., 1991). Gall formation can also involve the production of complex morphological structures in atypical places. For example, when forming leaf galls, grape phylloxera induce the formation of functional stomata on the adaxial surface of the leaf around the gall, even though stomata normally only occur on the abaxial surface (Nabity *et al*., 2013). Variation in gall morphology correlates closely with the phylogeny of galling aphids but not with the phylogeny of the host species, and so the structure of the gall is regarded as an 'extended phenotype' of the insect that is tightly controlled by the inducer, not by the host plant (Stern, 1995). However, the physical or chemical cues from the insect that trigger gall formation are as yet unidentified.

Gall induction by members of the Aphidoidea most probably involves coordinated manipulation of multiple plant hormones that regulate development, such as auxins, cytokinins and gibberellins (Bartlett and Connor, 2014). Galls induced by other Sternorryncha also show intriguing changes in the pectin composition of the cell walls and the orientation of cellulose microfibrils within the cells, both of which can influence division and expansion of plant cells and resulting tissue morphology (Formiga *et al*., 2013; Magalhães *et al*., 2014). Manipulation of cell walls, though, is not unique to gall-inducing aphids. As mentioned above, the saliva of free-living aphids is known to contain cell wall modifying enzymes; moreover, transcript profiling of aphid host plants has shown that aphids induce the expression of plant genes associated with cell wall remodelling (reviewed by Thompson and Goggin, 2006, and Goggin, 2007). A loss of function mutation in an aphid-inducible gene encoding a xyloglucan endotransglycolsylase/hydrolase in *Arabidopsis thaliana* increases infestations of *M. persicae*, which suggests that this cell wall remodelling enzyme contributes to effective defences against aphids (Divol *et al*., 2007). In contrast, transient silencing of an aphid-inducible wheat gene encoding (1,3; 1,4)-β-glucanase reduces *D. noxia* population growth and plant symptom development, indicating that this gene represents a susceptibility factor in compatible host plants (Anderson *et al*., 2014). These data support the hypothesis that cell wall remodelling modulates host suitability for aphids. Therefore, further work is warranted to characterize the effects of stylet probing and oral secretions on the plant cell wall, and to investigate how these changes may affect cytoskeletal rearrangements within cells, the growth and development of plant tissues and the process of infection by gall-forming and free-living aphids.

Cytological damage

Certain free-living Aphidoidea also induce marked cytological changes in plants. Such changes have primarily been studied in aphid species that induce

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chlorosis and macroscopic cell death at the feeding site. Light and electron microscopy studies indicate that feeding by the Russian wheat aphid on susceptible hosts can obstruct xylem vessels and occlude the plasmodesmatal connections that interlink phloem companion cells, phloem parenchyma cells and phloem sieve elements (Saheed *et al*., 2007a,b). These ultrastructural changes may perturb the translocation of water and photoassimilates in the plant. Russian wheat aphid feeding can also deform cell walls, plasmolyse mesophyll and vascular parenchyma cells, disrupt cell membranes, degrade organelles and cause cellular degeneration near the feeding site (Belefant-Miller *et al*., 1994; Saheed *et al*., 2007a,b). Cytological studies suggest that the chloroplasts may be a particular target for aphid virulence and a potential mediator of yield losses in response to aphid feeding. The Russian wheat aphid, the greenbug and the yellow sugar cane aphid all cause marked damage to the chloroplasts of mesophyll cells near the aphid penetration site, including increased starch accumulation and disorganization or loss of the thylakoid membranes (Ryan *et al*., 1990; Morgham *et al*., 1994; Gonzales *et al*., 2002). Damage to the chloroplasts probably contributes to chlorophyll loss, which in turn causes chlorotic symptoms. The Russian wheat aphid, the greenbug and the yellow sugar cane aphid are all classified as phytotoxic because they induce marked discoloration, chlorosis and necrosis at their feeding sites. However, two less symptomatic species, the bird cherry–oat aphid and *Metopolophium dirhodum* (the rose–grain aphid), have also been reported to cause modest cytological disruption, including changes in the chloroplast (Brzezina *et al*., 1986; Saheed *et al*., 2007b).

In the future, it would be useful to characterize the cytological effects of additional asymptomatic aphid species in order to assess whether cellular disruption contributes to the yield losses caused by these species. In addition, further studies are warranted to characterize changes in cell death patterns in response to Aphidoidea. Programmed cell death contributes to plant defences against many biotrophic pathogens (Dickman and Fluhr, 2013), and may also be associated with certain forms of aphid resistance (Belefant-Miller *et al*., 1994; Villada *et al*., 2009). However, other pathogens manipulate cell death programmes in their hosts to promote infection, either triggering runaway cell death in the case of necrotrophic pathogens or suppressing normal programmed cell death in the host in order to hijack host cells (Dickman and Fluhr, 2013). Similarly, insects that cause desistance may promote cell death, while species that cause deformation may, in some cases, suppress the host's normal cell death processes. The nature of cell death at insect feeding sites could be characterized by examining morphological changes in dying cells and testing for the presence of markers of programmed cell death such as cytochrome *c* release, caspase-like proteolytic activity and cleavage of DNA into fragments that are multiples of 180–185 base pairs in length (Reape *et al*., 2008). Furthermore, as molecular tools to enhance or inhibit plant cell death emerge, these could be utilized to test the impacts of cell death on symptom development and susceptibility to Aphidoidea.

Further work is also needed to establish which aspects of Aphidoidea injury are responsible for the cytological abnormalities observed at feeding sites. Differences in the nature and magnitude of cellular disruptions caused by different species could be due in part to differences in probing behaviour or in the composition of the insects' oral secretions. Ultrastructural damage caused by the Russian wheat aphid has been associated with intracellular probes and with saliva that appeared to coat the xylem vessels more smoothly than bird cherry–oat aphid saliva (Saheed *et al*., 2007b). Proteomic analyses of saliva from the Russian wheat aphid and greenbug have also identified several proteins that appear to be absent in the saliva of the non-phytotoxic species that have been examined to date (Cooper *et al*., 2011; Nicholson *et al*., 2012, Nicholson and Puterka, 2014). However, differences in symptom development between phytotoxic and non-phytotoxic species could also be due to quantitative rather than qualitative differences in feeding injury. For example, Madhusudhan and Miles (1998) have suggested that interspecfic differences in the mobility of aphid saliva may influence whether aphids cause strong symptoms at the feeding site (as in the case of phytotoxic species) or have weaker, more diffuse impacts (as in the case of asymptomatic species). When a complete genome is available for a phytotoxic aphid species, and as better protocols for RNA interference in aphids emerge (Coleman *et al*., 2014), these advances will enable functional genomic studies to test the impact of both species-specific and highly conserved oral secretions on symptom development in hosts.

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Disruption of resource allocation and transport

It has long been proposed that plants face trade-offs between growth and defence (Coley *et al*., 1985), and that herbivory compromises plant growth in part because it necessitates the redirection of metabolic resources into induced defences such as toxic allelochemicals. Consistent with this theory, transcriptomic and metabolomic profiling of responses to the corn leaf aphid (*Rhopalosiphum maidis*) in maize (*Zea mays*) reveal a shift from primary metabolism to defence signalling and synthesis of secondary metabolites such as benzoxazinoids (Tzin *et al*., 2015). The induction of salicylate-dependent defences in coyote tobacco (*Nicotiana attenuata*) by the green peach aphid also appears to contribute to the negative effects of aphid infestation on plant biomass and seed set (Donovan *et al*., 2013). However, there may also be synergistic interactions between primary metabolism and defensive signalling in plants. For example, a photosynthesis-related protein, Photosystem I Reaction Center Subunit 1 (PSAK1), that is differentially expressed in cotton (*Gossypium hirsutum*) in response to the green peach aphid, promotes salicylate-dependent responses and inhibits its aphid population growth when it is overexpressed in *Arabidopsis* (Zhang *et al*., 2014). Future studies on the interplay between primary metabolism and plant defence should shed light on the physiology of how herbivores influence plant productivity, as well as informing our understanding of plant–insect coevolution.

In addition to triggering induced defences, aphids – like any good parasite – also redirect plant resources to support their own growth and development. Simply by ingesting photoassimilates from the plant, Aphidoidea create an artificial sink that diverts resources from other parts of the plant. In fact, it is estimated that individual aphids ingest 0.5–3.0 µl of sap per hour (Kennedy and Mittler, 1953; Mittler, 1958; Weatherly *et al*., 1959) and so, cumulatively, aphid colonies can take a major toll on their hosts. Moreover, they induce transcriptional reprogramming that enhances the strength of this sink by shifting the tissues from an autotrophic to a heterotrophic mode (Nabity *et al*., 2013). Consistent with this shift, studies utilizing fluorescent or radiolabelled phloem-mobile probes suggest that certain aphids promote sugar leakage from the phloem at the feeding site and inhibit translocation of photoassimilates away from the infested area (Veen, 1985; Burd, 2002; Saheed *et al*., 2010). These effects on transport may be due to structural damage to the phloem and/or to local inhibition of phloem loading. Aphidoidea can also affect nutrient uptake, assimilation and partitioning in the whole plant. Most notably, phloem-feeding species influence the metabolism and allocation of nitrogen, a key limiting factor in their diet. Infestation by the green peach aphid on *Arabidopsis* upregulates the expression of nitrate reductase, an essential enzyme in nitrate assimilation that is a limiting factor on rates of nitrogen uptake from the soil (Wilson *et al*., 2011). The pea aphid also enhances the activities of enzymes associated with nitrogen assimilation and transamination in the nitrogen-fixing host plant *Medicago truncatula* (barrel medic) (Guo *et al*., 2013), and diverts nitrogen from the apical growth zones of lucerne to its feeding sites (Girousse *et al*., 2005). Furthermore, several aphid species have been shown to enhance the content of essential amino acids in phloem sap, thereby enhancing the nutritional quality of their food source (Sandström *et al*., 2000). The manipulation of amino acid content by aphids is achieved in part by the upregulation of genes required for essential amino acid synthesis (Thompson and Goggin, 2006; Guo *et al*., 2013), but it may also involve the catabolism of proteins in infested leaves (Dorschner *et al*., 1987). Thus, Aphidoidea increase the nutritional quality of their feeding sites by mobilizing local resources, blocking their export and increasing nutrient import from other sites in the plant, often at the expense of the plant's growth and development.

Further work is needed to establish how Aphidoidea induce changes in nutrient transport and allocation in their hosts, and also how they may impact the translocation of other agents that regulate host physiology, such as RNAs, proteins, hormones and other small molecules. Another active area of current research is to investigate whether modifications in photoassimilate metabolism can enhance aphid resistance in plants. For example, recent studies in *Arabidopsis* indicate that trehalose synthesis and reallocation of carbon into starch promote resistance to the green peach aphid (Singh *et al*., 2011), and that genetically engineering plants to translocate the complex sugar raffinose can also reduce green peach aphid infestations (Cao *et al*., 2013). Thus, just as aphids manipulate resource allocation to promote host susceptibility, plant biotechnologists may be able to manipulate resource allocation to enhance resistance. However, the

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practicality of this approach will depend greatly on how modifying the allocation of resources affects overall plant health and yields.

Perturbation of photosynthesis

When feeding on mature plant tissues, Aphidoidea can change these tissues from acting as a source to acting as a sink within the plant, and this shift is achieved in part by disturbing the photosynthetic machinery of host plants. These perturbations probably play a major causal role in yield losses and contribute to symptom development. Chlorosis, for example, results from chlorophyll loss. Moreover, in wheat, the development of leaf rolling and chlorotic streaks in response to the Russian wheat aphid requires exposure to light, which suggests that symptom induction by this aphid may possibly depend on dysfunctions of the light-dependent reactions of photosynthesis (Macedo *et al*., 2003a). Several studies also suggest that adaptations of the photosynthetic system to infestation play a role in tolerance, and possibly also in resistance mechanisms that limit aphid proliferation (Botha *et al*., 2006; Kerchev *et al*., 2012). Evidence for this is based both on the expression patterns of genes involved in photosynthesis and on the physiological measures of photosynthetic capacity in host plants. In order to describe the evidence that Aphidoidea impact photosynthesis in their host plants, it is necessary to outline briefly the steps in photosynthesis that can be impacted by stress and the techniques that are used to detect these physiological perturbations.

Photosynthesis and stress

Photosynthesis captures light energy to generate carbohydrates through light-dependent reactions that occur in the thylakoid membrane of the chloroplast and the light-independent reactions (i.e. the Calvin cycle) that occur in the chloroplast stroma. In brief, during the light reactions of photosynthesis, energy from light is absorbed by chlorophyll and powers the transfer of electrons from water through an electron transport chain to generate NADPH and ATP. The Calvin cycle in turn uses this ATP and NADPH to generate glycerol-3-phosphate (G3P), an essential building block for glucose synthesis, and to recycle ribulose bisphosphate (RuBP), a necessary substrate for G3P synthesis. The source of carbon molecules for G3P synthesis is carbon dioxide (CO_2) from the air, which enters the leaf through stomata. Stomata may close in response to water limitation or other stresses (Daszkowska-Golec and Szarejko, 2013; Sawinski *et al*., 2013), and the consequent reduction in stomatal conductance can limit the availability of CO_2 for the Calvin cycle. Certain biotic and abiotic stresses may also cause a decrease in chlorophyll content, thereby reducing the plant's light harvesting capacity. Other features of the photosynthetic machinery that may be perturbed by stress and so limit photosynthetic rates even under otherwise optimal conditions include: the electron transport chain in the light-dependent reactions; the activity of the first enzyme in the Calvin cycle (Rubisco); regeneration rates of RuBP; and utilization rates of the end product of the Calvin cycle (G3P) (Brestic and Zivcak, 2013). If photoassimilates are not utilized rapidly or translocated away from their site of synthesis, photosynthesis may be inhibited by a negative biochemical feedback loop.

Measuring limitations on photosynthesis

These possible limitations on photosynthesis are commonly detected and studied by measuring chlorophyll content, chlorophyll fluorescence properties and gas exchange rates of the foliage. Chlorophyll can be chemically extracted and quantified by spectrophotometric assays, or estimated in intact leaves using SPAD meter (i.e. a chlorophyll meter) to compare the amount of red and infrared light transmitted by the leaf, since chlorophyll absorbs red but not infrared light (Uddling *et al*., 2007). Measurements of chlorophyll fluorescence, in contrast, are used to estimate the efficiency of electron transport in the light reactions of photosynthesis, and can be measured *in vivo* with a fluorometer (Baker, 2008; Brestic and Zivcak, 2013). Light absorbed by photosystem II in the thylakoid membrane can either be used to power electron transport (i.e. photochemical quenching) or, if the electron transport chain is full and cannot accept further electrons, the excess energy can be dissipated through the generation of heat (non-photochemical quenching) or emission of longer-wavelength light (chlorophyll fluorescence). By measuring variation in chlorophyll fluorescence as the leaf is exposed to different light levels, and comparing fluorescence emission at light levels that will or will not saturate the electron transport chain, investigators can assess the efficiency of photosystem II and estimate rates of photochemical and non-photochemical quenching. Last, gas exchange rates can be measured with a

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photosynthesis system to estimate the overall photosynthetic rates, stomatal limitations on photosynthesis and biochemical limitations on the Calvin cycle (Long and Bernacchi, 2003). To measure gas exchange, a small area of the leaf surface is enclosed in a porometer in which the humidity and CO_2 of the incoming air can be controlled. CO_2 and water vapour are measured with an infrared light and compared in the incoming and outgoing air to estimate the amount of CO_2 taken up by the leaf (i.e. the assimilation rate) and the amount of water vapour emitted by the leaf (transpiration). Assimilation rates are often used as a measure of overall photosynthetic activity and, in combination with transpiration rates, are also used to estimate intracelllular CO_2 (C_i), stomatal conductance and stomatal limitations on photosynthesis. Furthermore, because the efficiency of different steps of the Calvin cycle vary depending on the availability of CO_2, assimilation rates (A) can be measured at a series of different ambient CO_2 concentrations to construct an A/ C_i curve, and the slope of different regions of this curve can then be used to estimate Rubisco activity, regeneration of RuBP and utilization of the G3P end product (Farquhar *et al*., 1980; Long and Bernacchi, 2003).

Impacts of Aphidoidea on photosynthesis

Measures of carbon assimilation in multiple plant hosts indicate that Aphidoidea, like other herbivorous insects, can decrease net photosynthetic rates (reviewed in Kerchev *et al*., 2012, and Zhou *et al*., 2015). Moreover, Aphidoidea have been variously reported to affect all of the major factors limiting photosynthesis, including chlorophyll content, stomatal conductance, the electron transport chain, Rubisco, regeneration of RuBP, or end-product utilization. However, there is as yet little consensus on which of these factors are most important in mediating the effects of Aphidoidea on photosynthetic rates, either in general or even within a single study system such as the interaction of the Russian wheat aphid with wheat.

Aphids have in some cases been reported to decrease stomatal conductance in their hosts (e.g. Ryan *et al*., 1987; Macedo *et al*., 2003a,b, 2009), but this does not appear to have a causal role in aphid inhibition of photosynthesis. In fact, Aphidoidea can in some cases increase stomatal conductance (Shannag *et al*., 1998; Shannag, 2007), and grape phylloxera have been shown to induce the formation of new stomata on the adaxial leaf surfaces around leaf galls (Nabity *et al*., 2013). Increases in transpiration as a result of increased stomatal conductance could contribute to water stress, but would not limit CO_2 availability for photosynthesis. Another much more commonly reported effect of aphid infestation is chlorophyll loss, which can result from cytological damage to chloroplast membranes (e.g. Ryan *et al*., 1990; Morgham *et al*., 1994; Gonzales *et al*., 2002) and/or to induction of chlorophyll-degrading enzymes. Whereas the enzyme pheophytinase regulates chlorophyll breakdown during leaf senescence (Schelbert *et al*., 2009), studies of chlorophyll breakdown in response to aphids suggest that the enzymes chlorophyllase or magnesium dechetelase may play a role in this stress response (Wang *et al*., 2004). For the Russian wheat aphid, greenbugs and other species that induce extensive chlorosis, the effects of infestation on photosynthesis are frequently attributed, at least in part, to chlorophyll degradation (Ryan *et al*., 1990; Botha *et al*., 2005). However, based on the relatively slow nature of chlorophyll loss in response to aphids, some authors hypothesize that it is a symptom rather than an initial cause of photosynthetic dysfunction (Franzen *et al*., 2007, 2008; Gutsche *et al*., 2009). Similarly, although some studies have detected a negative impact of aphids on the capacity and efficiency of photosystem II (Burd and Elliott, 1996; Haile *et al*., 1999), other studies have reported that significant decreases in carbon assimilation and the Calvin cycle can be detected before any dysfunctions of photosystem II are evident (Macedo *et al*., 2003b; Franzen *et al*., 2007, 2008; Gutsche *et al*., 2009). Based on these observations, it has been hypothesized that aphids negatively affect the Calvin cycle more strongly than the light reactions of photosynthesis, and that decreases in Rubisco activity, RuBP regeneration and/or G3P utilization are potential proximal causes of photosynthetic inhibition by aphids. Consistent with this hypothesis, aphids have been observed to suppress the expression of Rubisco subunits (Voelckel *et al*., 2004; Truong *et al*., 2015) and decrease J_{max}, a gas exchange parameter associated with RuBP regeneration (Franzen *et al*., 2007). Moreover, G3P accumulation and endpoint inhibition could result from the decreased transport of photoassimilates away from the aphid feeding site (Veen, 1985; Burd, 2002; Saheed *et al*., 2010). However, it is important to note that the functioning of photosystem II is studied through the analysis of chlorophyll fluorescence, whereas carbon assimilation and components of the Calvin cycle are assessed using a gas exchange system;

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therefore, any potential differences in the sensitivities of these detection systems could also lead to a lag between detection of changes in carbon assimilation and detection of dysfunctions in photosystem II.

In short, additional research is needed to define the causes of photosynthetic depression in aphid-infested plants, and to determine if adelgids and phylloxera have similar impacts. Furthermore, the fitness consequences for host plants of alterations in photosynthetic rates warrant further study. In susceptible hosts that support rapid insect population growth and sustain visible symptoms, decreases in photosynthetic capacity are typically interpreted as a consequence of insect injury and as a cause of insect damage. In contrast, when decreases in photosynthetic parameters or photosynthesis-related transcripts are observed in resistant cultivars, they are frequently attributed to an adaptive shift of resources from growth to defence (e.g. Carrillo *et al*., 2014). Identifying the processes that modify photosynthetic rates in response to Aphidoidea, and the plant and insect genes that regulate these processes, will enable functional analyses that can empirically test our assumptions about the adaptive significance of these changes for the plant and for the insect.

Environmental Effects on Insect Damage: Aphidoidea in a Changing Climate

A growing body of evidence suggests that climate change is promoting infestations by Aphidoidea and may expand the geographic ranges of many aphid species (Hullé *et al*., 2010). In addition to measuring how the climate influences the incidence and population growth of insect pests, it is also important to measure how environmental conditions such as temperature, carbon dioxide (CO_2) levels, water availability and soil fertility alter symptom development and yield losses in response to these infestations. This information is essential in order to project the economic impacts of climate change, and also to identify how cultural practices such as fertilization and irrigation affect losses to insect pests. Numerous studies indicate that the extent of aphid damage is influenced by water availability (Riedell, 1989; Archer *et al*., 1995; de Farias *et al*., 1995; Oswald and Brewer, 1997; Johnson *et al*., 1998), nitrogen fertilization (Throop and Lerdau, 2004) and CO_2 levels (Sun and Ge, 2011). For the majority of published studies, it is not possible to determine whether such environment changes influence the extent of damage caused by a fixed density of insects, or simply influence damage by influencing insect population dynamics. It is, for example, extremely difficult to study the effects of temperature on symptom development because temperature also dramatically impacts aphid development time and consequent population growth. However, there are some data to indicate that environmental conditions can influence quantitatively the response of susceptible plants to aphids. Certain studies suggest that fertilization can attenuate the negative effects of aphid infestation (Thomas and Miller, 1994; Morales *et al*., 2001), whereas elevated CO_2 can increase injury in response to aphids (Awmack and Harrington, 2000). For example, although the manipulation of environmental CO_2 levels did not influence the population growth of the pea aphid or *Aulacorthum solani* (the glasshouse-potato aphid) on broad bean, it dramatically increased the negative effects of these aphids on flower numbers and shoot and root weights, possibly as a result of altered resource allocation in the plant (Awmack and Harrington, 2000). Thus, further work is merited to study the effects of environmental conditions on plant responses to fixed population sizes of Aphidoidea, and to measure how environmental conditions influence specific physiological perturbations such as changes in photosynthetic rates or carbon partitioning.

Conclusions

As a result of their probing behaviour, oral secretions and withdrawal of plant sap, Aphidoidea can induce many changes in their host plants, including cytological damage, morphological aberrations, altered resource allocation and perturbations of the photosynthetic machinery. These changes can cause a wide diversity of symptoms including desistance (eg. chlorosis, necrosis, stunting) and deformation (e.g. galling, leaf rolling and other psuedogalls), and can also cause extensive damage to growth, reproduction and crop yields. The extent of damage depends on a complex interplay of effectors from the insect, resistance- and susceptibility-factors from the host and environmental conditions such as light and CO_2 levels. Research to understand this interplay and to characterize symptom development will advance crop protection dramatically in several ways. First, the development of new imaging approaches to identify and measure symptoms of infestation is contributing to novel approaches to detect and diagnose insect outbreaks. Second, better means of identifying and quantifying insect-responsive

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symptoms will empower better breeding programmes to select for tolerance and resistance. Third, an understanding of the basis for symptom development and the molecular underpinnings of the susceptible response to insect infestation can inform the rational design of new crop protection strategies. By studying the sequential process that renders plants susceptible and results in damage, we can identify steps at which to intercept this process. Last, just as previous basic research on the mechanisms of pathogenicity of *Agrobacterium tumefaciens* (crown gall) in plants and *Bacillus thuringiensis* in insects has ultimately enabled plant biotechnology and revolutionized crop protection (Patlak, 1998), current research on plant–aphid interactions may also have unexpected and far-reaching applications.

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15 Transmission of Plant Viruses[1]

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Introduction

As obligate parasites, plant viruses need to move from infected to healthy plants in order to survive. This is achieved either by mechanical means or, in the case of most plant viruses, by exploiting biological vectors such as arthropods, nematodes and fungi. Of the 700 or more plant viruses (van Regenmortel *et al*., 2000), about 70% are known, or suspected, to be transmitted by arthropod, nematode, or fungal vectors (Nault, 1997). Sap-feeding insects in the Auchenorrhyncha and Sternorryhncha are particularly important vectors, transmitting more than 380 viruses (Nault, 1997). The aphids (Aphididae) are by far the most important family among these vectors, transmitting many more viruses than whiteflies (Aleyrodidae), leafhoppers (Cicadellidae) or planthoppers (Delphacidae) (Fig. 15.1). More than 4700 aphid species have been described (Remaudière and Remaudière, 1997), and of these over 190 have been reported to transmit plant viruses (Nault, 1997), with many species able to transmit more than one virus (Eastop, 1983; Nault, 1997; Hull, 2002). The majority of reported aphid virus vectors belong to the genera *Myzus*, *Aphis*, *Acyrthosiphon* and *Macrosiphum* in the subfamily Aphidinae (Kennedy *et al*., 1962). Only a small proportion of aphid species (approximately 300 – Kennedy *et al*., 1962; Eastop, 1983; Nault, 1997) have been tested as virus vectors, and therefore the potential number of aphid vectors is probably very much larger. For example, in a study of the transmission of *Zucchini yellow mosaic virus* (ZYMV) by previously unrecorded vectors, 16 out of 19 species tested were found to transmit the virus (Katis *et al*., 2006).

Aphid-transmitted viruses belong to 19 of the 70 recognized virus genera and comprise approximately 275 virus species (i.e. about 50% of insect-borne plant viruses; Nault, 1997). Many of these viruses cause diseases of major economic importance in crops (Hull, 2002) such as cereals (Plumb, 2002), potatoes (de Bokx and van der Want, 1987; Salazar, 1996; Brunt and Loebenstein, 2001) and sugar beet (Stevens *et al*., 2004). In this chapter, we review virus transmission by aphids, with particular emphasis on the attributes that make aphids such well-adapted vectors, the different modes of transmission, determinants of transmissibility, factors affecting virus acquisition and inoculation, and control methods. Table 15.1 shows the names and standard acronyms for viruses used as examples throughout the chapter, as well as their genome type and classification to genus and family.

Virus–Vector Interactions

Virus transmission by an aphid (or any other vector) involves the transfer of virions (virus particles, complete with the RNA or DNA core and protein coat) from infected to healthy (or previously infected) plants. The transmission cycle comprises up to four phases:

1. *Acquisition* – the process by which the aphid takes up virions from an infected plant;
2. *Retention* – the carriage of virions at specific sites in or on the vector;
3. *Latency* – an inability to inoculate immediately following acquisition (the aphid is able to transmit the virus after the 'latent period' (LP) has passed);

[1] Much material from the first edition of this chapter has been included, and the contribution of Nikos Katis, John Tsitsipis and Glen Powell is gratefully acknowledged.

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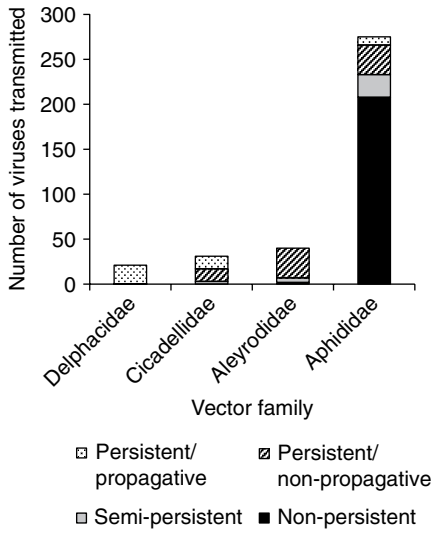

Fig. 15.1. Number of viruses transmitted by the four major homopteran vector families, divided into the four transmission categories. (From Nault, 1997.)

4. *Inoculation* – the release of retained virions into the tissues of a susceptible plant in such a way that they are able to establish a new infection.

Based on the period of retention by the vector, virus transmission by aphids has been divided into three major categories (Table 15.2):

1. *Non-persistent transmission* – where acquisition and inoculation require only very brief stylet penetration (<1 min). There is no LP and the entire transmission cycle may therefore be completed within a few minutes. Viruses transmitted in this way have also been referred to as 'stylet borne' and aphids rapidly lose the ability to inoculate them following acquisition (e.g. *Potato virus Y* (PVY)).
2. *Semi-persistent transmission* – where efficient acquisition and inoculation requires longer periods of plant access than for non-persistent viruses, often at least 15 min. There is no LP and the aphids retain the ability to inoculate for longer periods, and may continue to transmit for up to 2 days following acquisition (e.g. *Citrus tristeza virus* (CTV)).
3. *Persistent transmission* – where virus acquisition and inoculation require relatively long periods of plant access. An LP occurs between acquisition and inoculation, but once it has passed, the aphid can remain infective for life (e.g. *Cereal yellow dwarf virus*-RPV (CYDV-RPV)).

These categories are properties of the relationship between viruses and their vectors, but will often be used herein to describe the viruses. A given virus is always in the same category, regardless of its vector. A fundamental distinction regarding the mode of transmission is whether virions are circulative or non-circulative within the aphid vector. All viruses transmitted non-persistently and semi-persistently are non-circulative, residing on or in the aphid stylets and foregut, whereas those transmitted persistently are known as circulative, as they pass from the gut into the haemocoel and then to the accessory salivary glands (ASGs) before they can be inoculated. Persistent viruses may be propagative, that is, able to multiply in the aphid, but are mostly non-propagative (Table 15.2).

Aphids as Effective Virus Vectors

Certain characteristics of aphids predispose them to being effective virus vectors. Host selection and feeding behaviour are particularly important factors in virus epidemiology, and the host range and life cycle characteristics of aphid species are also key in determining the rate of spread of viruses. In this chapter, we consider the host-selection processes specifically related to virus transmission. Several reviews have previously covered feeding behaviour (Montllor, 1991; Chapter 9, this volume), host-plant selection (Dixon, 1998; Powell *et al.*, 2006; Chapters 8 and 9, this volume) and virus transmission by aphids (Sylvester, 1989; Harris, 1990; Nault, 1997; Gray and Banerjee, 1999; Pirone and Perry, 2002; Gray and Gildow, 2003; Ng and Perry, 2004).

Host selection related to virus acquisition and inoculation

A variety of sensory stimuli may influence aphid host-selection behaviour before plant contact and stylet insertion. Migrant aphids locate plant material primarily by responding to colour (Moericke, 1955; Kennedy *et al.*, 1959a,b; Kring, 1972). Olfactory stimuli may also play a role at this stage (Pettersson, 1970, 1973; Chapman *et al.*, 1987; Visser and Taanman, 1987; Pickett *et al.*, 1992; Park and Hardie, 2004; Chapter 9, this volume), but only a small fraction of the dispersing populations succeed in finding a suitable host plant (Ward *et al.*, 1998). Host recognition continues after alighting on plants, where physical (plant surface colour, texture and topology) and chemical (olfactory and gustatory)

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Table 15.1. Abbreviations of plant viruses included in the text and their classification to genus/family.

Acronym	Virus name	Genus/Family
AMV	*Alfalfa mosaic virus*	*Alfamovirus*/Bromoviridae
AYV	*Anthriscus yellows virus*	*Waikavirus*/Secoviridae
BBTV	*Banana bunchy top virus*	*Babuvirus*/Nanoviridae
BCMV	*Bean common mosaic virus*	*Potyvirus*/Potyviridae
BMYV	*Beet mild yellowing virus*	*Polerovirus*/Luteoviridae
BtMV	*Beet mosaic virus*	*Potyvirus*/Potyviridae
BWYV	*Beet western yellows virus*	*Polerovirus*/Luteoviridae
BYDV-MAV	*Barley yellow dwarf virus*-MAV	*Luteovirus*/Luteoviridae
BYDV-PAV	*Barley yellow dwarf virus*-PAV	*Luteovirus*/Luteoviridae
BYMV	*Bean yellow mosaic virus*	*Potyvirus*/Potyviridae
BYV	*Beet yellows virus*	*Closterovirus*/Closteroviridae
CABYV	*Cucurbit aphid-borne yellows virus*	*Polerovirus*/Luteoviridae
CaMV	*Cauliflower mosaic virus*	*Caulimovirus*/Caulimoviridae
CeMV	*Celery mosaic virus*	*Potyvirus*/Potyviridae
CMV	*Cucumber mosaic virus*	*Cucumovirus*/Bromoviridae
CTV	*Citrus tristeza virus*	*Closterovirus*/Closteroviridae
CtVY	*Carrot virus Y*	*Potyvirus*/Potyviridae
CYDV-RPV	*Cereal yellow dwarf virus*-RPV	*Polerovirus*/Luteoviridae
FBNYV	*Faba bean necrotic yellows virus*	*Nanovirus*/Nanoviridae
LMV	*Lettuce mosaic virus*	*Potyvirus*/Potyviridae
LYSV	*Leek yellow stripe virus*	*Potyvirus*/Potyviridae
MDMV	*Maize dwarf mosaic virus*	*Potyvirus*/Potyviridae
OYDV	*Onion yellow dwarf virus*	*Potyvirus*/Potyviridae
PEMV-1	*Pea enation mosaic virus-1*	*Enamovirus*/Luteoviridae
PEMV-2	*Pea enation mosaic virus-2*	*Umbravirus*/Tombusviridae
PLRV	*Potato leaf roll virus*	*Polerovirus*/Luteoviridae
PPV	*Plum pox virus*	*Potyvirus*/Potyviridae
PRSV	*Papaya ringspot virus*	*Potyvirus*/Potyviridae
PSbMV	*Pea seed-borne mosaic virus*	*Potyvirus*/Potyviridae
PVY	*Potato virus Y*	*Potyvirus*/Potyviridae
PYFV	*Parsnip yellow fleck virus*	*Sequivirus*/Secoviridae
SbDV	*Soybean dwarf virus*	*Luteovirus*/Luteoviridae
SMV	*Soybean mosaic virus*	*Potyvirus*/Potyviridae
SYVV	*Sowthistle yellow vein virus*	*Nucleorhabdovirus*/Rhabdoviridae
TBV	*Tulip breaking virus*	*Potyvirus*/Potyviridae
TEV	*Tobacco etch virus*	*Potyvirus*/Potyviridae
TuMV	*Turnip mosaic virus*	*Potyvirus*/Potyviridae
WDV	*Wheat dwarf virus*	*Mastrevirus*/Geminiviridae
WMV	*Watermelon mosaic virus*	*Potyvirus*/Potyviridae
ZYMV	*Zucchini yellow mosaic virus*	*Potyvirus*/Potyviridae

stimuli are evaluated by various sensilla located on the head, antennae, tarsi and labium (Pettersson, 1971; Wensler, 1974; Tjallingii, 1978; Eisenbach and Mittler, 1980; Yan and Visser, 1982; Anderson and Bromley, 1987; Backus, 1988; Nottingham *et al*., 1991; Pickett *et al*., 1992; Park and Hardie, 2004; Chapter 9, this volume). However, aphids attempt to make brief (<1 min) stylet insertions ('probes') as a behavioural reflex that follows tarsal contact with any solid surface (Powell *et al*., 1999), even when repellent or deterrent cues are present (Griffiths *et al*., 1982; Phelan and Miller, 1982). The aphids' propensity for landing on green surfaces and initiating probing behaviour helps explain their extraordinary capacity for transmitting plant viruses.

The aphid stylet bundle comprises two pairs of long stylets that taper to a sharp point at the tip. The two inner, maxillary stylets are tightly interlocked by ridges and grooves, forming the food canal (FC) and salivary canal (SC) (Fig. 15.2a). Although the FC and

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Table 15.2. Transmission and other characteristics of non-persistent, semi-persistent and persistent aphid-borne plant viruses.

	Transmission mode			
Transmission characteristic	NP	SP	PC	PP
Optimal acquisition time	Seconds (>5), minutes	Minutes to hours	Hours to days	Hours to days
Retention half-life	Minutes	Hours	Days to weeks	Weeks to months (often for lifetime)
Transtadial passage	No	No	Yes	Yes
Virus in vector haemolymph	No	No	Yes	Yes
Latent period	No	No	Hours to days	Weeks ('incubation')
Virus multiplication in the aphid's body	No	No	No	Yes
Transovarial transmission	No	No	No	Rarely
Aphid specificity	Low	Medium	High	High
Effect of pre-acquisition fasting	Enhances transmission	No effect	No effect	No effect
Mechanical transmission under laboratory conditions	All	Some with difficulty (Caulimo-, Sequi-, clostero- with difficulty, Waika: no)	Only few (PEMV-2), Umbravirus[a] (uncapsidated RNA is stable)	A number of rhabdoviruses infecting dicots[b]
Seed transmission	Some (species belonging to Cucumo-, Alfamo-, Poty-)	No	No	No
Common symptomatology	Mo, M, VN, LD, FB	Y, LR	Y, LR	Y, LR
Tissue acquisition	(Parenchyma) epidermis	Phloem	Phloem	Phloem
Inoculation	Parenchyma	Parenchyma/phloem	Phloem	Phloem

Notes: NP = non-persistent; SP = semi-persistent; PC = persistent/circulative (non-propagative); PP = persistent/propagative; M = mottling; Mo = mosaic; VN = vein necrosis; LD = leaf deformation; FB = flower breaking; Y = leaf yellowing; LR = leaf rolling. [a]Some rhabdoviruses infecting monocots are only transmitted mechanically by vascular puncture. [b]PEMV-2 is transmitted mechanically when plants are also infected with PEMV-1 *Luteovirus*. Co-infection of plants with PEMV-2 facilitates mechanical transmission of some luteoviruses such as PLRV and BMYV. (From Hull, 2002, and Nault, 1997.)

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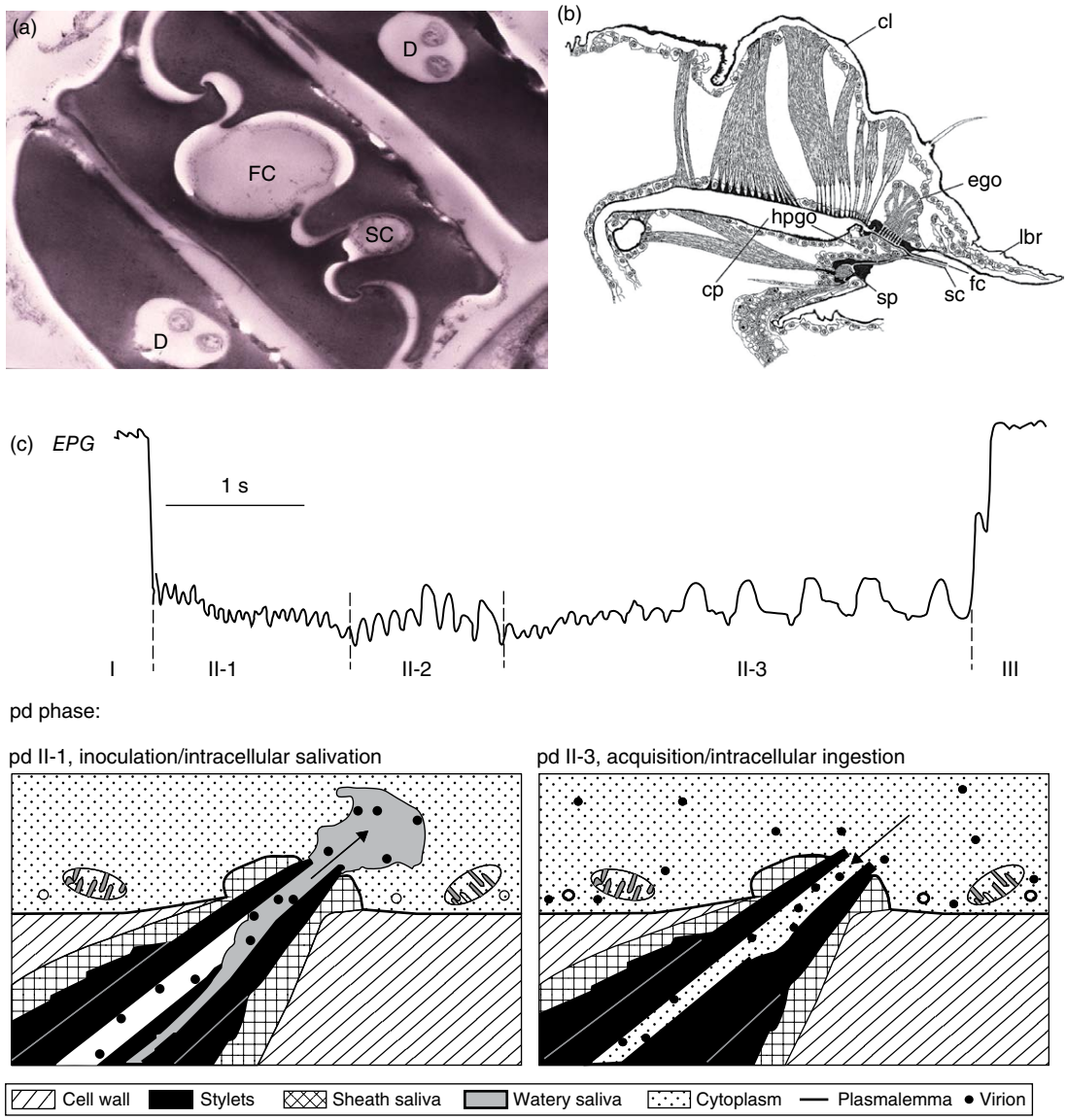

Fig. 15.2. Diagrammatic representations of aphid mouthparts. (a) Transmission electron micrograph showing transverse section of the stylet bundle of *Myzus persicae*. The inner pair of stylets (maxillae) form the larger food canal (FC; approximately 0.7 μm diameter) and smaller salivary canal (SC; approximately 0.3 μm diameter) (cf. Forbes, 1969). D = ducts in the mandibular stylets contain dendrites. (b) Longitudinal section through the head of an aphid; cl = clypeus; cp = cibarial pump; ego = epipharyngeal gustatory organ; fc = food canal; hpgo = hypopharyngeal gustatory organ; lbr = labrum; sc = salivary canal; sp = salivary pump. (From Ponsen, 1987.) (c) Longitudinal sections of the stylet tips introduced into an epidermal or mesophyll plant cell (bottom) and associated electrical penetration graph (EPG) waveforms (top). The EPG signal shows the three successive intracellular subphases: II-1, II-2 and II-3. The first subphase (II-1) is associated with the inoculation of non-persistent viruses, possibly involving the release of virions from the common duct during salivation (bottom left). The third subphase (II-3) is linked with acquisition, and therefore represents the ingestion of cytosol (bottom right). pd = potential drop. (From Martin *et al*., 1997.)

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SC are distinct canals for almost the entire length of the aphid stylet bundle, they merge to form a common duct (CD) at the maxillary stylet tips (terminal 2–4 μm region; Forbes, 1969). The outer pair of 'mandibular' stylets plays an important role in physical penetration of plant cell walls, but it is the maxillary stylets that enter plant cells (Tjallingii and Hogen Esch, 1993). The maxillary FC, SC and CD are therefore the channels through which aphids acquire and inoculate virions.

Probing behaviour is a particularly important feature of host-plant selection by aphids because it provides a means of assessing internal plant chemistry (Powell and Hardie, 2000; Powell *et al*., 2006). The mandibular stylets have been found to be innervated, each containing a pair of dendrites (Fig. 15.2a; Forbes, 1966; Parrish, 1967), but these probably function as proprioreceptors and allow the insect to monitor stylet movement and position (Wensler, 1974, 1977). The stylets therefore apparently lack chemoreceptors, and aphids need to ingest plant sap through the maxillary FC to the pharyngeal area of the foregut to allow chemosensory assessment using a gustatory organ (Fig. 15.2b; Wensler and Filshie, 1969; Ponsen, 1972; McLean and Kinsey, 1984).

Stylet penetration activities can be monitored by attaching a fine gold wire to the aphid, making the insect and plant part of an electrical circuit (McLean and Kinsey, 1965; Tjallingii, 1988; Chapter 9, this volume) to produce an electrical penetration graph (EPG) signal. When this technique is based on a direct current (DC) circuit, it enables researchers to discriminate stylet penetration of the apoplast (the extracellular environment) from puncture of the symplast (the intracellular compartment). The fluid-filled FC and SC enable the maxillary stylets to function as microelectrodes, recording the transmembrane potential of plant cells. Maxillary puncture of a cell membrane is therefore recorded as a distinct drop to a lower (intracellular) voltage level of the EPG (Tjallingii, 1988).

Since plant viruses have no independent means of movement into or out of the symplast, their acquisition and inoculation by aphids occurs during intracellular punctures by the maxillary stylets. Aphids usually initiate stylet penetrations in the anticlinal grooves between epidermal cells (Nault and Gyrisco, 1966; Yoshii, 1966), and much of the stylet pathway remains intercellular (apoplastic) (Tjallingii and Hogen Esch, 1993). However, DC-EPG reveals that aphids regularly puncture the symplast during their host selection, phloem location and feeding behaviours. Even initial epidermal probes, lasting less than 30 s, usually include a brief (5–10 s) maxillary puncture of one cell (Powell, 1991, 2005; Martin *et al*., 1997). Such brief cell punctures always include ingestion of a cytosolic sample (Powell *et al*., 1995; Martin *et al*., 1997), presumably allowing chemosensory evaluation via the gustatory organ in the foregut (Wensler and Filshie, 1969).

Virions of non-persistent viruses are acquired and inoculated during these brief epidermal cell punctures (Powell, 1991; Powell *et al*., 1992). Aphids typically make several brief probes following contact with a new plant and, regardless of whether the plant is a host or non-host species, this behaviour is often followed by plant rejection (departure). Alate aphids will then often make a short flight before landing on and probing another plant. Flight and landing/probing continue to alternate as antagonistic reflexes (Kennedy, 1965), leading to brief probes on a series of plants. If one of the plants in the series is already infected with a non-persistent virus, the result may be very rapid spread to one or more plants visited later. In newly inoculated plants, virions delivered into cells multiply and spread to neighbouring cells through plasmodesmata and eventually become systemic via the phloem, infecting the whole plant (Carrington *et al*., 1996) and providing a new source of virus inoculum and further spread.

The virus acquisition and inoculation processes occur as a direct consequence of various stylet activities that enable aphids to select appropriate host plants, suppress plant defensive processes and extract nutrients. Depending on the mode of transmission, virions may adhere to the cuticular lining of the stylets and the foregut, or be ingested and pass through the gut into the circulatory system and salivary glands and then be inoculated via salivation.

Early molecular events in aphid–plant interactions

The molecular basis of aphid–plant–virus interactions continues to develop and has emerged as a very complex and dynamic series of relationships (Giordanengo *et al*., 2010). It appears that early plant responses to phytophagous insects might, to some degree, be conserved to those displayed by other pathogens including local (protein phosphorylation and release of reactive oxygen species) and systemic responses (phytohormone-dependent pathways such as ethylene- and jasmonate-dependent responses) (for a review see Giordanengo *et al*., 2010). This

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highlights the ongoing molecular 'arms race' between plants and pathogens, where plants deploy an array of defence mechanisms to combat invading pathogens and where insects and viruses counterattack by deploying a means to evade or manipulate their hosts for their own benefit (Pitino and Hogenhout, 2013) (see below and Chapter 2, this volume).

During probing, aphids insert their stylets into the leaf tissue between the epidermal and mesophyll cells and secrete different types of saliva. Gelling saliva (or sheath saliva) is secreted continuously from the stylet tip to form a protective sheath, which may provide a means to counteract host defences (Tjallingii, 2006). This early event is relatively short (less than 1 min), and epidermal cells are most likely targeted (Powell *et al*., 2006) but none the less might condition plant rejection (resulting in the aphid flying away from the probed leaf) or acceptance and probing until reaching vascular tissue and hence phloem sap ingestion (Powell and Hardie, 2000; Powell *et al*., 2006).

Once phloem tissues are reached, watery saliva is secreted prior to phloem uptake and during the feeding period (Prado and Tjallingii, 2007). In addition to their mechanical role in facilitating and protecting the stylets' transit in the leaf cell layers (Tjallingii *et al*., 1993; Tjallingii, 2006), the composition and the role of these different types of saliva have been the focus of recent proteome studies. Gelling saliva composition appears to be relatively conserved and includes, among others, phenoloxidases, peroxidases, pectinases and glucosidases (Cherqui and Tjallingii, 2000; Tjallingii, 2006). Watery saliva is a complex mixture of enzymes (some of them capable of degrading plant cell walls or preventing occlusion of sieve tubes) and other components capable of eliciting plant defence responses. Watery saliva differs significantly between aphid species and varies depending on the aphids' diets (Harmel *et al*., 2008; Will *et al*., 2009, 2012; Bak *et al*., 2013). This suggests that watery saliva composition might influence aphid host range.

Recent studies combining proteomic, transcriptomics and genetic approaches helped to define the aphid saliva secretome (for a review, see Giordanengo *et al*., 2010) and identified a wide range of secreted effectors. The role of these effectors appears to be extremely complex and diverse (Atamian *et al*., 2013; Elzinga and Jander, 2013; Pitino and Hogenhout, 2013). Some effectors will trigger plant defence responses and will have a negative effect not only on aphid colonization but also on the fitness of other pathogens. For example, overexpression of *Myzus persicae* (peach–potato aphid) candidate effectors Mp10 and Mp42 were found to reduce aphid fecundity (Bos *et al*., 2010; Rodriguez *et al*., 2014). Mp10 and Mp42 showed distinct subcellular localization *in planta*, either found respectively in the cytoplasm or associated with cell membranes including the plasma membrane and nuclear envelope, suggesting that both effectors target different host compartments and hitherto display different functions. Strikingly, Mp10 affected gene expression at the transcriptional level, suggesting a wider generic role in inhibiting gene expression. Differential behaviour of both effectors was further exemplified, as transient overexpression of Mp10 (but not Mp42) activated jasmonic acid and salicylic acid signalling pathways and increased resistance to *Phytophthora capsici*. Therefore, these two *M. persicae* effectors can elicit host defences through different mechanisms (Rodriguez *et al*., 2014). Conversely, some effectors have a beneficial effect on aphid colonization. Indeed, Pitino and Hogenhout (2013) found that *M. persicae* reproduction was enhanced on *Arabidopsis thaliana* plants expressing *M. persicae* effectors C002, PIntO1 and PIntO2. Using the same approach, the expression of orthologue effectors from *Acyrthosiphon pisum* (pea aphid) did not result in significant increase of *M. persicae* reproduction, suggesting that these effectors acted in a species-specific manner and might control aphid host range. This hypothesis was supported by the fact that orthologues of C002, PIntO1 and PIntO2 were identified in multiple aphid species with distinct plant-host ranges. Further commonality between effector functions was reported in *Macrosiphon euphorbiae* (potato aphid), whereby *in planta* delivery of *M. euphorbiae* effectors Me10 and Me23 enhanced aphid fecundity (Atamian *et al*., 2013).

Virus-induced changes in plants on aphid vectors

While aphids interfere with and manipulate host defence and plant metabolism for their own benefits, plant viruses have also developed ways to control plant–aphid interactions to fulfil their life cycle and ultimately transmission to other plants. Many plant viruses depend on aphids and other phloem-feeding insects for transmission. Thus, viruses may promote their own transmission by manipulating plant physiology to attract aphids and increase

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aphid reproduction. This phenomenon led scientists to propose the terms 'host manipulation hypothesis' (Holmes and Bethel, 1972) or 'vector manipulation hypothesis' (Ingwell *et al*., 2012), whereby natural selection pressure on the virus has favoured its ability to elicit host behaviour with the overall outcome of enhancing transmission.

Consistent with this hypothesis, *M. persicae* was observed to settle preferentially on plants infected with *Turnip mosaic virus* (TuMV), resulting in increased fecundity on TuMV-infected plants compared to uninfected controls (Casteel *et al*., 2014). Interestingly, TuMV infection was seen to suppress callose deposition and increase the amount of free amino acids, an important source of nitrogen for aphids. Furthermore, from all the TuMV genome-encoded proteins expressed in transgenic plants, only the nuclear inclusion a-protease domain (NIa-Pro) increased *M. persicae* reproduction in their host plants. This suggests that TuMV NIa-Pro protein has the ability to manipulate host-plant physiology by promoting aphid reproduction, and therefore promoting its own transmission. The influence of virus-induced changes within infected plants on aphid vectors has been demonstrated in numerous pathosystems in monocot and dicot hosts, exemplifying the broad nature of this phenomenon (Ren *et al*., 2015). For example, mixed infections of heterologous viruses such as PVY and *Potato leaf roll virus* (PLRV) resulted in increased fecundity of *M. persicae* and *M. euphorbiae* than on singly infected or non-infected plants (Srinavasan and Alvarez, 2007). In cereals, the rate of population increase of the *Sitobion avenae* (English grain aphid) was observed on barley infected with *Barley yellow dwarf virus* (BYDV) as opposed to uninfected barley plants (Hu *et al*., 2013). The effect of virus infection can also be observed on infected plants towards aphids that are not vectors of the virus. Hu *et al*. (2013) monitored the feeding behaviour of *S. avenae*, a non-vector of *Wheat dwarf virus* (WDV) and CYDV, on virus-infected and virus-free barley. *Sitobion avenae* exhibited a shorter non-probing phase and longer phloem sap-ingestion phase, with more aphids ingesting phloem sap on infected plants, suggesting that WDV-/CYDV-infected host plants positively affected the feeding behaviour of the non-vector aphid, *S. avenae* (Hu *et al*., 2013).

The molecular mechanisms underlying these different types of plant–virus–insect interactions are likely to be as diverse and complex as those regulating other plant–pathogen(s) interactions. While some studies have found that aphids are attracted to plants showing chlorosis as a consequence of virus infection (Macias and Mink, 1969), volatile signals can attract aphids released by plants infected with non-persistently transmitted viruses like *Cucumber mosaic virus* (CMV) (Mauck *et al*., 2010). Deletion of the CMV genome-encoded 2b protein from CMV, an inhibitor of antiviral RNA silencing, induced stronger resistance to *M. persicae*, as sustained phloem ingestion was observed in CMV-infected plants in comparison to plants infected by a CMV-2b deleted variant (Ziebell *et al*., 2011). The latter example illustrates a distinctive mode of action of virus-encoded effectors, whereby the CMV 2b inhibits plant resistance mechanisms to insects, which ultimately increases aphid fitness.

Transmission Modes of Plant Viruses by Aphids

Non-persistent transmission

Approximately 75% of viruses with aphid vectors are transmitted in a non-persistent manner (Fig. 15.1; Nault, 1997). Non-persistently transmitted viruses cause a number of important diseases in cultivated plants (Raccah, 1986; Nault, 1997; Hull, 2002) and belong to six genera (Murphy *et al*., 1995; Ng and Perry, 2004) (Table 15.3). These viruses are usually distributed in many tissues of their host plants, including the epidermis, and they cause stunting, leaf distortion, vein clearing, vein necrosis, leaf mosaic and mottling and, in some cases, flower breaking (e.g. *Tulip breaking virus* (TBV) and TuMV in certain hosts). In some cases, as with *Alfalfa mosaic virus* (AMV) and some virus species of the genus *Carlavirus*, they do not cause any symptoms (latent infections). All non-persistent viruses are readily transmitted mechanically under laboratory conditions, and some are seed-borne (e.g. *Lettuce mosaic virus* (LMV) and CMV). For transmission and other characteristics, see Table 15.2.

Transmission characteristics

Non-persistent transmission is virtually exclusive to aphids (Fig. 15.1), and acquisition and inoculation occur optimally during very brief stylet penetrations (<1 min). During these probes, aphid stylets penetrate the epidermal layer, where virus concentration can be high. As the stylet insertion period increases

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Table 15.3. Aphid-transmitted viruses: families, genera, particle morphology and type of genome.

Mode of transmission	Genus/Family	Particle morphology	Genome[a]
Non-persistent	*Alfamovirus*/Bromoviridae	Quasi-isometric to bacilliform (18 nm diameter, 30–56 nm long)	Tp/+ssRNA
	Carlavirus/Flexiviridae	Slightly flexuous filamentous (470–580 nm long, 13 nm diameter)	Mp/+ssRNA
	Cucumovirus/Bromoviridae	Isometric to bacilliform (26–35 nm)	Tp/+ssRNA
	Fabavirus/Comoviridae	Isometric (22–32 nm)	Bp/+ssRNA
	Macluravirus/Potyviridae	Short flexuous rods (650–675 nm long, 11–15 nm diameter)	Mp/+ssRNA
	Potyvirus/*Potyviridae*	Flexuous rods (680–900 nm long, 12–15 nm diameter)	Mp/+ssRNA
Semi-persistent	*Badnavirus*/Caulimoviridae	Bacilliform (95–130 nm, or 60–900 nm long and a width of 24–35 nm)	Circular dsDNA
	Caulimovirus/Caulimoviridae	Isometric (35–50 nm)	Circular dsDNA
	Closterovirus/Closteroviridae	Flexuous filamentous (1250–2000 nm long, 12 nm diameter)	Mp/+ssRNA
	Sequivirus/Sequiviridae	Isometric (31 nm)	Mp/+ssRNA
	Waikavirus/Sequiviridae	Isometric (30 nm)	Mp/+ssRNA
Persistent/non-propagative	*Enamovirus* /Luteoviridae	Isometric (25–30 nm)	Mp/+ssRNA
	Luteovirus/Luteoviridae	Isometric (25–30 nm)	Mp/+ssRNA
	Polerovirus/Luteoviridae	Isometric (24 nm)	Bp/+ssRNA
	Umbravirus/not assigned to a family	Do not form conventional virions except in coat protein of a helper luteovirus	Mp/+ssRNA
	Nanovirus/Nanoviridae	Isometric (17–26 nm)	Mc/ssDNA
Persistent/ propagative	*Cytorhabdovirus*/ Rhabdoviridae	Bullet-shaped or bacilliform, membrane enveloped (42–130 nm diameter, 100–360 long)	Mp/–ssRNA
	Nucleorhabdovirus/ Rhabdoviridae	Bullet-shaped or bacilliform, membrane enveloped (43–100 nm diameter, 95–500 long)	Mp/–ssRNA

Notes: [a]Viruses with monopartite (Mp) or undivided genome have only one molecule of nucleic acid as a genome, whereas viruses with divided or segmented genome (multipartite) may have two (bipartite, Bp) or three (tripartite, Tp) molecules. Multi-component (Mc) genome = with more RNA segments (6–11 in the case of nanoviruses); +ssRNA = single-stranded RNA of positive polarity acting as messenger RNA; –ssRNA = single-stranded RNA of negative polarity; ssDNA = single-stranded DNA; dsDNA = double-stranded DNA.

beyond approximately 30 s to 1 min (representing penetration beyond the epidermal cell layer), the subsequent transmission rate decreases rapidly. Pre-acquisition fasting of aphids for 15 min to 4 h can result in increased transmission efficiency (Hull, 2002). Initially, this 'pre-acquisition starvation' (PAS) effect was attributed to behavioural changes, as starved aphids had the propensity to make short probes, favouring the acquisition and inoculation of non-persistent viruses (Bradley, 1952). However, more recent studies have indicated that non-behavioural factor(s) also contribute to the PAS effect (Powell, 1993; Powell *et al*., 1995; Wang and Pirone, 1996). Aphids lose their infectivity after moulting, since the stylets and cuticular lining of the foregut are shed with any retained virions. The aphids remain viruliferous for only a few minutes to hours, and lose the ability to inoculate more rapidly when given access to a plant (irrespective of whether it is a host for either the aphid or virus) than when fasted (Watson and Roberts, 1940; Bradley, 1959). Although the rate of loss tends to be exponential in fasted aphids, it is correlated positively with temperature (Kassanis, 1941). In a few cases, aphids can retain their vectoring ability for a longer period if they are not feeding on plants, for at least 18 h in

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the case of *Maize dwarf mosaic virus* (MDMV) (Berger *et al*., 1987).

Mechanisms of transmission

ACQUISITION. The retention of virions in the aphid foregut, particularly the maxillary FC (see below), indicates that non-persistent viruses are acquired via ingestion (Pirone and Perry, 2002) during maxillary puncture of an epidermal cell. The DC-EPG technique has revealed that three successive intracellular activities occur after the maxillary stylet tips puncture the plasma membrane, designated subphases II-1, II-2 and II-3 (Powell *et al*., 1995; Martin *et al*., 1997; Powell, 2005; Fig. 15.2c). The third intracellular activity, occurring immediately before stylet withdrawal from the cell, is associated with efficient acquisition of both PVY and CMV (Martin *et al*., 1997), and therefore represents active ingestion of cytosol by the aphid (Powell and Hardie, 2000; Fig. 15.2c).

RETENTION. Localization studies have focused particularly on potyviruses, where a virally encoded helper component (HC; or 'helper factor' or 'aphid transmission factor'; reviewed by Pirone and Blanc, 1996) accessory protein is required for transmission. Evidence suggests that the CD and FC of the maxillary stylets and the cibarium (Berger and Pirone, 1986; Ammar *et al*., 1987, 1994; Childress and Harris, 1989; Ammar and Nault, 1991; Wang *et al*., 1996) are the sites where virions of potyviruses are attached to the cuticular surfaces of the stylets. However, virions are particularly associated with the distal third of the maxillary stylets (Wang *et al*., 1996). The HC acts as a bridge to facilitate binding between a putative aphid cuticular receptor (ACR) and the viral capsid-protein (CP) subunit (Raccah *et al*., 2001). With cucumoviruses, such as CMV, there is no viral HC, and only an ACR–CP bridge exists (Perry, 2001). Therefore, among non-persistently transmitted viruses, two strategies have developed, either helper-dependent or helper-independent transmission. Attached virions provide the inoculum for viral infection of healthy plants.

INOCULATION. In common with the acquisition process, inoculation of virions requires maxillary puncture of the plasma membrane (Powell, 1991). Cell puncture interruption experiments have been performed to investigate which of the three intracellular subphases is associated with efficient inoculation by viruliferous aphids. This approach showed that only the first intracellular activity (II-1) was necessary for delivery of PVY, CMV and TuMV virions into the cell (Martin *et al*., 1997; Moreno *et al*., 2012). Virions are therefore released very rapidly (within 2 s) after puncture of the plasma membrane. However, the inoculation mechanism has been the subject of controversy, and two hypotheses have been advocated, presenting alternative scenarios.

The 'ingestion–egestion' hypothesis suggests that virions carried in the maxillary FC and more proximal areas of the foregut are expelled into the inoculated cell during egestion (regurgitation) (Watson and Plumb, 1972; Garrett, 1973; Harris and Bath, 1973; Harris, 1977; Harris and Harris, 2001). Microscopic observations of aphid stylets during penetration of an *in vitro* artificial feeding system suggested that the aphid cibarial pump might function bidirectionally: ink particles were reported to move both into and out of the FC (Harris and Bath, 1973). However, while aphids may be capable of egestion under such artificial conditions, it is not clear whether or when egestion occurs during penetration of plant tissues. There is no evidence that the behavioural event associated with non-persistent virus inoculation (subphase II-1) represents egestion. It has been argued that experiments demonstrating the transfer of radioisotopes from labelled plants to unlabelled plants provide evidence for the transfer of plant sap via ingestion and subsequent egestion (Garrett, 1973; Harris, 1977). However, efficient acquisition and transfer of the label required longer probes by the aphids (3–5 min; Garrett, 1973) than those that typically characterized the non-persistent acquisition and inoculation processes (<1 min).

Martin *et al*. (1997) have put forward an alternative ('ingestion–salivation') hypothesis whereby virions are inoculated via salivation. They pointed out that the anatomy of the aphid stylets, with the FC and SC merging near the maxillary tips (forming the CD), provided a point of convergence where retained virions were exposed directly to the flow of saliva. Aphids are able to secrete two types of saliva (Miles, 1999). Gelling saliva is produced during penetration of the apoplast and forms a sheath around the stylet bundle. This sheath material is excluded from the cell when the maxillary stylets puncture the plasma membrane (Tjallingii and Hogen Esch, 1993), and intracellular salivation involves the production of non-gelling, 'watery' saliva (Cherqui and Tjallingii, 2000). Initiation of the II-1 EPG waveform immediately

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following cell entry may therefore represent a sudden switch from the production of gelling saliva to watery saliva. Virions retained at the common duct may be released at this point if factors present in watery saliva have the ability to reverse binding between virions and their cuticular retention sites (either direct or HC mediated).

Support for the ingestion–salivation hypothesis comes from EPG experiments investigating inoculation of the persistent (circulative) *Pea enation mosaic virus* (PEMV) (Powell, 2005). Unlike many other persistent, non-propagative viruses, PEMV is not phloem limited and can be inoculated to superficial plant tissues. Inoculation of this virus can therefore be used as a marker for early intracellular salivation by aphids. During brief epidermal probes, inoculation of PEMV was linked to the occurrence and duration of subphase II-1, but not to the other two subsequent intracellular subphases. When considered together with the results of the previous study associating II-1 with the inoculation of non-persistent viruses (Martin *et al*., 1997), these results suggest that the non-persistent inoculation process involves the injection of watery saliva into the cell cytoplasm, with the implication that the CD represents the likely functional retention site. The CD occupies an extremely small (2–4 μm) region of the stylets, that is <1% of the stylet bundle (Forbes, 1969), and virions retained here will be a very small proportion of those acquired. However, the retention of virions at more proximal sites does not provide evidence that they function in transmission (Pirone and Perry, 2002).

Semi-persistent transmission

Viruses transmitted by aphids in a semi-persistent manner occur in six genera (Nault, 1997) (Table 15.3). *Cauliflower mosaic virus* (CaMV), the type member of the genus *Caulimovirus*, was considered initially to be an atypical non-persistent virus (Hamlyn, 1955; van Hoof, 1958). Later, it was thought to be transmitted bimodally, that is in both a non- and a semi-persistent manner (Chalfant and Chapman, 1962; Bouchery *et al*., 1990), but it is now considered to be transmitted semi-persistently (Markham *et al*., 1987).

Transmission characteristics

Similar to the non-persistent viruses, some semi-persistent viruses may be acquired within minutes, but the efficiency to inoculate virions subsequently to a new host increases with the length of acquisition access (Palacios *et al*., 2002). Efficient virus acquisition appears to be a function of feeding rather than probing. In common with non-persistent viruses, semi-persistent viruses do not require an LP in the vector, are not present in vector haemolymph and cannot be transmitted after injection into the vector haemocoel. Infectivity may be retained for a few days, but it is lost after moulting (Fereres and Collar, 2001). However, unlike non-persistent viruses, pre-acquisition fasting does not affect transmission efficiency.

Mechanisms of transmission

ACQUISITION. Using the DC-EPG technique, Palacios *et al*. (2002) showed that the principal vectors of CaMV (*M. persicae* and *Brevicoryne brassicae* (cabbage aphid)) were able to acquire virions during brief punctures of epidermal cells. Such rapid acquisition probably occurs via the same process as the acquisition of non-persistent viruses, with virions ingested into the FC during intracellular subphase II-3. However, the efficiency of acquisition (measured by subsequent transmission to test plants) increased significantly if aphids reached a phloem sieve element and ingested phloem sap for at least 15 min on CaMV-infected plants (Palacios *et al*., 2002). Other semi-persistent viruses may be limited to the phloem (particularly closteroviruses; Hull, 2002), and their acquisition therefore may have a more rigid requirement for phloem-sap ingestion (Limburg *et al*., 1997).

RETENTION. The transmission characteristics of semi-persistent viruses suggest the functional retention of a much larger number of virions than for non-persistent viruses. Harris and Harris (2001) pointed out that the surface area in the proximal part of the maxillary FC and the pre- and post-cibarial area was extensive, providing for the binding of a large number of virions. Transmission electron microscopy has indicated that semi-persistent viruses are retained in the aphid foregut (Murant *et al*., 1976), whereas Lopez-Abella *et al*. (1988) suggested that they might use two binding sites, one in the aphid stylets and another in the foregut. The exact location of cuticular receptors for semi-persistent viruses in aphids remains unclear and, as with non-persistent viruses, retention of virions at particular sites does not prove that they are functional in the transmission process.

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INOCULATION. It is widely accepted that semi-persistent virus transmission occurs via an ingestion–egestion mechanism (Fereres and Collar, 2001; Harris and Harris, 2001). However, further research is required to determine when aphids egest during plant penetration. Moreno *et al.* (2005b) recently investigated inoculation of CaMV using the DC-EPG technique. Both *M. persicae* and *B. brassicae* were able to inoculate the virus very rapidly during the first (epidermal) cell puncture. Both vector species inoculated CaMV more efficiently when allowed several short cell punctures during a longer (5 min) period of plant access, and inoculation efficiency increased further when aphids made sustained (>15 min) contact with a phloem sieve element. However, the occurrence of inoculation during initial brief cell punctures is a finding that has important implications for the CaMV inoculation process and retention site. Since subphases II-2 or II-3 have not been linked with the ejection of stylet contents into the cell (Martin *et al.*, 1997; Powell, 2005), the likely mechanism of such rapid CaMV inoculation is via intracellular salivation (during subphase II-1; Moreno *et al.*, 2005b). The maxillary CD may therefore function as a retention site for semi-persistent viruses, as seems to be the case for non-persistent ones. However, a definitive association between II-1 and CaMV inoculation will require interrupting cell punctures during the various subphases (Martin *et al.*, 1997), an approach that has not yet been reported with CaMV. The study by Moreno *et al.* (2005b) suggests that aphids are able to inoculate CaMV during early brief cell punctures and later sustained sieve element punctures, but it is not clear whether egestion occurs during such behaviours. There is currently no experimental evidence that aphids egest during penetration of superficial cells (Powell, 2005) or the phloem (Prado and Tjallingii, 1994).

Virus–aphid molecular interactions during transmission of non- and semi-persistent (non-circulative) viruses

As all non- and semi-persistent viruses have a simple structure with their nucleic acid (RNA or DNA) encapsidated in simple virus particles (Hull, 2002), it is the CP that is available for interaction with cuticular surfaces of the aphid stylets and foregut. Two forms of interaction have been identified between the CP and aphid retention sites: direct interaction (called the capsid protein strategy) and indirect interaction (the helper component(s) strategy), in which one (e.g. potyviruses) or two (e.g. caulimoviruses) non-structural virus-coded protein(s) are involved.

CAPSID PROTEIN (CP) STRATEGY. The transmission of cucumoviruses, alfamoviruses and carlaviruses does not require a helper component, and aphids can therefore acquire virions from purified virus preparations through an artificial membrane feeding system and then transmit them to host plants (Pirone and Megahed, 1966; Pirone, 1977; Weber and Hampton, 1980). In the case of CMV and other cucumoviruses, transmissibility depends solely on the CP, as was found in *in vitro* dissociation and reassembly experiments with highly aphid-transmissible and poorly aphid-transmissible virus isolates (Gera *et al.*, 1979; Chen and Francki, 1990). Although CMV transmission by aphids does not require a helper component, it is considered that the transmission mechanism(s) involved are very similar to those of potyviruses and other viruses, transmission of which is mediated by HC.

HELPER STRATEGY (NON-PERSISTENT). Aphid transmission of potyviruses involves the so-called helper strategy (Fig. 15.3). In addition to virions, the acquisition by aphids of a virus-coded helper protein is required for successful potyvirus transmission. For this reason, aphids cannot transmit purified potyviruses (Pirone and Megahed, 1966) unless they have previous or simultaneous access to HC (Kassanis and Govier, 1971a,b; Govier and Kassanis, 1974a,b).

The viral HC-Pro (to denote the dual functional role of HC in both aphid transmission and proteolysis) has been identified in many potyvirus–host-plant systems and seems to be a general phenomenon (Raccah *et al.*, 2001). Potyviral HCs can assist the transmission of virions belonging to the same (homologous) or different (heterologous) virus species, although transmission efficiency is often higher with homologous HC (Pirone, 1981; Sako and Ogata, 1981; Sako *et al.*, 1984; Lecoq *et al.*, 1991). Potyviral HC appears to act as a link between virions and aphid mouthparts (Govier and Kassanis, 1974a,b). The 'bridge' hypothesis (Pirone and Blanc, 1996) has been supported experimentally by introducing mutations within the highly conserved proline–threonine–lysine (PTK) motif of HC-Pro (Peng *et al.*, 1998). This hypothesis presumes that HC-Pro contains two domains: one specifically binding to the aphid stylets and the second binding to the CP of

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the virion. Experimental data have identified the two domains in HC-Pro: the N-terminal domain lysine–isoleucine–threonine–cysteine (KITC) motif, which might be involved in the specific binding to the aphid's stylets (Blanc *et al*., 1998), and the C-terminal domain PTK motif, which has been shown to be involved either directly or indirectly in HC-Pro binding to the amino acid triplet aspartic acid–alanine–glycine (DAG) motif, located at the N-terminus of CP (Peng *et al*., 1998). Experimental evidence supports the bridging role of HC-Pro (Blanc *et al*., 1998; Wang *et al*., 1998). The inability of aphids to acquire different potyviruses from purified preparations has been attributed to their failure to retain the virus in the stylets (Revers *et al*., 1999), and retention in the maxillary FC and foregut occurs only when active HC is present (Ammar *et al*., 1994; Wang *et al*., 1996).

HC-Pro is a multifunctional protein (Maia *et al*., 1996) with numerous functional domains such as a zinc-finger motif involved in viral synergism between co-infecting viruses (Vance *et al*., 1995; Pruss *et al*., 1997), nucleic acid-/RNA-binding domains (Urcuqui-Inchima *et al*., 2000), peptidyl domains involved in viral genomic RNA replication and systemic movement (Cronin *et al*., 1995, Kasschau *et al*., 1997) and cysteine-protease-like domains (Oh and Carrington, 1989; Guo *et al*., 2011). Apart from mediating aphid transmission (Govier *et al*., 1977), HC-Pro appeared to be involved in almost all processes of the viral cycle, such as movement through plasmodesmata, cell-to-cell and long-distance potyvirus movement in the plant (Rojas *et al*., 1997; Kasschau and Carrington, 2001; Saenz *et al*., 2002), pathogenicity (Revers *et al*., 1999; Redondo *et al*., 2001) and suppression of antiviral RNA silencing (Llave *et al*., 2000).

HELPER STRATEGY (SEMI-PERSISTENT). Studies with caulimoviruses suggest that these also depend on a helper strategy, but instead of a single HC protein, there are two proteins mediating interactions between the ACR and CP (Blanc *et al*., 2001). At the cellular level, CaMV forms two types of specialized inclusion bodies within infected plant cells: virus factories, which are intracellular aggregates forming the sites for viral replication and virion assembly by concentrating required cellular and viral proteins, and a single transmission body (TB), which is specialized for virus transmission by aphid vectors and contains helper components and virions (Drucker *et al*., 2002). The TBs are dynamic structures and react within seconds to aphid feeding, whereby TBs in adjacent cells punctured by the aphid's stylets undergo disruption and redistribution of the viral transmission helper protein P2 on to microtubules throughout the cell. At the same time, CaMV virions will also associate with microtubules. This redistribution of P2 and virions facilitates transmission while the TB reforms within minutes after vector departure (Bak *et al*., 2013; Blanc *et al*., 2014). Transmission of CaMV involves the virus-encoded proteins P2 and P3, together with the CP (P4) (Espinoza *et al*., 1992; Leh *et al*., 1999) (Fig. 15.3). Aphid transmission of CaMV requires a bridge between P2 and P3 (Drucker *et al*., 2002) to link virions to the aphid's cuticular surfaces. The P2–P3 virion complex is formed within the aphid alimentary canal and not in infected plant tissues, as was believed originally (Drucker *et al*., 2002). Aphids may acquire P2 first during stylet penetration of infected mesophyll cells, and subsequently ingest P3 and virions from other mesophyll or phloem cells (Drucker *et al*., 2002). The attachment of CaMV

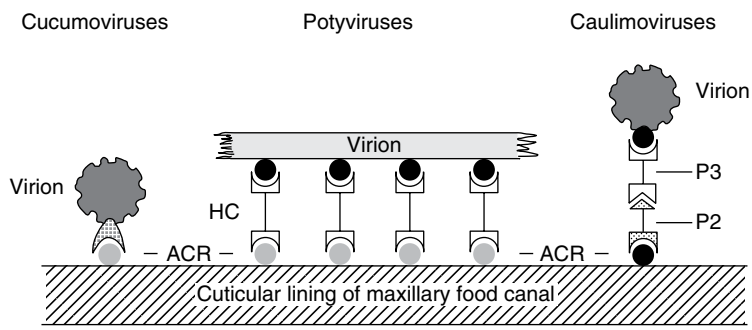

Fig. 15.3. Diagrammatic representation of the attachment of different categories of non-circulative viruses to the cuticular lining of maxillary food canal/common duct of aphids. ACR = aphid cuticular receptors; HC = helper component protein; P2, P3 = proteins.

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virions to the aphid is mediated by the N-terminal domain of P2, which recognizes a cuticular receptor at the tip of the stylets (Uzest *et al*., 2007), while the P2 C-terminus binds to the P3 N-terminus (Leh *et al*., 1999). The C-terminal domain of P3 is responsible for the interaction with the virion (Leh *et al*., 2001). An additional interaction is required to ensure the formation of the stable P2–P3 complex. There are three possible roles for P2 and P3 in the aphid transmission of CaMV (Blanc *et al*., 2001): (i) P2 is indeed the only helper, and P3 would be more correctly referred to as a capsid component; (ii) both P2 and P3 equally can be considered helpers; (iii) neither P2 nor P3, but rather the complex P2–P3, is the helper. One striking difference between helper proteins is that CaMV P2 does not seem to be involved in other viral-associated functions apart from transmission in contrast to the multifunctional HC-Pro potyviruses.

Helper components are also implicated in the semi-persistent transmission of sequiviruses, and are attributed to a helper virus belonging to the genus *Waikavirus* (Harrison and Murant, 1984). Aphid transmission of *Parsnip yellow fleck virus* (PYFV) is dependent on the acquisition of a helper produced by plants infected with *Anthriscus yellows virus* (AYV) (Elnagar and Murant, 1976). Helper components may also be implicated in the transmission of closteroviruses (Murant *et al*., 1998). The evidence for helper component dependency is based on the observation that, as in the case of potyviruses and caulimoviruses, aphids cannot acquire and transmit them from purified preparations. However, such factors have not been identified and further work is needed to investigate this.

Vector specificity in non- and semi-persistent (non-circulative) viruses

'Vector specificity' refers to the degree of interdependence between a specific virus and a particular aphid vector species. As would be expected, the vector specificity of non-persistent viruses, because of their relatively transient relationship with the vector, is lower than that of the other aphid-borne viruses (Pirone and Harris, 1977). Aphids acquire and inoculate non-persistent viruses during brief probes, and many different aphid species (including some that are unable to feed on virus host plants) may be vectors (e.g. Radcliffe and Ragsdale, 2002; Jones *et al*., 2006).

A given virus may be vectored with varying efficiency according to the aphid species, clone, or biotype. Aphid species or clones may or may not transmit CMV, and if they do, have varying vector efficiencies (Bhargava, 1951; Badami, 1958; Conti *et al*., 1979). Clones of *A. pisum* differ considerably in their ability to transmit *Bean yellow mosaic virus* (BYMV), and this is not related to the geographic origin or the colour of the clone (Jurík *et al*., 1980). Also, *M. persicae* transmits efficiently both *Beet mosaic virus* (BtMV) and PVY, whereas *Rhopalosiphum padi* (bird cherry–oat aphid) transmits both viruses inefficiently (Katis and Gibson, 1984, 1985). There have been many studies of the efficiency with which various aphid species transmit PVY, including van Hoof (1980), Sigvald (1984), Harrington *et al*. (1986), Gibson *et al*. (1988), Harrington and Gibson (1989), de Bokx and Piron (1990), Verbeek *et al*. (2010) and Pelletier *et al*. (2012). These studies usually allocate a relative transmission efficiency factor (REF) to each species, this being the efficiency compared to *M. persicae*, which is given an REF of 1.0. Unsurprisingly, different studies produce different REFs, because different methodologies, aphid clones, virus isolates and test plants are used. REFs are often used to help assess PVY risk to the crop (vector pressure), but should be seen as only a very approximate guide, even if mean values from a range of studies are used. The susceptibility of crops varies with their growth stage, and the rate of change varies with crop cultivar and virus strain. This needs taking into account when using REFs to determine vector pressure, but quantitative data are limited.

Using PCR-based methods on aphids collected from pan traps allowed the detection of PVY from aphid stylets (Pelletier *et al*., 2012). From the 65 aphid taxa identified from PVY positive samples, 45 taxa had never been evaluated for PVY transmission and 7 had been previously reported as non-vectors. While this study does not prove the ability of these species to transmit PVY, a larger number of aphid species could potentially act as vectors than has previously been recognized.

Kirchner *et al*. (2011) adopted a more holistic approach to determine the relative importance of aphid species as PVY vectors in potato crops. They modelled aphid counts in traps, aphid REFs, virus resistance of potato cultivars and initial tuber-borne infection rate as explanatory variables in general linear mixed models. They demonstrated that the incidence of seed-borne infection and early-season aphid flights were the main components contributing to PVY incidence in the field. Interestingly, by

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comparing models with all aphid species surveyed, the best model fit was obtained with *Aphis fabae* (black bean aphid), suggesting that in this geographical area *A. fabae* was the most important PVY vector and that the contributions of other aphid species were negligible.

Strains of CMV and CTV also differ in the efficiency with which they are transmitted by aphids (Simons, 1957a; Raccah *et al*., 1976; Gera *et al*., 1979). The CP determines transmission specificity at least in the case of CMV (e.g. Gera *et al*., 1979), and a conserved CP surface domain of CMV that is essential for efficient transmission by aphids has been identified (Liu *et al*., 2002).

For non-circulative viruses with a helper component, it is likely that helper proteins play a very important role in vector specificity. It was shown that in the case of potyvirus transmission, specificity was conferred by HC and transmissibility was highly correlated with retention of virus in the stylets (Wang *et al*., 1998). In the P2 HC of CaMV, changing a single amino acid residue can alter the spectrum of aphid-vector species (Moreno *et al*., 2005a).

The question remains as to what makes an aphid such as *M. persicae* an efficient vector of many potyviruses whereas, for example, *Myzus ascalonicus* (shallot aphid) cannot transmit, or transmits very inefficiently, potyviruses such as TuMV, *Tobacco etch virus* (TEV), PVY, LMV and BtMV (Doncaster and Kassanis, 1946; Wang *et al*., 1998).

Other factors affecting transmission of non- and semi-persistent viruses

Apart from interactions between virus and aphid genotypes, abiotic factors such as temperature and humidity, and the presence of satellite RNA (satRNA), can greatly affect virus transmission by aphids (Robert and Lemaire, 1999). Temperature affects aphid behaviour during acquisition and/or inoculation (Robert *et al*., 2000) and also affects host plants, both as virus sources and new virus hosts, and has direct effects on virus survival (Syller, 1987). The transmission rate of ZYMV by *M. persicae* was greater at 21°C than at 8°C, and *Aphis gossypii* (cotton aphid or melon aphid) failed to transmit it at lower temperatures when relative humidity was less than 80% (Fereres *et al*., 1992). High humidity was correlated positively with the transmission efficiency of PVY by different aphid species (Singh *et al*., 1988).

Persistent transmission

Persistent viruses are usually, but not exclusively, confined to the phloem tissue (sieve elements and companion cells) of their host plants and cause symptoms such as stunting, leaf discoloration and leaf rolling (Table 15.2). Such viruses either replicate (propagative viruses) or not (non-propagative viruses) within the aphid vector.

Non-propagative circulative transmission

LUTEOVIRIDAE. Non-propagative, aphid-transmitted viruses belong mainly to the family Luteoviridae, which comprises four genera: *Luteovirus*, *Polerovirus*, *Enamovirus* and *Umbravirus*. Viruses belonging to the unassigned genera *Nanovirus* and *Sobemovirus* are also transmitted in this manner (Ng and Perry, 2004). The Luteoviridae comprises eight fully recognized and assigned viruses, along with 12 unclassified and 20 tentative members that have many characteristics of the type species of the four genera (Smith and Barker, 1999). PEMV represents an obligate symbiosis between an enamovirus (PEMV-1, a member of the family Luteoviridae) and an umbravirus (PEMV-2) (de Zoeten and Skaf, 2001). PEMV-1 confers transmission by aphids in a circulative (non-propagative) manner and, as in the case of luteoviruses, acquired PEMV virions accumulate in the accessory salivary glands and are inoculated via salivation (de Zoeten and Skaf, 2001; Reavy and Mayo, 2002; Gray and Gildow, 2003). PEMV-2 is not known to play any role in determining interactions with aphid vectors, but influences the site of successful virus inoculation within plants by conferring cell-to-cell movement and escape from phloem limitation.

Transmission characteristics. As luteoviruses are phloem limited, aphids need to ingest phloem sap in order to acquire them (Prado and Tjallingii, 1994). The minimum recorded virus acquisition access period (AAP) therefore reflects the time taken for aphid stylets to reach the phloem and has been determined as 15 min for BYDV and 1 h for PLRV (Gray *et al*., 1991; Taliansky *et al*., 2003). However, the transmission efficiency of both viruses increases with a rise in the AAP to 2 or more days, as in the case of PLRV. The LP is at least 24 h and may extend to as much as 4 days. LP length depends on several factors, such as the aphid species, virus concentration in the host plant tissue and environmental

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factors such as temperature (van der Broek and Gill, 1980; Power and Gray, 1995). An inoculation access period (IAP) of about 10–30 min is required for most virus species, but efficiency is higher when IAP is increased (Power *et al*., 1991). EPG experiments with *R. padi* indicate that some aphids are able to inoculate BYDV-PAV without showing sustained contact with a phloem sieve element. All such aphids showed numerous short cell punctures (presumably including brief puncture of sieve elements or companion cells where the virus could be inoculated), and virions were therefore probably delivered during the very brief initial intracellular salivation activity (subphase II-1). Transmission of BYDV-PAV occurred at a higher frequency when aphids showed sustained puncture of a sieve element, and efficient inoculation was linked with the sieve-element salivation EPG waveform E1 (Prado and Tjallingii, 1994). Aphids retain the capability to transmit luteoviruses for several days, and in some cases throughout their lifespan. The interactions between luteoviruses and their aphid vectors have been reviewed by Gray and Gildow (2003).

Uptake route in the vector. For successful transmission, virions have to pass at least two barriers: the gut wall and the salivary gland membranes. Virions first enter the aphid's body via the ingestion of phloem sap, then are transported across the gut wall to the haemocoel and finally accumulate in the ASGs. The particles are delivered into the SC, from where they are injected into a plant during subsequent stylet penetration (Gildow, 1999). Endocytosis and exocytosis at the two epithelial barriers (alimentary tract and ASG) involve specific interactions between virus CPs and receptors present in these two locations within the aphid (Gildow, 1987, 1993; Stevens *et al*., 2005).

Luteovirus–aphid vector molecular interactions and vector specificity. Viruses transmitted by aphids in a persistent manner are usually vectored by one, or only a few, aphid species that colonize the virus host plants. The molecular interactions determining transmission and vector specificity have been researched in some detail, particularly with the *Luteovirus* species BYDV and CYDV (Gray and Banerjee, 1999). As aphids can acquire and transmit purified luteoviruses, it is likely that no additional proteins, other than the CP, are involved. Studies with different luteoviruses have suggested that both the CP and the minor CP (CPm) structural proteins play key roles in the aphid transmission process (Mayo and Ziegler-Graff, 1996), as point mutations in or near conserved domains of *Beet western yellows virus* (BWYV) CPm affect aphid transmissibility (Brault *et al*., 2000).

There is good evidence that symbionin, a 60 kDa protein produced by the endosymbiotic bacterium *Buchnera* spp. and found in *M. persicae* haemolymph, interacts with PLRV and other *Polerovirus* species to assist virus retention in the haemolymph (van den Heuvel, 1999). Symbionin possibly mediates the longevity of virus particles by binding and protecting them from proteolysis (Hogenhout *et al*., 1998). However, the binding of symbionin to virus particles or to P5 (the coat protein readthrough structural proteins) has only been demonstrated *in vitro* (Reavy and Mayo, 2002). As symbionin homologues from vector and non-vector aphid species bind, *in vitro*, to six different purified luteoviruses (van den Heuvel, 1999) and the binding capacity is not correlated with transmission ability or efficiency, it has been suggested that if symbionin plays a role in virus transmission, it does not play a major role in determining vector specificity (van den Heuvel *et al*., 1997).

Barriers within the aphid act as 'filters' to the passage of luteoviruses and thereby contribute to vector specificity. The key barriers are the gut and the ASG walls. After ingestion, the virions in the gut lumen cross the gut wall, via receptor-mediated endocytosis, at two possible regions: the posterior midgut and the hindgut. Previous studies have shown that BYDV-PAV passes through the hindgut of *S. avenae* (grain aphid) and *R. padi*, as does BYDV-MAV in *S. avenae* (Gildow, 1999) and *Soybean dwarf virus* (SbDV) in *Aulacorthum solani* (glasshouse and potato aphid) and *M. persicae* (Gildow *et al*., 1994). In contrast, PLRV (Garret *et al*., 1993) and BWYV (Reinbold *et al*., 2001) penetrate through the posterior midgut of *M. persicae*. In some aphid–virus combinations, such as *Cucurbit aphid-borne yellows virus* (CABYV) in *M. persicae* and *A. gossypii*, both areas of the gut allow virus transport (Reinbold *et al*., 2003). Also, specificity can occur within the same aphid species. For example, in *M. persicae*, SbDV passes through the hindgut while PLRV passes through the posterior midgut. Having crossed the gut wall, viruses are transported via the haemolymph to the ASG. Specificity at the ASG involves two barriers: the extracellular basal lamina (basement membrane) and the basal plasmalemma (cell membrane). Strains of SbDV have been found to

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have different properties with regard to ASG membrane penetration. Virions of the SbDV-D strain can penetrate the basal lamina in *A. solani* but not in *M. persicae*. The SbDV-Va20 strain can penetrate the basal lamina in both species, but the basal plasmalemma membrane can be penetrated in *M. persicae* only (Gildow *et al*., 2000). In the ASG, the basal plasmalemma forms the physical barrier, in contrast to the gut wall, where the apical plasmalemma membrane forms the barrier. The mechanism of the passage through the cellular membrane presumably involves a receptor-mediated endocytosis. In the basement membrane, however, attachment of the capsid protein of the virus is postulated to cause loosening of cross-linking bonds of the collagen and laminin matrix, allowing the passage of virions larger than the membrane pore (Peiffer *et al*., 1997; Gray and Gildow, 2003). Little is known about the molecular mechanisms of receptor-mediated endocytosis. It is believed that parts of the capsid protein are involved. Evidence has been obtained supporting the hypothesis of involvement of the N-terminal half of the readthrough domain encoded by open reading frame 5 of SbDV (Terauchi *et al*., 2003). A review of virus–vector specificity has been given by Gildow (1999). The nature of the viral determinants governing tissue specificity (posterior midgut, hindgut, or both) in the aphid body during virus acquisition has not been identified, and sequence comparisons of viral structural proteins do not show any obvious sequence motifs that could be correlated with tissue specificity (Reinbold *et al*., 2003). However, the minor CP of BWYV plays an important role in the transport of virions through midgut cells, and is also necessary for the maintenance of virions in the haemolymph and their passage through ASG cells (Reinbold *et al*., 2001).

Factors affecting luteovirus transmission. As with non- and semi-persistently transmitted viruses, the transmission of persistent viruses such as luteoviruses may also be affected by the aphid species, clone or biotype and/or virus strain. This has been reviewed by Gray (1999). It has been shown that the transmission efficiency of PLRV and BYDV is affected not only by the aphid species but also by the clone, morph and instar (Björling and Ossiannilsson, 1958; Hinz, 1966; Robert and Maury, 1970; Robert, 1971; Upreti and Nagaich, 1971; Tamada *et al*., 1984; Zhou and Rochow, 1984; Bourdin *et al*., 1998; Gray and Gildow, 2003). A twofold difference in transmission efficiencies of BYDV-PAV was found between the least and most effective clones of *R. padi*, and an 8-fold difference was found between *S. avenae* clones tested (Guo *et al*., 1997). Similarly, Bourdin *et al*. (1998) showed that some PLRV isolates were poorly transmitted by clones of *M. persicae* and *M. persicae nicotianae* (tobacco aphid), and this could not be related to the intrinsic properties of either the virus particle, as was suggested initially (Tamada *et al*., 1984), or the aphid clone; the transmission process and its specificity depend on interactions between them. Variation in the percentage of *S. avenae* individuals that transmitted BYDV-PAV ranged from 3.7 to 92.5%, and this was affected by the aphid clone, the plant species on which the clone was collected and the reproductive mode of the clone (Dedryver *et al*., 2005). Populations of *A. solani* originating from Japan were more efficient vectors of SbDV than those originating from the USA and New Zealand (Damgsteeght and Hewings, 1986).

Abiotic factors such as temperature and humidity may also affect the ability of aphids to transmit luteoviruses. Temperature affects aphid behaviour during acquisition and/or inoculation (see Robert *et al*., 2000), and also host plants, both as virus sources and new virus hosts (Syller, 1987). The effect of temperature on BYDV transmission is related to the aphid species involved, and seven clones of *R. padi* have been shown to differ in their vectoring ability at 5 or 10°C but not at 15°C (Smyrnioudis *et al*., 2001b), whereas no interclonal variation in the transmission efficiency by *S. avenae* was observed at any temperature. Humidity was correlated positively with the transmission efficiency of PLRV by different aphid species (Singh *et al*., 1988).

Umbraviruses do not encode for a CP and therefore require a helper *Luteovirus* CP for aphid transmission. Seven *Umbravirus* species have been described so far, each associating with a different *Luteovirus* (Robinson and Murant, 1999). The system has the following characteristics: (i) both the *Umbravirus* and its *Luteovirus* helper are non-propagative; (ii) the *Umbravirus* is mechanically transmitted via sap, but the helper *Luteovirus* is not; (iii) aphids can only transmit the *Umbravirus* if they acquire it from plants dually infected with both the *Umbravirus* and the helper *Luteovirus*; (iv) the *Umbravirus* is transmitted by the aphid only when its RNA is packaged in a protein shell comprising the helper virus protein (Harrison and Murant, 1984); and (v) the *Umbravirus* may be helped by several different luteoviruses.

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NANOVIRUSES. The minimum AAP is 15–30 min for *Faba bean necrotic yellows virus* (FBNYV) and 4 h for *Banana bunchy top virus* (BBTV) (Hu *et al*., 1996), with a 5–15 min IAP required for both viruses. Aphids retain the viruses throughout the aphid lifespan. Purified FBNYV is not transmitted by its vectors, which indicates that possibly a yet unidentified helper component is involved in the circulative transmission of this nanovirus. It has been shown that this regulates virus transport across the haemocoel–salivary gland interface (Franz *et al*., 1999). If that is the case, this would represent the first example of helper component-mediated transmission of a circulative virus (Franz *et al*., 1999; Blanc *et al*., 2014).

Propagative circulative transmission

Rhabdoviruses have a unique ability to propagate in the body of aphid vectors (Jackson *et al*., 1999). The requirement for long LPs and virus retention throughout vector life is indirect evidence for replication in aphids. Transovarial passage also occurs (see below) and is consistent with propagation in the insect. More direct evidence for virus replication has been obtained by continued transmission after repeated serial dilution passages from aphid to aphid (Sylvester *et al*., 1974; Sylvester and Richardson, 1981). It is assumed that the virus particles produced in aphid cells are released into the haemolymph, find their way to the salivary glands and finally are injected into the plant along with saliva. Bacilliform particles of *Sowthistle yellow vein virus* (SYVV) have been observed in the nucleus and cytoplasm of cells in the brain, suboesophageal ganglion, salivary glands, ovaries, fat body, mycetome and muscles of aphid vectors (Sylvester and Richardson, 1970), and the virus is assembled in the nucleus.

The aphid gut appears to be a potential barrier to transmission because bypassing it by injection of the virus into the haemolymph increases transmission efficiency and often allows transmission by non-vector aphid species (Sylvester and Richardson, 1992). Conversely, *M. euphorbiae* (potato aphid) remained an inefficient vector of SYVV when the virus was acquired via experimental injection into the haemolymph, indicating that additional factors (other than a gut barrier) constrained transmission in this case (Behncken, 1973).

As with non-propagative viruses, the acquisition and inoculation efficiency of propagative viruses increases when the plant access periods (AIP and IAP) are increased. Usually, they have much longer mean LPs (latent periods of >1 week) than non-propagative viruses (1 or 2 days), and LP may be affected by temperature (Hull, 2002). Plant rhabdoviruses are not normally transmitted from parent vectors to their offspring (Redinbaugh and Hogenhout, 2005): only about 1% of the offspring of viruliferous *Hyperomyzus lactucae* (black currant–sowthistle aphid) were able to transmit SYVV (Sylvester and Richardson, 1971; Sylvester and McClain, 1978). Plant rhabdoviruses usually do not cause disease in their insect vectors (Redinbaugh and Hogenhout, 2005), but serial transmission of some SYVV isolates from aphid to aphid (by haemolymph injection) was associated with increased aphid mortality (Sylvester, 1973). However, as infected aphids lived beyond the period of maximum reproduction, the intrinsic rate of population growth was little affected (Sylvester, 1973).

Epidemiology

Patterns of spread of aphid-borne viruses depend on interactions between the virus, its host plant(s), the aphid vector(s), the environmental conditions and the cultural practices undertaken by the growers. Epidemiological aspects have been reviewed many times, including by Harrison (1981), Maramorosch and Harris (1981), Raccah (1986), Nault (1997), Burgess *et al*. (1999), Dewar and Smith (1999), Lecoq (1999), Robert (1999), Robert and Lemaire (1999), Ragsdale *et al*. (2001) and Fereres and Raccah (2015). Evaluation and knowledge of the impact of various factors, discussed below, on the epidemiology of a specific virus allows the design of the most effective control measures against that virus (Madden *et al*., 1987; Jones, 2001, 2004; for reviews see Chapter 9 in Smith and Barker, 1999).

Biological factors

Virus

HOST RANGE AND SURVIVAL IN NATURE (VIRUS SOURCES). Viruses differ in their host range and this may affect their spread. For example, more than 1000 host species, both cultivated and non-cultivated, are susceptible to CMV, whereas *Leek yellow stripe virus* (LYSV) infects a very limited number of species. The presence of virus sources is usually a prerequisite for the appearance and spread

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of viral disease in a specific area, although aphids are able to carry viruses, even non-persistent ones (see MDMV example above), over long distances and provide new infection sources. Infection of a crop by a specific virus may originate from:

1. *Infected seed* – seed transmission plays an important role in the epidemiology of non-persistently transmitted virus species that belong to the *Potyvirus*, *Cucumovirus* and *Alfamovirus* genera (Brunt *et al*., 1996).

2. *Perpetuating sources (tubers, groundkeepers and volunteer plants)* – infected propagules play an important role in the epidemiology of viruses with a narrow host range, such as *Onion yellow dwarf virus* (OYDV), LYSV in different *Allium* species (Dovas *et al*., 2001), PLRV and PVY in potato (Robert *et al*., 2000) and fruit tree viruses (Garsney and Lee, 1987; Thresh, 1988). Groundkeepers left behind after the harvest, and fodder beet or mangold clamps kept too long, are important reservoirs of *Beet mild yellowing virus* (BMYV) (Smith, 1986). Volunteer potato plants are potential sources for all potato viruses (Wright and Bishop, 1981; Thomas, 1983; Robert *et al*., 2000) and for *Carrot virus Y* (CtVY) (Jones *et al*., 2005).

3. *Other susceptible crops in the vicinity* – nearby sugar beet crops, for example, are important sources of aphid-borne beet viruses (Peters, 1988; Dewar and Smith, 1999; Dusi, 1999), and potato crops act as sources of all aphid-borne potato viruses (Chapter 29, this volume) and of PVY for other solanaceous crops such as tobacco, pepper and tomato (Chatzivassiliou *et al*., 2004). In many countries, vegetable crops are grown successively in the field, and in these cases the older crops can act as major virus reservoirs. Overlapping or successive crops play important roles in the epidemiology of viruses that are not seed-borne and have a narrow host range such as OYDV, where overlapping of onion and shallot crops results in serious epidemics (Chamberlain and Bayliss, 1948; van Dijk, 1993).

4. *Weeds of arable crops* – weeds are implicated in the ecology and epidemiology of most aphid-borne viruses (Duffus, 1971; Adlerz, 1981; Chapter 29, this volume) as they may be hosts of both the virus and the aphid vectors, and in many cases are the most important overwintering or summer hosts. Their importance is related to the mode of virus transmission by aphids. They play a crucial role in the epidemiology of non-persistent viruses such as CMV (Quiot *et al*., 1979a,b; Fotopoulos *et al*., 2011), a virus with a wide host range, but are less important for PVY (Orsenigo and Zitter, 1971; Chatzivassiliou *et al*., 2004), which has a relatively narrow host range. They also act as serious sources of persistently transmitted viruses such as the BYDV/CYDV complex and the beet poleroviruses (Stevens *et al*., 1994; D'Arcy, 1995).

VIRUS MUTABILITY AND STRAIN SELECTION. New virus strains appear readily in nature, and this is the result of mutation and selective adaptation, heterologous encapsidation, pseudorecombination or genetic recombination due to direct interaction between strains of a virus or between different viruses in the host plant (Hull, 2002). Mutation has been the primary source of genetic variation in plant viruses, particularly RNA viruses (Garcia-Arenal *et al*., 2001). Viruses differ in their rate of mutation, with CMV showing high genetic diversity (Palukaitis and Garcia-Arenal, 2003), whereas others such as PLRV are more stable genetically (Hull, 2002). The new virus strains that appear in nature may differ in their host range, pathogenicity and transmissibility by their aphid vectors, characteristics that may affect their epidemiology.

The effect of environmental conditions on the diversity of plant viruses has not been studied extensively. However, temperature seems to be an important factor in strain selection, and CMV thermosensitive strains dominate in spring tomato and pepper crops in southern France, whereas thermoresistant strains are prevalent in the summer (Quiot *et al*., 1979b).

DISPERSAL. Field spread of aphid-borne viruses takes place in two phases. Primary infections are brought into the field by either winged aphids and/or infected seed. Secondary infections within the field may then result from alatae moving locally and/or apterae walking from plant to plant, especially when they are in contact. Frequently, the spread of non- and semi-persistent viruses is by alatae on their host-selection flights, whereas only colonizing aphid species contribute to the spread of persistent viruses. The rate and pattern of spread of an aphid-borne virus within a specific field depends on many factors, including: the source and the amount of inoculum; its relationship (whether non-persistent, semi-persistent or persistent) with the aphid vectors; the time at which the aphids appear in relation to the host's age; and weather

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conditions, which affect both aphid biology and host physiology.

In early studies, attempts were made to relate aphid populations to virus spread by counting aphids on host plants (Doncaster and Gregory, 1948), but more recently, different types of trap have been used to assess the number of flying aphids (see Irwin and Ruesink, 1986; Chapter 16, this volume). However, in order to understand virus epidemiology, it is necessary to know the number of infective aphids that will visit the crop, and this can be done either by using sensitive detection techniques (Chapter 16, this volume) or by placing trapped aphids on to indicator plants (Harrington *et al*., 1986). The 'infection pressure' to which a crop is exposed can be assessed by exposing indicator plants for successive periods in the field (van Hoof, 1977).

Virus spread over long distances can be the result of either human activities moving infected propagative material (potato, fruit trees) and/or the movement of aphid vectors, especially in the case of persistent viruses (Thresh, 1983) such as BYDV, which moves into northern USA and Canada during the spring migration of aphids in jet streams from southern states (Irwin and Thresh, 1988).

Cultural practices

Cultural practices such as planting date, crop rotation, field size and other characteristics, plant population density and plant size may have pronounced effects on the dispersal of aphid-borne viruses (Thresh, 1982a). Planting date in relation to the build-up of aphid populations affects the spread of aphid-borne viruses such as BYDV (Wyatt *et al*., 1988; Foster *et al*., 2004) and potato viruses (Ragsdale *et al*., 2001). Crop rotation may also affect the incidence of viruses that overwinter in weeds and/or volunteer plants, as in the case of potato viruses (Doncaster and Gregory, 1948). The effect of field size and other physical characteristics of the field on viruses and their vectors is little studied and is probably complex, although persistent viruses have been reported as more common in larger fields and non-persistent viruses in smaller ones (Watson, 1967). This may be due to the greater perimeter/area ratio in small fields and the exposure of plants around the margin to greater risk from vectors introducing virus from adjacent sources (Vanderplank, 1948). However, Foster *et al*. (2004), who studied BYDV incidence in 623 untreated autumn-sown cereal crops in the UK in relation to a wide range of field characteristics, reported aphid and virus incidence to be greatest in fields of 2–9 ha and lower in both smaller and larger fields. They also found a virus strain-dependent effect of field aspect, and more virus in crops near the coast and in areas with little arable land, the latter probably because it was associated with an increased area of grassland, which could act as a reservoir of the virus and aphids at times when crops were absent or unsuitable. Crop spacing and plant size may also affect the landing behaviour and response of migrating aphids, and therefore the incidence of the viruses they carry. Heathcote (1974) noted that the incidence of viruses causing yellowing symptoms in sugar beet was higher in low-density crops. Similarly, large cauliflower plants in seedbeds become infected more readily with insect-borne viruses than do small ones, because they are visited more often by aphid vectors (Broadbent, 1957).

Weather

Air temperature, rainfall and wind are key weather components in aphid-borne pathosystems. Air temperature is particularly influential, as it has marked effects on the rate of development and activity of aphid vectors and the phenology of the virus hosts (either cultivated or arable weeds and wild hosts). Potentially, virus diseases such as BYDV could increase with a changing future climate (Trebicki *et al*., 2015).

Cool conditions do not favour the flights of aphids, and very high temperatures may reduce aphid populations and the incidence of the viruses they are vectoring. Temperature also affects the transmission efficiency of aphid-borne viruses (see above). Heavy rainfall may reduce the aphid population, with consequences for virus spread (Wallin and Loonan, 1971). Wind also affects virus incidence, as winged aphids do not fly when wind speed is too high and flight direction is affected by the prevailing wind. MDMV epidemics in the USA were favoured by low-level jet winds and resulted in the rapid transport of the virus from southern areas north to Minnesota (Zeyen *et al*., 1987).

Disease Forecasting

Various virus forecasting systems and warning schemes have been developed. For further details, see Chapters 16 and 17, this volume.

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Disease Management Strategies

The direct control of viral diseases is not possible. Control is based on preventative measures, and virus–vector relations are of major importance in determining the best strategies. As already mentioned, cropping practices play an important role in virus spread, and their manipulation is often used to achieve some degree of control (Zitter and Simons, 1980). However, the control of viruses, particularly those transmitted in a non-persistent manner, has proved to be difficult to accomplish by chemical control of aphids, as insecticides usually do not act quickly enough to stop transmission (Rains and Christensen, 1983; Jayasena and Randles, 1985; Collar *et al*., 1995). In general, preventative measures aim at reducing virus sources (virus-free propagative material, weed control, etc.) and also at reducing and/or avoiding aphid-vector populations. Conventional breeding has also been effective in successfully combatting a number of aphid-borne virus diseases of potato, tobacco, etc. (Valkonen, 1994). In addition, introducing genes for virus resistance into existing crop varieties may produce transgenic crop plants resistant to viruses. Genes derived from the viruses themselves, in a concept referred to as 'pathogen-derived resistance', have been used for this purpose (Beachy, 1993, 1997; Fitchen and Beachy, 1993; Barker and Waterhouse, 1998; Kaniewski and Lawson, 1998; Berger and German, 2001; Hull, 2002). Below, we describe conventional preventative measures for the control of aphid-borne viruses. Effective control should be based on the integration of different control measures, as in most virus–host systems, the adoption of only one method is usually insufficient (Jones, 2001).

Use of genotypes resistant to the virus and/or to the aphid vectors

The use of resistant cultivars has been an attractive, effective and environmentally friendly way of combatting viral diseases (Hammond, 1998), particularly those caused by non-persistent viruses (Walker *et al*., 1982), as these viruses are more difficult to control by other means. In potato, there are two main types of resistance to PVY (for a review, see Karazev and Gray, 2013), either through a hypersensitive response mediated by *N* resistance genes (such as *Ny*, *Nc*, *Nz*; Gebhardt and Valkonen, 2001) or extreme resistance mediated by *Ry* genes (Valkonen *et al*., 1996) conferring immunity and complete failure to replicate. However, due to the relatively high level of recombinant viruses that are now found in most potato-growing areas worldwide, the impact of *N* genes on PVY control is very limited. Indeed, while present in a number of widely grown potato cultivars, *N* genes provide only partial resistance against certain PVY strains, such as PVY^{C} and PVY^{O}, but not against many new recombinant PVY^{NTN} strains and variants (Karasev and Gray, 2013). On the other hand, *Ry* genes such as Ry_{sto} and Ry_{chc} have been shown still to provide strong resistance to most of the PVY strains and isolates identified so far. However, many Ry_{sto} cultivars display cytoplasmic male sterility caused by mitochondrial genome derived from the parent *Solanum stoloniferum* (Lössl *et al*., 2000), thus limiting their deployment.

Resistance to CMV and *Papaya ringspot virus* (PRSV) has been incorporated into commercial melon cultivars, and resistance to potato viruses has been incorporated into potato (Berger and German, 2001; Brown and Corsini, 2001; Solomon-Blackburn and Barker, 2001). Genotypes resistant to seed transmission (Khetarpal and Maury, 1987; Wang *et al*., 1993) have been selected and used for the control of *Soybean mosaic virus* (SMV) and LMV in soybean and lettuce, respectively.

Breeding for resistance to the aphid vector(s) may be effective (Chapter 22, this volume), particularly if there is only one or a few vector species involved in the transmission of several viruses of a given crop. If the aphid vectors are also serious crop pests in their own right, then resistance is of double benefit. Host resistance to aphids has been studied extensively and exploited in different plant–aphid systems such as cowpea, cucurbits, maize, *Solanum berthaultii*, tobacco, peach and tomato (Kennedy, 1976; Gibson and Plumb, 1977; Jones, 1987).

Although resistance to one or a few aphid species may not prevent the transmission of non-persistent viruses, since non-colonizing aphids also transmit them, this can be an important component in an integrated control programme. For example, muskmelon (*Cucurbita pepo*) genotypes resistant to *A. gossypii*, an efficient vector of PRSV, *Watermelon mosaic virus* (WMV) and ZYMV, show resistance to these viruses when *A. gossypii* is their main vector (Lecoq *et al*., 1980; Risser *et al*., 1981). However, the plants are not protected against these viruses if other aphid vectors are also involved. Some peach

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selections resistant to *M. persicae* and *Myzus varians* (cigar-rolling peach aphid) are also resistant to *Plum pox virus* (PPV) transmission by these species (Massonie and Maison, 1980; Maison and Massonie, 1982; Massonie *et al*., 1982), and this resistance can be useful under field conditions if these aphid species are the only species involved in PPV epidemiology, a rather unusual situation. However, in some crops such as lupins, resistance to aphids also confers field resistance to the viruses they transmit (Wilcoxson and Peterson, 1960; Jones, 1979, 1987; Gray *et al*., 1986).

While the use of resistant cultivars to control aphid vectors offers great opportunities as a chemical-free control measure of pests in pathogens, there are potentially some limitations. In tomato, a single dominant resistance gene, *Mi-1.2*, confers race-specific resistance against certain phloem-feeding herbivores including aphids (*M. euphorbiae*), whiteflies (*Bemisia tabaci*), psyllids (*Bactericera cockerelli*) and root-knot nematodes (*Meloidogyne* spp.) (Milligan *et al*., 1998; Rossi *et al*., 1998; Nombela *et al*., 2001; Casteel *et al*., 2006). All of these pests feed on phloem sap, and studies indicate that resistance acts mainly by inhibiting the establishment of a feeding site in the vascular tissue of the plant (Kaloshian *et al*., 2000). This suggests that *Mi-1.2* may protect only against phloem-feeding organisms; however, more recent studies indicate that Mi-mediated resistance displays a deterrent action to herbivores prior to phloem sap ingestion (Jiang *et al*., 2001; Pallipparambil *et al*., 2010). Recent studies have highlighted non-target effects on beneficial organisms such as the phytophagous predator *Orius insidiosus* displaying lower survival rates in *Mi-1.2* background (Pallipparambil *et al*., 2014). This suggests that the ecological impact of *Mi-1.2*-mediated host resistance can be broader than expected and requires study under field conditions.

Elimination of virus sources (see also Chapter 29, this volume)

Use of virus-free seed and vegetative propagative material through seed certification programmes

Seed transmission provides early within-crop foci of infection from which subsequent secondary spread by aphids can occur early in the growing season, when the crop plants are more susceptible to virus infection. A number of non-persistently transmitted viruses such as LMV, BYMV and *Bean common mosaic virus* (BCMV) are transmitted by seed. The use of virus-free lettuce seed minimized both LMV dissemination and virus-induced yield losses in California and the UK (Grogan *et al*., 1952; Tomlinson, 1962; Grogan, 1980). Seed certification programmes have also been the fundamental management tools for the control of tuber-borne potato viruses (Hall, 1993; Slack, 1993; Slack and Singh, 1998).

Weed control

Weeds serve as both virus reservoirs and hosts for their insect vectors (Duffus, 1971; Bos, 1981; Thresh, 1982b). Weed removal and/or destruction can contribute to the prevention or elimination of crop infection by the virus(es) they harbour, if they are important sources of primary infection. However, weed control may be expensive and will only stop short-range spread, such as in that of the non-persistent viruses CMV (Rist and Lorbeer, 1989) and *Celery mosaic virus* (CeMV), and PVY in celery and pepper crops, respectively (Orsenigo and Zitter, 1971).

Roguing of diseased crop plants

The eradication of infected plants is a long-established method of controlling the spread of many virus diseases (Thresh, 1988). The approach has been applied more widely, and with more success, in woody perennial crops, but has also been effective in some annual herbaceous crops. In general, roguing should begin as soon as symptoms appear, and in potato is easier to accomplish before the aphids arrive and the canopy closes (Woodford and Gordon, 1990; Salazar, 1996).

Eradication of volunteer plants

Volunteer plants play an important role in the epidemiology of PVY and PLRV in potato crops (Robert, 1999), and also of PVY in tobacco and possibly other solanaceous crops in Greece (Chatzivassiliou *et al*., 2004). Therefore, the eradication of volunteer plants can reduce the spread of these viruses greatly.

Isolation from virus sources

The isolation of crops in time or space from virus sources might give a useful reduction in virus incidence. The production of virus-free seed potatoes is

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carried out frequently in areas isolated from ware potatoes (Ragsdale *et al*., 2001). A crop-free period may help reduce the incidence of viruses with limited host range, such as OYDV in onions (Chamberlain and Bayliss, 1948) and CtVY in carrots (Latham and Jones, 2004).

Prevention or reduction of virus spread

Plant spacing

The spread of plant viruses may also be affected by plant density, and this has been documented, for example, by Hull (1964) and A'Brook (1964, 1968) for groundnuts and rosette virus disease. A'Brook demonstrated that higher plant populations in groundnut crops decreased the incidence of rosette disease as well as aphid populations. However, high plant density was costly, and also decreased crop yield. It is recommended that the planting rate should achieve complete ground cover as soon as possible without reducing yield due to competition. Similarly, the incidence of BMYV and *Beet yellows virus* (BYV) in sugar beet was reduced when plants were closely spaced (Johnstone *et al*., 1982), whereas low plant density resulted in considerably higher incidence of BYMV in narrow-leaved lupin (*Lupinus angustifolius*) (Jones, 1993, 1994).

Control or avoidance of vectors

CHEMICAL CONTROL OF APHID VECTORS (SEE ALSO CHAPTER 18, THIS VOLUME). Insecticides reducing aphid populations may also prevent or reduce the spread of viruses they transmit (Loebenstein *et al*., 1964; Broadbent, 1969). However, vector control strategies are often associated with adverse effects on beneficials, aphid resistance, environmental pollution, recolonization of the crop and induction of vector movement, causing further virus spread (Irwin and Thresh, 1990). Field application of pyrethroids, which have a knock-down effect, can reduce PVY spread in potato crops (Gibson *et al*., 1982; Gibson, 1983; Gibson and Cayley, 1984) and the spread of a range of potyviruses in flower bulbs, provided that aphid populations are not resistant to the insecticides. However, in other cases, insecticides do not act quickly enough to stop the transmission of non-persistent viruses, and insecticides may actually increase vector activity and the incidence of potyviruses (Ferro *et al*., 1980). On the other hand, the spread of persistent viruses can be managed effectively by aphid control (Plumb and Johnstone, 1995; Perring *et al*., 1999; Mowry, 2005). Imidacloprid seed treatment reduced the incidence of yellowing viruses of sugar beet by 72%, but yield benefits were recorded only when virus incidence in untreated plots was above 10% (Dewar *et al*., 1996).

USE OF OIL SPRAYS. It has been known for more than 40 years that mineral oils can reduce PVY transmission substantially (Bradley *et al*., 1962). Field application has been used successfully for the control of many non-persistent viruses, especially in high-value ornamental bulb crops (lilies, hyacinths) and PVY in seed potato crops (Simons and Zitter, 1980; Simons, 1982; Kerlan *et al*., 1987; Chapter 29, this volume). Although mineral oils generally are considered effective in inhibiting the transmission of non-persistent viruses, they fail to control some non-persistent viruses such as MDMV in sweetcorn (Szatmari-Goodman and Nault, 1983), TuMV, BCMV and BYMV (Walkey and Dance, 1979). Oil applications do not reduce the transmission of persistent and semi-persistent viruses such as PEMV (Vanderveken, 1977), PLRV (Hein, 1971) and BYV (Walkey and Dance, 1979). Generally, their use for virus control is rather limited due to phytotoxicity, inadequate efficacy, volatility or viscosity, oil removal by rain and/or irrigation and non-covering of new vegetation (de Wijs, 1980). In a recent study, foliage spray of potato crops with mineral oil reduced PVY incidence by 43–58% (Kirchner *et al*., 2014). Combining insecticides with mineral oils has improved the control of non-persistently transmitted viruses such as MDMV, PVY and BtMV (Ferro *et al*., 1980; Gibson and Rice, 1986). The mechanisms involved in the protective action of oils are still a matter of debate. While some studies suggest that oils may impede the binding of the virus particle to the stylet (Bradley *et al*., 1962; Loebenstein *et al*., 1964; Powell, 1992; Boquel *et al*., 2013), mineral oil has also been shown to reduce virus replication and accumulation in inoculated plants, possibly due to a general activation of the defence mechanisms of the plant (Loebenstein *et al*., 1964; Peters and Lebbink, 1975; Martoub *et al*., 2010; Al-Daoud *et al*., 2014). The protective action of mineral oil varies greatly depending on the frequency and time of application, as mineral oil has been shown to be more effective on older plants in reducing PVY systemic movement in the plant (Al-Daoud *et al*., 2014). Other factors such as high level of vector pressure and level of

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susceptibility to viruses in potato cultivars might affect oil efficacy (Steinger *et al*., 2014).

BIOLOGICAL CONTROL OF APHID VECTORS. Although biological control has been used as an alternative strategy for aphid control, the effect on virus spread has not been well documented. Parasitoids are thought to have little effect on virus transmission and spread (e.g. Carter and Harrington, 1991). Parasitization of *S. avenae* by *Aphidius ervi* did not obstruct BYDV transmission, and in some experiments, parasitized aphids were more efficient vectors (Christiansen-Weniger *et al*., 1998). Parasitism may also cause increased aphid movement (Höller, 1991) and perhaps exacerbate virus spread in the field (Weber *et al*., 1996). Fewer plants were infected with BYDV by *R. padi* when the parasitoid *Aphidius rhopalosiphi* was present, whereas more plants were infected in the presence of the predator *Coccinella septempuncata* (7-spot ladybird) (Smyrnioudis *et al*., 2001a). In South America, the introduction and establishment of several coccinellid predators and aphelinid and aphidiid parasitoids decreased BYDV transmission in the field (Zuniga, 1990). Further work is needed to clarify the role of beneficials in the epidemiology of aphid-borne viruses in different virus-host systems.

SOIL COVERAGE BY USING COLOURED OR REFLECTIVE MULCHES (SEE ALSO CHAPTER 21, THIS VOLUME). Aphids, like most insects, respond preferentially to certain wavelengths of light. Alatae are attracted initially to short wavelength light and therefore show a dispersive phase of flight behaviour (Chapter 10, this volume). Their responses subsequently change and they are attracted to yellow and green wavelengths, searching for a suitable host (Moericke, 1950; Kennedy, 1960; Johnson, 1969; Chapter 10, this volume). This aphid behaviour led Smith *et al*. (1964) to investigate the possibility of using different reflective mulches in order to deter winged aphids from landing on virus-susceptible crops. Coloured or reflective mulches consisting of aluminium foil, or aluminium-coated paper, polythene or straw have been used with some success to reduce the incidence of non-persistent viruses such as WMV in cucurbits (McLean *et al*., 1982), *Pea seed-borne mosaic virus* (PSbMV) in broad bean (Tachibana, 1981) and BYMV in narrow-leaved lupin crops (Jones, 1991). Straw mulch has also been used to reduce aphid infestation and the incidence of non-persistent viruses in several crops (Heimbach *et al*., 2002; Jones, 2004). Straw mulch has been shown consistently to affect PVY transmission, resulting in 50–70% reduction of PVY in comparison to untreated crops over a 3-year period (Kirchner *et al*., 2014). Although mulching is more effective in controlling non-persistent viruses than others, it also delayed the spread of CABYV, a persistent virus (Lecoq, 1999). More recently, the use of UV-absorbing covers has limited the impact of CMV and LMV, as the covers have been found to interfere with host finding by aphids, thereby decreasing virus transmission (Legarrea *et al*., 2012).

The use of coloured or reflective mulches has limitations. Their effectiveness is reduced as the crop plants grow and cover the mulches. Placement and removal increase the cost of the crop, and mulches are ineffective in cloudy weather. Therefore, the practice is only economically justifiable in high-value crops or germplasm collections (Loebenstein and Raccah, 1980; Zitter and Simons, 1980; Jones, 1991), and even in these cases, only as part of an integrated control programme (Lecoq and Pitrat, 1983; Jones, 1991).

BARRIER CROPS AND INTERCROPPING. The use of barriers of immune plants surrounding virus-susceptible crops is another cultural practice to reduce/eliminate the spread of non-persistent viruses (Broadbent, 1952; Jenkinson, 1955; Simons, 1957b; Fereres, 2000; Jones, 2005). Different host plants such as sunflower, barley, wheat, maize, okra (*Abelmoschus esculentus*), sorghum, cotton, oats, pot marigold (*Calendula officinalis*), potato and kale have been used as barrier crops (Fereres, 2000). More recently, the olfactory signals of border plants to deflect aphids away from commercial wheat crops have been investigated (Schröder *et al*., 2015). In Florida, a barrier of sunflower plants reduced the incidence of PVY in pepper crops (Simons, 1957b). Similarly, a wheat barrier protected muskmelon crops from non-persistent viruses in California (Toba *et al*., 1977). The effectiveness of this strategy depends on various factors such as the height of the host used as a barrier crop at the time of maximum risk of infection and the extent of competition between the barrier and the protected crop (Fereres, 2000). Barrier crops may act as a sink for non-persistent viruses by cleaning the mouthparts of the infective aphids that land on the barrier crop (Fereres, 2000), and hence reducing the aphids' ability to transmit the virus to the adjacent protected crop (Toba *et al*., 1977; Difonzo *et al*., 1996).

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In some cases, instead of having a barrier crop as a border, the immune crop is integrated into the susceptible crop, thus providing camouflage and impeding both aphid movement and virus spread, and possibly acting as a source of natural enemies of the aphid vectors (Thresh, 1982a).

MANIPULATION OF PLANTING DATES. As the spread of aphid-borne viruses is affected greatly by aphid population size, the avoidance of high populations, especially at the beginning of the growing season when the crop is more susceptible to virus infection, may decrease virus incidence. Early sowing reduces the incidence of groundnut rosette virus disease greatly (Naidu *et al*., 1998), whereas infection of autumn-sown cereal crops by BYDV can be avoided by delaying sowing (Plumb and Johnstone, 1995; Chapter 17, this volume).

CULTIVATION IN ISOLATED AREAS UNFAVOURABLE TO APHIDS. This practice has been used for the production of virus-free potato seed in areas with relatively cool and windy conditions during the growing season and where the relatively low aphid populations appear rather late in the growing season (Todd, 1961; de Bokx and van der Want, 1987; Hutton *et al*., 2015). Such climatic conditions do not favour the spread of aphid-borne potato viruses. In such areas, aphid populations are monitored during the cultivation period, and in years when an early aphid invasion is recorded, the entire potato crop is sprayed with a foliar desiccant in order to prevent tuber infection (de Bokx and van der Want, 1987).

Conclusions

Aphids have an extraordinary ability to transmit plant viruses. The virus–vector interactions vary widely from superficial binding with aphid cuticular surfaces associated with a rapid transmission cycle (non-persistent/non-circulative), to more long-term processes involving selective transport across gut and salivary gland membranes (persistent/circulative) and, in some cases, multiplication within the aphid (circulative/propagative). Since persistent viruses accumulate in accessory salivary glands, the link between their inoculation and salivation is very well established, but salivation seems also to provide a means of intracellular delivery of non-circulative viruses. The immediate injection of watery saliva into punctured cells is likely to allow aphids to subvert early defensive plant signalling processes. If aphids are able to use salivary components to manipulate plant physiology and suppress cellular defences, these changes may also benefit inoculated viruses by facilitating the successful establishment of infection. Understanding the molecular mechanisms regulating interactions between aphid salivary components, aphid-transmitted viruses and plant cell biology will be an important area for future research, as well as the use of novel remote-sensing technologies and precision agriculture methods (Jones, 2014) to monitor the population dynamics of aphids and ultimately control the viruses they spread.

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16 Monitoring and Forecasting[1]

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Introduction

This chapter covers the monitoring and forecasting of aphids: why, what, where, when and how? Attention to the first four questions is a prerequisite for proper consideration of the fifth.

Why Monitor and Forecast?

Within the context of aphids as crop pests, monitoring and forecasting are aimed ultimately at optimizing the nature, location and timing of control measures, although background research will be necessary ahead of that directly supporting the decision making of individual growers. For example, samples from traps involving attraction to colour could not be translated into sound advice without knowledge of how different species vary in their response to colour. Optimization of control measures involves economic and environmental considerations to varying degrees, depending on the nature of the problem and of the individual trying to solve it. For example, prophylactic use of chemicals may be more desirable for the control of aphids causing virus spread in seed potato crops, where there may be very low tolerance levels for the virus, and hence for the vectors, than for control of aphids causing direct feeding damage in a ware potato crop, where tolerance levels will be higher. A prophylactic approach may suit a wealthy, risk-averse grower with little concern for the environment or longer-term problems such as the build-up of insecticide resistance, whereas advice to reduce inputs may be adopted more readily by those at the other end of the wealth and environmental concern spectra. The degree to which monitoring and forecasting influence the grower community depends ultimately on the proven robustness of the method, and on political agendas that impact on the cost of control.

More recently, there has been interest in longer-term forecasting in order to assess the likely impacts of global environmental change. Here, instead of trying to predict the values of population variables a few days to months ahead on the basis of known, measured explanatory variables, the need is to predict mean population measures decades ahead on the basis of environmental change scenarios provided by experts in that field.

What Should be Monitored and Forecast?

Monitoring aphid abundance can lead directly to control decisions, provided that economic threshold levels in the crop and their relationship with the monitoring data are known. These thresholds and relationships vary according to a range of factors associated with, for example, location, weather, soil conditions, cultivar, aphid species and aphid genotype, and are therefore not known for the vast majority of situations. This limits the value of some monitoring programmes. However, in many cases, especially in seed crops where aphids are important as virus vectors, any aphid activity may be unacceptable during the susceptible stages of crop growth. Thus, as soon as aphids appear, control is necessary, and hence monitoring simply for presence can provide an immediate return. Where thresholds are used, it is important that they are biased towards ensuring that farmers are not told to take no action (e.g. spray) when action is necessary (i.e. avoid a 'type 2

[1] Material from the first edition of this chapter has been included, and the contribution of Manuel Plantegenest is gratefully acknowledged.

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error' or a 'false negative'). Such occurrences would lead to immediate mistrust of thresholds. 'False positives', leading to unnecessary spraying, are undesirable but less critical. Even without accurate knowledge of thresholds, long-term standardized monitoring programmes enable comparisons of abundance in current and past seasons, and thus demonstrate whether the current season is high compared to the mean or to specific years in which the species was known to have caused economic problems.

Forecasting and then monitoring the time of the start of aerial activity can prevent monitoring in the crop being undertaken too early or too late. Other aspects of phenology are also important in relation to control decisions, for example, the timing of population crashes in crops caused by mortality or emigration.

Most important pest aphids are ubiquitous at a national scale, occurring wherever the crop is present. Abundance, and hence the need for control, varies regionally and locally. However, the presence of aphids does vary at larger scales, and so monitoring changes in distribution are worthwhile in relation to predicting future arrivals in a country or in specific regions of larger countries.

As well as the distribution, abundance and phenology of aphids, it may be useful to monitor or predict certain aphid attributes such as whether they are carrying parasitoids or viruses, or are resistant to certain insecticides. It may also be useful to know the morph of the aphids, as, for example, winged gynoparae of heteroecious species feed on different host plants to winged virginoparae of the same species. As more is known about differences in the pest potential of different aphid clones, it is becoming more useful to understand the population structure at a subspecific level, and techniques are developing rapidly to achieve this (Chapters 1 and 3, this volume). For example, Dedryver *et al*. (2005) found different clones of *Sitobion avenae* (English grain aphid) to transmit a particular isolate of *Barley yellow dwarf virus* (BYDV) with efficiencies varying from 3.7–92.5%. There are many proven and suspected examples of different host-plant preferences within particular currently designated species (Chapters 1 and 3, this volume), meaning that not all individuals of a recognized species will necessarily pose the same threat to crops.

Where Should Monitoring and Forecasting be Done?

Monitoring and forecasting may be done at various spatial scales depending on objectives and available resources. Crop monitoring provides data that are of more local value than aerial monitoring but, because of the generally aggregated distribution patterns of aphids in crops, multiple samples are needed in single fields to assess the variance. With aerial monitoring, the higher above ground the sample is taken, the less will be the aggregation. As a result, the area for which the catch is representative will be greater, especially where there is little topographical variation, but samples will not take account of local variation between crops (Taylor, 1979).

When Should Monitoring and Forecasting be Done?

For most purposes relating to aphids as crop pests, aerial monitoring is of more value when aphids are entering crops than when leaving them. However, numbers leaving may give an indication of the potential risk to subsequent crops, especially when several crops are planted sequentially or the time gap between one crop becoming unsuitable and another emerging is short.

It is necessary to tailor crop-specific monitoring programmes to crop phenology. For example, new infections of BYDV are not thought to damage small grain cereal crops once these reach Zadoks growth stage 31 (Doodson and Saunders, 1970). As potato crops mature, the chance of newly acquired virus reaching the tubers is reduced and vectors become less important (Beemster, 1972; Sigvald, 1986).

In general, the greater the frequency of sampling, the better. Inevitably, costs dictate limitations.

How Can Aphids be Monitored and Forecast?

Monitoring

Table 16.1 lists a range of methods commonly used for sampling aphids, together with some of the major considerations when assessing their suitability for the intended purpose of the sampling programme. Some of these are pictured in Fig. 16.1. Heathcote (1972) gives additional detail on sampling, extraction and counting techniques for evaluating populations on plants, and Taylor and Palmer (1972) provide the same for aerial sampling. Taylor and Palmer (1972) give an account of factors relating to the physical properties of traps and to aphid behaviour that affect the interpretation of data from various aerial sampling systems.

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Table 16.1. Advantages and disadvantages of sampling methodologies.

Methodology	Advantages (+) and disadvantages (–)
Crop sampling	
In situ counts on plants	Measure absolute abundance per plant or plant part + Part of plant colonized can be recorded + Can monitor progress on individual plants + Suitable in a sequential sampling programme + Provide immediate results – Time-consuming in the field – Difficult and sometimes uncomfortable – Results will be weather dependent – Results will depend on observer efficiency – Cannot record non-colonizers adequately – Problem with inaccessible aphids (between leaves, on roots, etc.)
Destructive counts on plants	Measure absolute abundance per plant part + Part of plant colonized can be recorded if bagged separately + Quick in the field + Exhaustive – Time-consuming in the laboratory, although counting and identification can be postponed to a convenient time provided that plants are stored at 3°C or lower to prevent further aphid development
Vacuuming from plants	Measures absolute abundance per unit area + Quick in the field – Time-consuming in the laboratory, although counting and identification can be postponed to a convenient time – Tends to bias towards older/larger and winged aphids – Results will be weather dependent – Reliable quantification is difficult
Sweeping	Measures numbers per sweep + Quick in the field + Suitable for presence/absence sampling – Time-consuming in the laboratory, although counting and identification can be postponed to a convenient time – Results will be weather dependent – Appropriate quantification is virtually impossible, although it may be possible to compare different samples made under similar conditions in similar crop species – No use for tall plants – Only suitable for assessing presence/absence
Beating	+ Quick in field and laboratory – Results will be weather dependent – Quantification is not possible – Only suitable for assessing presence/absence
Aerial sampling	
Impaction traps	*Sample size depends on wind speed and shape of trap surface.* *Colour of the surface will affect the sample size in a species-specific manner*
Coloured water traps	Measure relative abundance and can be used to compare catches of a given species over space or time, assuming similar behaviour of different clones, but not to compare across species + Many individuals caught if yellow used – Species bias depending on colour preferences – Aphids cannot be collected alive – Reflections may affect alighting behaviour – May dry out in hot weather unless emptied regularly (overflowing in wet weather can be prevented by using mesh drains on the sides)

Continued

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Table 16.1. Continued.

Methodology	Advantages (+) and disadvantages (–)
Clear/plant-coloured water traps	Measure absolute numbers alighting per unit area + Sample should be representative of individuals landing in crop + Non-colonizing species can be recorded – Very few individuals caught compared to yellow traps – Reflections may affect alighting behaviour – Aphids cannot be collected alive
Sticky traps	Measure relative abundance + Can be vertical, horizontal, laminar or cylindrical – Dealing with samples is difficult – Samples may be in poor condition – Aphids cannot be collected alive
Sex pheromones	Measure relative local abundance of males + Can be used in conjunction with many of the above methods + Can select species – Synthetic pheromone is not available for many species
Filter traps	*These traps collect air and filter aphids from it*
Nets (pivoted or non-pivoted)	Measure relative abundance of different species flying at a given height + Aphids can easily be trapped alive and transferred immediately to plants to test for virus infectivity – The volume of air sampled depends on wind run, but can be controlled if vehicle mounted – Need constant attendance
Suction traps	Measure absolute abundance per unit volume of air + Constant, known volumes of air can be sampled + Efficiency is almost independent of wind speed + Aphids can be collected alive or dead + Samples can be divided automatically according to time – Require electricity – Sampling is usually at a single height Low-level traps sample aphids that are not randomly distributed Aphids are randomly distributed above about 10 m

This account is still essential reading prior to expenditure on resources for aerial sampling. Aphids are still generally identified by eye. However, automated methods of identifying flying insects are progressing rapidly.

It is possible, by using specialized entomological radars, to identify large individual insects to order, family and, occasionally, even species level (Chapman *et al*., 2010, 2011); smaller insects such as aphids can only be detected by radars when flying en masse, but even so, existing weather radar networks can play an important role in forecasting pest aphid invasions when combined with trapping information (Leskinen *et al*., 2011; Shamoun-Baranes *et al*., 2014).

In the laboratory, automated species identification involving, for example, immunological techniques or pattern analysis is currently impracticable when dealing with the large number of individuals sampled in most monitoring programmes, although Zhang *et al*. (2006) were able to count (but not identify) aphids from sticky yellow pan traps automatically with 94% accuracy using imaging technology. Perhaps the most significant recent advance is the ability to identify aphids, monitor the genetic structure of populations and screen individuals in this respect with ever-increasing speed (Chapter 3, this volume). The International Barcode of Life Project (Ratnasingham and Hebert, 2007, 2013) database includes more than 1200 aphid species (BOLD, 2016). Such molecular methods are particularly useful with respect to strategic research, but are still little used in more immediately applied programmes, except in relation to monitoring insecticide resistance status.

Here, we summarize, only briefly, techniques that have changed little since the reviews mentioned above and concentrate more on areas where subsequent progress has been evident.

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Fig. 16.1. Examples of methods for trapping flying aphids: (a) yellow water pan trap; (b) sticky wire trap; (c) 'mist net'; (d) suction trap. (Photographs courtesy of Rothamsted Research, UK.)

Monitoring in crops

Direct assessment of aphid densities in crops must be made by researchers attempting to determine economic control thresholds and by agronomists and growers wishing to apply them. The use of such thresholds is fraught with difficulties, and they provide, at best, rather crude guidelines. This is because they are inevitably based on work carried out under a limited set of conditions but applied under a much wider range of conditions. The aphid density at which control becomes justified is affected by biotic and abiotic factors, and by complex interactions between them. For example, susceptibility to damage will vary with crop growth stage, planting density, variety and environmental stress. Although quantifying these effects is not inherently difficult, it is very laborious and only a narrow range of each variable is usually considered in published thresholds. In general, younger plants are more susceptible than older plants to yield loss from aphids, including that caused by viruses. However, damage to product quality or appearance may occur at specific growth stages, depending on the product. For example, the milling quality of

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grain can be greatly affected by *S. avenae* feeding on the ears of cereal crops. Crop variety and density will affect susceptibility to damage and the degree of compensatory growth that occurs. Damage will also vary with aphid species. Assessors who have had little training can identify species that look very different, but often different species look very similar. For example, agronomists examining sugar beet crops in the UK for potential virus vectors are asked to look for 'green aphids', which may comprise *Myzus persicae* (peach–potato aphid), *Macrosiphum euphorbiae* (potato aphid), or *Aulacorthum solani* (glasshouse and potato aphid). It is also likely to be the case that there will be differences in the damage caused by different aphid genotypes, which cannot be identified during routine field counts. For example, different genotypes of *S. avenae* vary in their ability to transmit BYDV (Dedryver *et al.*, 2005). Weather conditions subsequent to sampling cannot be predicted easily, but may have a profound effect on the need for control and the ability to carry it out.

Strategies for making control decisions almost inevitably involve *in situ* sampling. They must take into account the spatial distribution of aphids. This varies with time, often quite rapidly, because of reproduction, movement of apterae, dispersal of alatae and mortality caused by, for example, weather and natural enemies. Knowledge of the form of the frequency distribution of aphid counts, or of the form of the relationship between the mean and its variance, enables sequential sampling programmes to be devised whereby sampling continues only until a preset probability that the threshold for control will, or will not, be exceeded is reached.

A classical statistical text on this topic is that of Binns *et al.* (2000). Robert *et al.* (1988) provide a good summary of the theory and practice of sequential sampling relating specifically to aphids. By this approach, determination of a summary statistic to describe spatial pattern only requires random sampling of aphids, and the statistic does not require the spatial coordinates of the data points. In contrast, Perry *et al.* (1999) devised a methodology for assessing the spatial distribution of organisms, which utilized two-dimensionally spatially referenced count data. Termed SADIE (Spatial Analysis of Distance Indices), the methodology takes direct account of behavioural mechanisms leading to distributions. It has been used, for example, to investigate the spatial distribution of *S. avenae* in winter wheat (Winder *et al.*, 1998) and of *Nasonovia ribisnigri* (currant–lettuce aphid) in lettuce (Diaz *et al.*, 2014). Such methods that describe spatial pattern help to inform choice of sampling scheme and thus provide considerable improvements in accuracy (Alexander *et al.*, 2005). They have the potential for use in precision spraying programmes, where only areas at particular risk are targeted.

Aerial monitoring

The methods listed in Table 16.1 for sampling flying aphids do not, on their own, provide any information on the distances flown by aphids. Indeed, it is still remarkably difficult to estimate this because most species of interest are very widespread and do not provide clues that help to distinguish between local and distant arrivals in trap samples (Loxdale *et al.*, 1993). Where discrete centres of aphid population are known, the distribution of migratory ranges of individuals can be estimated by trapping at different distances from the sources (Taylor *et al.*, 1979). Some evidence for long-distance migration has been obtained by placing traps a long way from the nearest possible host plants (e.g. Wiktelius, 1984), or by estimating trajectories of aphids using low-level jet streams modelling (Zhu *et al.*, 2006). Molecular techniques may enable the rate of spread of clones to be estimated and, in some cases, may hint at the origin of individuals (Chapters 3 and 10, this volume).

MONITORING NETWORKS. Several trap networks have been permanently or occasionally operated in order to monitor and forecast aphid flight dynamics. The most extensive involves aerial monitoring using 12.2 m suction traps (Macaulay *et al.*, 1988; Fig. 16.1d). In 2014, there were 58 such traps operating in Europe, Tunisia and South Africa, together with a network of 47 suction traps 7 m tall in eleven states of the USA (Bahlai *et al.*, 2014) and 32 suction traps 8.8 m tall in China (Zhang *et al.*, 2013). The distribution and use of suction traps is summarized in Fig. 16.2 and in NJF (2013). Most traps are emptied daily during the aphid season. For some, all aphids are identified to species, species group, or genus. At other sites, only a few species are identified.

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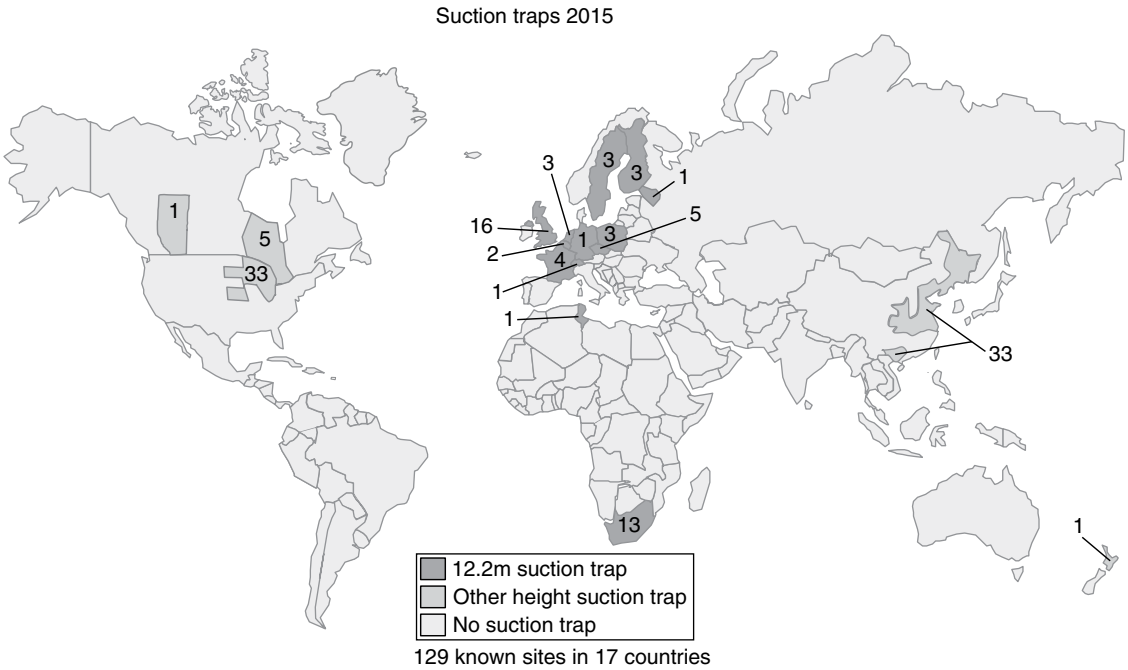

Fig. 16.2. Sites of suction traps, 2015.

The area represented by a trap varies according to topography, but Taylor (1974) found that there was an extremely strong correlation between the composition of samples in 12.2 m traps 80 km apart, and still a significant correlation in traps nearly 400 km apart. Cocu *et al*. (2005a) found the abundance of *M. persicae* in north-west Europe to be correlated between sites over distances up to 700 km. In agronomically and topographically homogeneous regions, the correlation between traps is linearly related to the distance between them (Hullé and Gamon, 1989). Halbert *et al*. (1998) showed that collections from the 7 m traps in Idaho reflected aphid activity within a 30-km radius of the traps.

The first trap began operating in 1964 in Europe and in 1983 in the USA. During the 1980s, the European Union (EU) sponsored meetings under the title 'EURAPHID', reports from which show the variety of uses to which the European trap data have been put (Taylor, 1981; Bernard, 1982; Cavalloro, 1987, 1989). However, the data were stored independently and in different formats by different individuals. In 2000, an EU Thematic Network ('EXAMINE') was set up in order to bring the data together in a single, integrated database to facilitate Europe-wide analyses (Harrington *et al*., 2004). In 2017, a new database, 'Paul', was launched. All data owners are encouraged to place their data on this database. Data can be downloaded via the Internet.

While suction traps can provide a regional picture of aphid activity and samples have been shown to be correlated with abundance in fields (Fabre *et al*., 2010), there will be much variability in aphid activity within a region according to local factors. In the UK, networks of yellow water pan traps have been used to provide complementary information relating to individual fields (Harrington *et al*., 2009; Northing, 2009).

Monitoring aphid attributes

MORPH. Aerial sampling, of course, deals only with winged aphids, whereas crop sampling can be used to gather information on winged and wingless aphids. Wingless aphids may be fundatrices, other virginoparae, males, oviparae, or sexuparae.

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The first four forms are generally easily distinguishable morphologically. Sexuparae are usually morphologically similar to virginoparae, but if trapped alive, may be distinguished on the basis of their morphologically distinctive offspring. Winged aphids may be virginoparae, gynoparae, or males. Males generally are easy to distinguish from the two female forms by their heavily pigmented genitalia. They are also often morphologically distinct from conspecific females in other ways. For example, they tend to have thinner abdomens and more rhinaria on their antennae. However, gynoparae and virginoparae are usually very difficult to distinguish morphologically. This is an important practical issue when, for example, monitoring *Rhopalosiphum padi* (bird cherry–oat aphid) in order to assess the risk of BYDV. While all three winged forms are capable of introducing the virus to an autumn-sown cereal crop, only the virginoparae will colonize the crop and produce offspring that may spread the virus. BYDV risk assessment programmes that use information on the aerial abundance of vectors thus require a quick, cheap and reliable method for distinguishing virginoparae from gynoparae in regions where both forms are known to be present. Morphometric analysis (Simon *et al*., 1991; Taylor *et al*., 1994) and microscopic observation of embryos (Hardie and Tatchell, 1989) are extremely time-consuming and impracticable as a routine when many aphids must be tested. Trapping aphids alive, offering them a choice of the primary or secondary host plant, and noting on which they reproduce (Tatchell and Parker, 1990), is also time-consuming and causes a delay in the provision of data on aphid morph. Lowles (1995) found that if embryos of *R. padi* were teased out into alcohol, those of gynoparae were yellow-green and those of virginoparae were red-brown (Fig. 16.3). This test is cheap, rapid and reliable, but requires living, or very recently killed, aphids and is not suitable for specimens stored in alcohol or for other species tested so far, including the closely related *Rhopalosiphum oxyacanthae* (apple–grass aphid).

More recently, molecular techniques have been developed to infer the reproductive mode of aphids from their genotypic profile. For example, allele sizes of seven microsatellite markers were linked to the reproductive mode and allowed sexual, asexual, male-producing and intermediate clones of *R. padi* to be separated (Halkett *et al*., 2005).

INSECTICIDE RESISTANCE. Routine monitoring of the insecticide resistance status of aphids can provide valuable information for control programmes involving insecticides (Chapter 19, this volume).

Molecular diagnostics are available for all known mutations conferring resistance in *M. persicae* and *S. avenae*, and these can be used with fresh specimens or with alcohol-stored specimens such as those from field or suction-trap samples (Harrington *et al*., 2014).

VIRUSES IN INDIVIDUAL APHIDS. Immunological techniques such as enzyme-linked immunosorbent assay

Fig. 16.3. Differentiating virginoparae and gynoparae of *Rhopalosiphum padi* using the test of Lowles (1995). The teased-out embryos of virginoparae (left) are reddish-brown and those of gynoparae (right) are greenish-yellow.

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(ELISA) for the detection of viruses in individual aphids have been largely superseded by molecular diagnostics, which are far more sensitive and quicker. They can be applied readily regardless of the transmission mode, whereas ELISA is rarely successful in detecting non-persistent viruses because of the very low virus titre. Singh *et al*. (1996) developed a duplex reverse transcription-polymerase chain reaction (RT-PCR) for detecting non-persistent viruses. Olmos *et al*. (1997) described a print capture (PC)-hemi-nested-PCR technique, which successfully detected a range of isolates of *Plum pox virus* (PPV) in *Aphis gossypii* (melon aphid or cotton aphid). Varveri (2000) used a combined immunological and molecular technique (PC-RT-PCR-ELISA) to detect *Potato virus Y* (PVY). Detection of the virus by this method closely matched the transmission efficiency of a parallel batch of aphids and was quick and reliable enough for routinely testing large numbers. Olmos *et al*. (2005) used a TaqMan® real-time RT-PCR to detect PPV. The sensitivity was 100 times greater than nested RT-PCR and 1000 times greater than ELISA and conventional RT-PCR. Saponari *et al*. (2008) used high-throughput Taqman® real-time RT-PCR to detect *Citrus tristeza virus* (CTV). Chen and Hu (2013) used the same technique to detect *Banana bunchy top virus* (BBTV). The method was highly sensitive, quantitative and took less than 2 h.

Nie *et al*. (2011) found that 50% propylene glycol, which was more suitable for use in aphid traps than ethanol because of its lower volatility, facilitated the detection of PVY in single *M. persicae* using RT-PCR as effectively as 70% ethanol, with no loss of detection efficiency after 10 days. Pelletier *et al*. (2012) used 50% propylene glycol successfully in yellow pan traps to test a range of non-colonizing aphids for their ability to acquire PVY, identifying many new potential vectors as a result.

The presence of a virus in an aphid does not necessarily mean that the aphid is capable of transmitting that virus (Plumb, 1989; Barker and Torrance, 1990; Smith *et al*., 1991). The only way to get round this problem, essential in epidemiological studies, is to revert to time-consuming bioassays, or to ensure that work has been done to relate numbers that are viruliferous to numbers that are infective so that an appropriate conversion can be made.

NATURAL ENEMIES IN APHIDS. Migrant aphids may host and therefore disseminate their own natural enemies such as fungal pathogens and parasitoids. The detection of parasitized winged aphids can be done by biological assays or with biochemical or molecular tools applied to dead aphids. In the first case, aphids have to be captured alive and reared until the appearance of mycosis or mummification (Feng *et al*., 2007; Chen *et al*., 2008). In the second case, aphids can be captured by standard monitoring programmes. By monitoring carboxylesterase activity and using previously described electrophoretic 'keys', Walton *et al*. (2011) identified the parasitoids *Aphidius ervi* and *Aphidius rhopalosiphi* in airborne alate *S. avenae*, captured by suction trapping in Hertfordshire, UK. Methods based on DNA barcoding were implemented to identify parasitoids within their aphid hosts. The 16S rRNA mitochondrial gene allows the detection and identification of immature stages of parasitoids as early as 24 h after egg injection by adult wasps (Derocles *et al*., 2012). This method was applied to decipher aphid–parasitoid interactions in cultivated and non-crop habitats (Derocles *et al*., 2014a) and to evaluate the contribution of long-range aphid flight to the dispersal of their parasitoids (Derocles *et al*., 2014b).

Forecasting

Aphid forecasting models are often based on aphid responses to environmental factors, in particular temperature, which drives aphid development. Two categories of forecasting tool have been developed. First, large data sets have been used to develop phenomenological models based on a statistical approach. Second, process-based simulation models have been produced by making use of accumulated scientific knowledge on the biology of the target species. Chapter 13, this volume, covers process-based models in the context of population dynamics theory, and so the current chapter will concentrate on phenomenological models. Phenomenological models are easy to build from a technical point of view, but require a huge data set. Many methods have been proposed for statistical approaches: single or multiple linear regressions, discriminant analysis, multivariate analysis and, more recently, Bayesian statistics and neural networks. Examples of phenomenological forecasting models are shown in Table 16.2 and some of them are described briefly below.

The most common approach is based on regression analysis, relating aspects of aphid phenology or abundance to environmental variables, often

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Table 16.2. Modelling approaches for aphid forecasting.

Methodology	Example
Phenomenological models	
Linear regression	Prediction of peak density Pierre and Dedryver (1984, 1985); Entwistle and Dixon (1986, 1987); Dedryver *et al*. (1987); Latteur and Oger (1987); Parker (1997); Thacker *et al*. (1997); Chattopadhyay *et al*. (2005) Prediction of migration phenology Turl (1980); Way *et al*. (1981); Wiktelius (1982); Thomas *et al*. (1983); Walters and Dewar (1986); Harrington *et al*. (1990); Worner *et al*. (1995); Rispe *et al*. (1998); Chattopadhyay *et al*. (2005); Hansen (2006)
Linear mixed model	Predicting impacts of environmental change on phenology Harrington *et al*. (2007) Forecasting of aphid-transmitted virus diseases Kirchner *et al*. (2011)
Logistic regression	Forecasting of aphid-transmitted virus diseases Fabre *et al*. (2003)
Artificial neural networks	Predicting impacts of environmental change on abundance Cocu *et al*. (2005b); Lankin-Vega *et al*. (2008)
Multivariate descriptive analysis	Study of patterns of flight phenology Hullé *et al*. (1994); Masterman *et al*. (1996)
Regression and discriminant analysis	Linking migration and colonization processes Klueken *et al*. (2009)
Time series analysis	Search for density-dependent effects Woiwod and Hanski (1992)
Bayesian statistics	Linking migration and colonization processes Vialatte *et al*. (2007); Fabre *et al*. (2010)
Combination of approaches	
Statistical + process-based model	Forecasting of aphid-transmitted virus diseases Northing *et al*. (2004)
Bayesian approach	Forecasting of aphid-transmitted virus diseases Fabre *et al*. (2006)

climatic. This implies that the predicted variable is a simple scalar variable and that the relationship between the predicted variable and the predictors is linear, or can be transformed to be linear. In order to have confidence in such models for forecasting, it is important that the statistical relationships between predicted and explanatory variables can be explained, at least in qualitative terms. If the model fails, it may be difficult to pinpoint why and hence revise it. For example, Pierre and Dedryver (1985) have shown that the regression model they developed from data collected in Brittany, France, was not able to predict accurately aphid densities in the Parisian basin, probably because of differences in the biology of the aphids and their natural enemies in the two areas. Similarly, multiple regression models developed by Hansen (2006) to predict the migration date of two cereal aphid species, *S. avenae* and *R. padi*, worked well in areas where both aphid species were entirely holocyclic. Worner *et al*. (1995) found similar disparities when using predictive sample reuse and day-degree methodologies to forecast the time of 50% migration of *Phorodon humuli* (damson–hop aphid) at two sites in the UK. Thacker *et al*. (1997) have also shown that, although linear regressions may describe the existing data well, they are not always good at predicting future patterns, especially when there is a large ratio of predictor variables to data points. However, as variables change, provided that the monitoring system is still operational, forecast equations can be updated to take account of the change.

More complex linear or non-linear patterns can be modelled by the use of alternative approaches such as artificial neural networks (ANN). For example Cocu *et al*. (2005b) explored the role of geographical, climatic and land-use factors on the phenology and spatial patterns of the aphid

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M. persicae at the European regional scale and showed that ANN was more accurate (better coefficient of determination) than multiple linear regression (MLR) to describe such relationships. Several methods (MLR, Jackknife) were also used to improve the prediction of ANN models of the number of *R. padi* during the autumn flight at Canterbury, New Zealand (Lankin-Vega *et al.*, 2008).

To be of potential value in statistical forecasting models, data must have been collected using a standardized methodology for a long period (for example, A'Brook (1983) considers 13 years insufficient). Twenty years is, perhaps, about the minimum period necessary to reduce adequately the probability that explanatory variables – in a year in which aphid populations are to be forecast – will be sufficiently outside the range used to construct the forecast as to render it unreliable. Unfortunately, there are very few aphid data sets that meet both these criteria of standardization and duration, the suction-trap networks being notable exceptions. Some short-term data have shown strong correlations, but these have not been tested over a long period. For example, the timing of peak aphid populations in potato crops has been related to temperature in January and February (Parker, 1997). Peak density of *S. avenae* on wheat has been related to aphid density and rate of increase (Entwistle and Dixon, 1986, 1987), to aphid density, percentage mummified and number of syrphids at flowering (Latteur and Oger, 1987), and to aphid density at ear emergence, temperature in February and number of rainy days in May (Pierre and Dedryver, 1984, 1985; Dedryver *et al.*, 1987). Thacker *et al.* (1997) used the same methodology to predict the summer population density of *Aphis fabae* (black bean aphid), *M. persicae* and *Acyrthosiphon pisum* (pea aphid).

One of the earliest successful uses of long-term aphid data in forecasting was for *A. fabae* on spring-sown field beans in southern England (Way *et al.*, 1981). The numbers of *A. fabae* in suction-trap samples in spring gave the most accurate estimate of the size and timing of crop infestation, but autumn trap samples, also numbers of eggs and fundatrigeniae on spindle trees (*Euonymus europaeus*), provided useful, though less accurate, earlier warnings. Egg counts have been used to forecast outbreaks of *R. padi* in areas where it is largely dependent on the egg stage for successful overwintering (Leather, 1983; Kurppa, 1989). The phenology of primary host-plant flowering and temperature have been shown to be correlated very strongly with the migration phenology of *P. humuli* in England (Worner *et al.*, 1995). However, the model used temperature right up to the migration event, so the prediction of migration phenology was not early enough to be useful in planning control programmes. Chattopadhyay *et al.* (2005) developed a model to predict the rapeseed crop age at which *Lipaphis pseudobrassicae* (mustard aphid) first appeared on the crop, the peak number of aphids and the crop age at peak number, all at least 1 week ahead of the first appearance of the pest on the crop. Such predictions allow growers to apply insecticides in a more timely and effective manner. Slightly less accurate predictions using temperature alone were used by Thomas *et al.* (1983) for the start and end of *P. humuli* migrations into hops far enough ahead to be used to recommend when control should begin and end, without the need for laborious crop inspection.

Strong relationships have been found between winter or early spring temperature and the timing and size of spring migrations of aphids, as recorded by suction traps, particularly for species that are largely anholocyclic in the region of interest (Turl, 1980; Wiktelius, 1982; Walters and Dewar, 1986; Harrington *et al.*, 1990; Fig. 16.4). Such relationships can be particularly useful on a regional basis in warning of the likely timing and abundance of aphids with respect to crop colonization.

Other statistical approaches have been used less frequently to produce phenomenological models, such as multivariate descriptive analysis for the study of global patterns of flight phenology (Hullé *et al.*, 1994; Masterman *et al.*, 1996) or time series analysis in search of density-dependent effects (Woiwod and Hanski, 1992).

Other models focus on migration and crop colonization by winged aphids alighting on crops. For example, binary response variables corresponding to thresholds of migrant cereal aphid abundance in autumn and spring were linked to suction-trap catches using discriminant analyses and cross-classification methods (Klueken *et al.*, 2009). These made it possible to forecast aphid migration in the short term and pointed out the role of wind speed on aphid flight behaviour. These models were more efficient at predicting low thresholds (days with more than one aphid) than high thresholds (days with more than 10 aphids). Other strong relationships have been found between the numbers of *S. avenae* in suction traps and the numbers alighting

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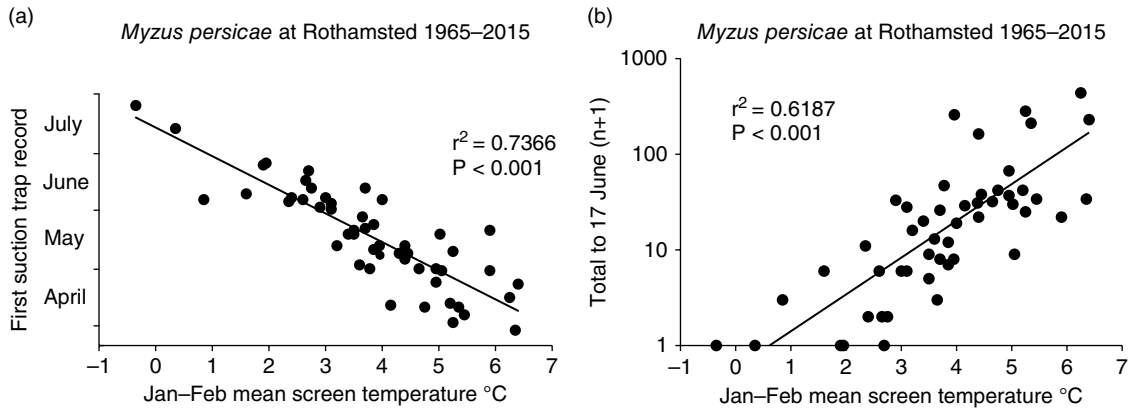

Fig. 16.4. Relationship between mean January and February temperature at Rothamsted, UK, and (a) time of first record and (b) abundance to 17 June of *Myzus persicae* in the Rothamsted suction trap.

on cereal crops in spring (Vialatte *et al*., 2007; Fig. 16.5), when one aphid caught by the suction trap corresponded to 0.25 aphids/m^2 colonizing the field. Genetic analysis of migrating and landing populations showed that this colonization rate was valid when long-distance migrating aphids were the only source colonizing crops. In some years, local populations flying at lower altitude (and therefore not sampled by suction traps) can also contribute to crop colonization. Bayesian models were developed to tackle the question of plant colonization at a larger spatial scale. For example, the model developed by Fabre *et al*. (2010) is detailed in Chapter 17, this volume. In this study, the deposition rate of *R. padi* flying during the autumn and landing on winter cereals (estimate of the number of aphids deposited per m^2 of crop for one individual caught in a suction trap) is shown to be correlated negatively to winter severity, ranging from 0.15 in eastern France, where holocycly is dominant, to 0.35 in western France, where anholocycly is dominant. This quantifies the fact that the pool of autumn *R. padi* migrants is a mixture of individuals migrating to bird cherry (*Prunus padus*) (holocycly) or to Poaceae (anholocycly).

Bayesian probability theory provides to ecology an accurate modelling structure to exploit diverse sources of information, to accommodate sources of uncertainty and to draw inference on large numbers of variables that describe complex relationships (Clark, 2005). While they have experienced significant growth in ecology, these methods have been little applied to forecasting aphid populations. For example, and in addition to the study cited above, they have been applied to the assessment of BYDV risk in cereal fields based on the population dynamics of its main vector in Western Europe, *R. padi* (Fabre *et al*., 2003, 2006), and to decipher the possible invasion route of *Myzus persicae nicotianae* (tobacco aphid) in South America (Zepeda-Paulo *et al*., 2010).

Uptake and outcomes

Numerous industry bulletins report results from monitoring and forecasting programmes, but there are few published assessments of their impact on farming practice. Examples of the thresholds used for aphids in different crops are given in the IPM Case Studies in Chapters 24–33, this volume. In the case of UK sugar beet, the whole crop is grown under contract to British Sugar plc, which employs agronomists to advise its growers. The agronomists are provided with preseason forecasts of the incidence of aphids and aphid-transmitted viruses causing sugar beet yellows (Qi *et al*., 2004). The forecasts are issued in early March (e.g. Stevens, 2016) and are based on the relationships between virus incidence and winter temperature, the timing and size of the spring aphid migration as recorded by suction traps, crop emergence date and the use of insecticides, including seed treatments (Qi *et al*., 2004). The widespread use of neonicotinoid-treated seed (99% in the UK in 2015) has reduced the crop area to which the forecasts are relevant, and even though it is now possible to provide forecasts by the middle of February, this cannot influence the amount of seed that is treated as, for

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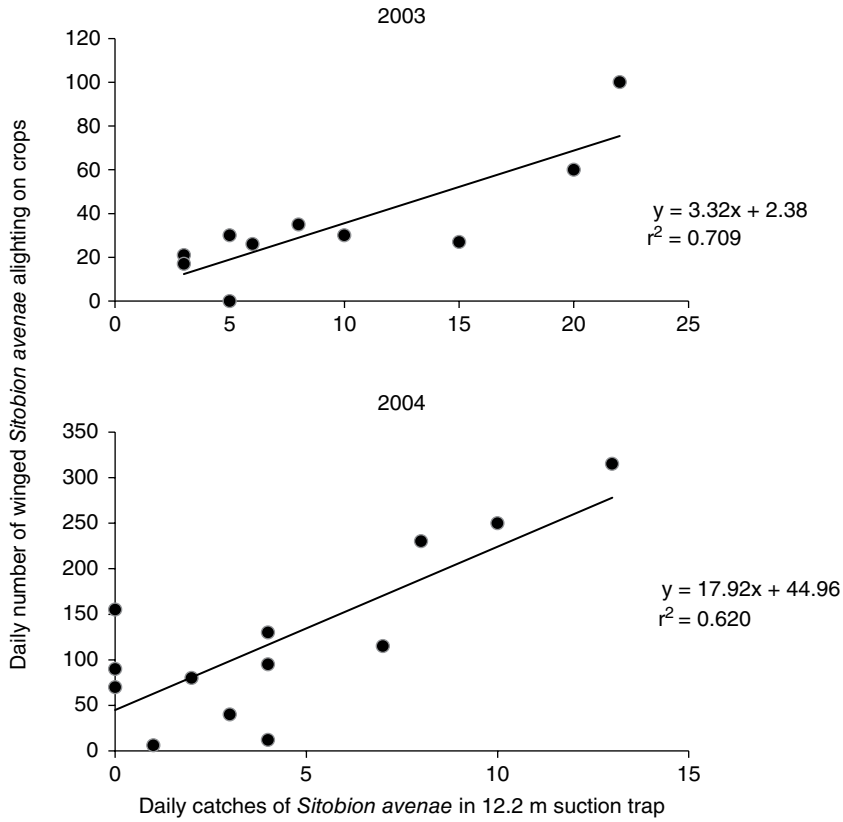

Fig. 16.5. Correlation between the number of winged *Sitobion avenae* caught each day in wheat fields (landings sampled on a total surface of 20m^2) and suction-trap catches (Brittany, France) on the same dates. (From Vialatte *et al*., 2007.)

practical reasons, the treatment process is completed by the previous November. The use of neonicotinoid-treated seed is only economically justifiable if virus incidence is expected to be at least 12% (Dewar *et al*., 2001). Running the model of Qi *et al*. (2004) assuming no seed treatment, shows that, with an average temperature of 4°C from January to mid-February, virus yellows incidence would remain well below the 12% threshold, even if only 25% of fields were treated. If resistance to neonicotinoids reaches the UK, or treated seed cannot be used for other reasons, the relevance of the forecast will once again be extremely high. The forecast is supplemented by season-long information on the incidence of vector aphids in suction traps and yellow pan water traps (Harrington *et al*., 2009; Stevens, 2016), their insecticide resistance status and the viruses they are carrying. This information helps growers who have not used treated seed to decide on the value of a spray programme. As a result of the information provided and the resulting action by growers, the incidence of virus was reduced by over 50% between 1984 and 1999, giving a net annual benefit of about 1.7% (worth approximately £5.5 million) (Dewar and Smith, 1999).

Other examples of the use of suction-trap data in crop protection include: an IPM programme for *R. padi* in Finland; assessing the risk from potato viruses in the Netherlands, Scotland, South Africa, Sweden and Tunisia; monitoring the aphid pests of soybean and cereals in China and monitoring the aphid pests of a wide range of crops in the Czech Republic (NJF, 2013); and monitoring *Aphis glycines* (soybean aphid) (North Central IPM Center, 2016).

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The system SOPRA has been developed as a forecasting tool in order to optimize the timing of monitoring, management and control measures of insect pests, including *Dysaphis plantaginea* (rosy apple aphid), in fruit orchards. Through a web interface, the simulation results are made available to consultants and growers (SOPRA, 2016). Phenology is directly linked to a detailed decision support system and to extended information about the pest insects, as well as to the registered plant protection products. Fourteen climatic regions cover all the fruit-growing areas of Switzerland. SOPRA is applied as a decision support system for fruit orchards on a local and regional scale in Switzerland and southern Germany (Samietz *et al*., 2015).

Forecasting the impacts of environmental changes

Statistical modelling approaches have been used to assess the potential impacts of environmental changes on aphid dynamics. These include simple linear regressions (Harrington *et al*., 1990) and linear and non-linear mixed-effects models (Harrington *et al*., 2007; Bell *et al*., 2015). These models, based on suction-trap data, suggest that most aphids are now flying earlier in the season than before as a result of climate change, especially those that are largely anholocyclic, although the rate that phenology is advancing varies with species, location and the model involved. Harrington *et al*. (2007) used data from a climate change scenario (HADCM3 A1F1) in a mixed-effects model and predicted that, over the next 50 years, the first appearance of 29 economically important aphid species in suction traps throughout Europe would occur on average 8 days earlier over the 50 years from 2000 to 2050. The results for *M. persicae* at Rothamsted, UK, are shown in Fig. 16.6. Total annual abundance of alatae has not changed greatly (Bell *et al*., 2015), although abundance in spring can be greater following warmer winters (Harrington *et al*., 1990). Van der Waals *et al*. (2013) used climate models to simulate past, and to predict future, climate in parts of South Africa and its effect on the relative development rates of *M. persicae* (and other pests and diseases) in potato. Pressure from *M. persicae* was predicted to increase up to 2050, and the results were used to suggest the impact of expected changes in potato planting times on viruses transmitted by *M. persicae*. The number of aphid species recorded from suction traps has increased in proportion to increasing temperature by 2–15 species per °C (Hullé *et al*., 2010).

It is not only the mean values of aphid population parameters that are of interest in predicting future pest issues but also the variance around those means and the stability of populations, as these will determine the frequency and intensity of outbreaks. Estay *et al*. (2012) used a combination of statistical and mathematical approaches to identify structural changes to the variance in the population dynamics, as seen in data from 11 UK suction traps, of *Elatobium abietinum* (green spruce aphid) and *Drepanosiphum platanoidis* (sycamore aphid). Thirteen out of 21 time series showed changes in variance, with increases in 11 of these cases. In the case of *D. platanoidis*, the change in variance was generally accompanied by an abrupt change in population stability, which was not the case to the same extent in *E. abietinum*. In both cases, an increase in outbreak frequency was predicted.

Manipulative experiments examining the potential impact of elevated CO_2 levels on aphid abundance have suggested a range of responses. Bezemer *et al*. (1999) found the complete range of responses (increase, decrease, no change) in *M. persicae* and *Brevicoryne brassicae* (cabbage aphid) depending on the aphid–host plant combination and duration of the experiments. They review the results of other work that, collectively, shows a great range of responses.

Newman (2005) produced a mechanistic model that predicted a decline in the abundance of *R. padi* in the face of increasing CO_2 emissions and attempted to explain the various responses of aphid species by considering their requirements for nitrogen and their density-dependent response in alata production.

The results described above illustrate that no one methodology is a panacea. The multivariate statistical approaches account implicitly for variability in all the relevant conditions experienced over the period of data collection, but involve extrapolation to new combinations of values for the variables. The manipulative experiments and the mechanistic model take account of only a very limited range of environmental and biological variation. All provide important pieces in a jigsaw that will take some time to complete.

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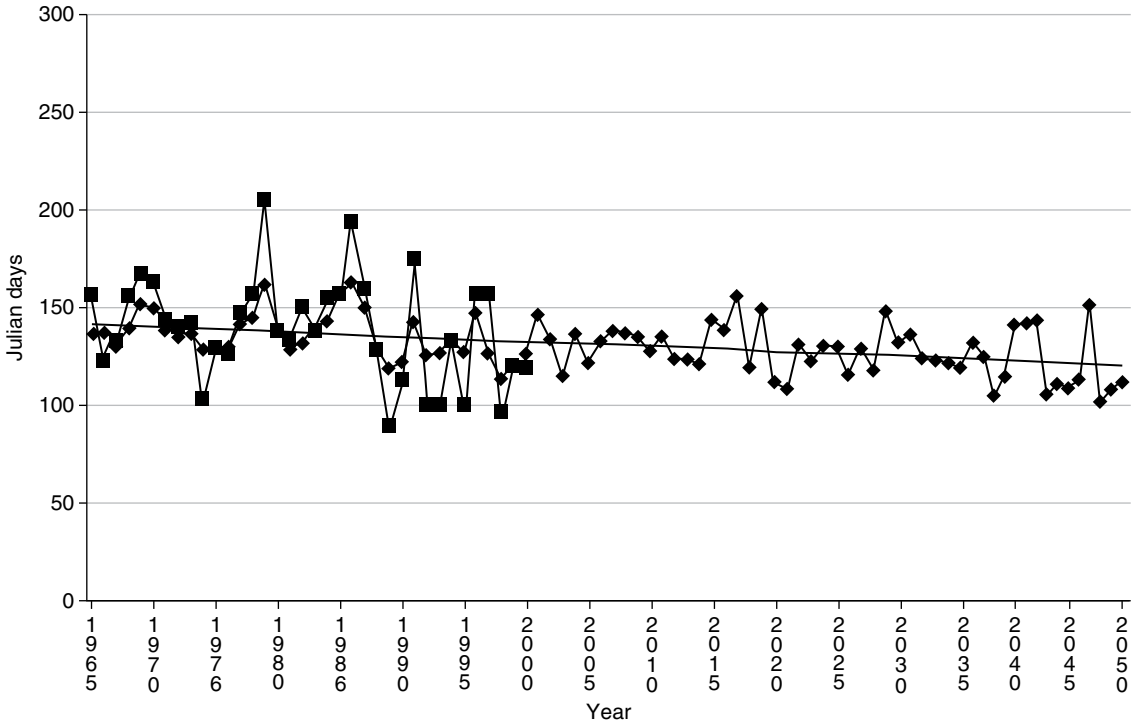

Fig. 16.6. Observed and predicted dates of first flight of *Myzus persicae* at Rothamsted and projected values on the basis of climate changes predicted by the HADCM3 A1F1 scenario. (From Harrington *et al*., 2007.)

Conclusions

Much effort, building on fundamental and strategic studies, has gone into monitoring and forecasting programmes dealing with various aphid and crop species around the world. For many reasons, few of these programmes have, as yet, had a sustained impact. This is sometimes because technology transfer has not been planned properly or implemented, or because the scientists involved in development have moved on to other problems, and resources for updating systems are not available. This is especially true in the case of process-based approaches, which are often used in specific short-term projects aimed at one problem and are rarely adequately validated to be of general use (Chapter 13, this volume). In the case of statistical approaches using data sets of adequate length, some stability is possible as a result of the wide range of strategic and applied applications to which the data can be put. This does not make such approaches inherently superior, and the desirability of complementary approaches is clear. However, the reality is that for any forecasting system to be adopted widely, it must be proven to have economic benefits over space and time. In relation to climate change issues, the importance of a long-term outlook is further emphasized.

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17 Decision Support Systems

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Introduction

Decision support systems (DSSs) can be defined as user-friendly systems which, through some combination of expert knowledge, simulation models and databases, provide support to decision makers (Knight, 1997). In plant protection, DSSs typically estimate the need for and the timing of one or several protection measures along the cropping season: they support tactical decisions with short-range objectives ('one season in a field'), most often when responsive (rather than preventive) tactics are available (Pedigo *et al*., 1986). DSSs bridge the gap between scientific knowledge and users making day-to-day management decisions. They help farmers to make the right decision, by interpreting complex biological information within an economical context, and by proposing simple choices.

Historically, aphids have contributed much to the theory underlying DSSs. The concept of economic injury level (EIL) defined as 'the lowest population density of a pest that will cause economic damage' was proposed by Stern *et al*. (1959) for the control of *Therioaphis trifolii maculata* (spotted alfalfa aphid). This is a key concept in reducing pesticide input and, as such, a key concept for integrated pest management (Pedigo and Higley, 1992). By explicitly linking pest dynamics, host responses to injury and the resultant economic losses, the EIL concept grounded (for now more than 50 years) decision making for pest control in a bioeconomical framework.

Aphids have several features that make them good subjects for DSSs. They cause quantitative and qualitative losses in most agricultural products, due to sap feeding and virus transmission (Tatchell, 1989; Wellings *et al*., 1989; Chapter 14, this volume). Several crop aphids can cause high direct losses, among them *Sitobion avenae* (English grain aphid) on wheat in Europe, *Schizaphis graminum* (greenbug) and *Diuraphis noxia* (Russian wheat aphid) on cereals in northern America, South Africa and central Asia, *Aphis fabae* (black bean aphid) on field beans in Europe and *Aphis gossypii* (cotton aphid) on cotton in Africa and the USA (see IPM Case Studies, this volume). Virus transmission by aphids on cereals (e.g. *Barley yellow dwarf virus* (BYDV)), beets (e.g. *Beet yellows virus* (BYV)), potatoes (e.g. *Potato virus Y* (PVY), *Potato leaf roll virus* (PLRV)), rape and turnips (e.g. *Cauliflower mosaic virus* (CaMV), *Turnip mosaic virus* (TuMV)) and most vegetable crops (e.g. *Cucumber mosaic virus* (CMV), *Zucchini yellow mosaic virus* (ZYMV), *Watermelon mosaic virus* (WMV) on cucurbits), frequently decreases yields around the world (Chapter 15, this volume). Importantly, outbreaks are often sporadic in time and space. For example, in western France, *S. avenae* have caused severe losses to wheat (more than 1000 kg/ha) only four times in 30 years (Dedryver *et al*., 2009). In the UK, *S. avenae* caused important damage to cereal crops about 1 year in 3 during the 1970s (Watt, 1983). Mastering aphid control ('Should I spray?' 'At which time?') is thus a hard task for farmers, as sporadic occurrence limits the opportunities for learning by experience.

The need for aphid DSSs is also reinforced, as for any pests and diseases, by laws reducing the number of pesticides authorized and their frequency of application (e.g. Pesticide framework in the EU, directive 2009/128/EC). Farmers must thus use fewer pesticides in a better way. Aphids still being

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controlled mostly by insecticides, the management action considered in this chapter is insecticide spray. However, DSSs could apply to any control measures such as cultural management practices, plant resistance or biological control that are increasingly available (Dedryver *et al*., 2010).

In this chapter, the steps involved in DSS development are first described by paying particular attention to the biological constraints specific to aphids, as well as to the methodological constraints specific to most DSSs. These points are then illustrated in the case of a recent aphid DSS. Next, existing aphid DSSs are reviewed. Finally, the long-standing questions of the adoption of DSSs by farmers and of their real impact for aphid management are tackled in the light of recent reviews of this topic (Gent *et al*., 2013; Shtienberg, 2013).

Making a DSS: the Biological Constraints of Dealing with Aphids

The development of DSSs is a straightforward perspective of the study and modelling of aphid population dynamics. Being grounded in a bioeconomical framework, DSSs require a basic understanding of the relationship between aphid densities and crop losses.

Forecasting aphid populations *ex nihilo* is impossible: it requires a sound knowledge of aphid biology and population dynamics (Chapter 13, this volume). Some major biological processes, such as ageing and birth as a function of temperature (Dean, 1974), are classically measured in controlled conditions. They can be incorporated into age-structured models of population dynamics using, for example, Von Foerster's partial differential equations (Plantegenest *et al*., 2001). However, switching from models built up from laboratory data to models suitable under field conditions is a further big step. It requires extensive field data sets to validate models properly. The validation of a DSS forecasting aphid outbreak in lupin crops was realized with a 14-year field data set from six sites in the Australian grainbelt (Thackray *et al*., 2004). In Sweden, Larsson (2005) used 161 fields experiments carried out from 1977 to 2002 to evaluate the relationship between *S. avenae* density and crop yield. The parameters of models of population dynamics can nowadays be estimated directly from field data sets, including possibly diverse types of sampling , thanks to modern statistical methods (e.g. mechanistic-statistical models). For example, the forecast of the colonization of barley fields by winged *Rhopalosiphum padi* (bird cherry–oat aphid) from suction-trap data (Fabre *et al*., 2010) relied on a hierarchical Bayesian model (a way to gain knowledge on hidden (i.e. unobserved) processes and to account explicitly for all sources of uncertainty in the data) but would not have been possible without a long-term survey of aphid dynamics over 13 years in 15 locations in several regions of France (Fig. 17.1).

Under field conditions, several important processes impacting aphid dynamics (e.g. predation by natural enemies, alatae dispersal) most often remain black boxes because their study is expensive and time-consuming (Plantegenest *et al*., 2001). If statistical methods allow, to some extent, to account properly for these sources of uncertainty, black boxes *de facto* limit model accuracy, and thus DSS adoption (see later in this chapter). Currently, these constraints are certainly the most important ones and are likely to remain so in the near future for modelling aphid dynamics.

A model of aphid injury is needed to take economically sound decisions from outputs of a population dynamics model. The relationship between aphid population dynamics and crop damage is complex, typically depending on aphid*plant*soil*climate interactions (Miles, 1989; Chapter 14, this volume). Despite this complex array of factors, statistical relationships sometimes capture simple 'damage functions' cumulating the effect of aphid densities due to sap feeding, but also to the effect of honeydew on CO_2 assimilation (Wellings *et al*., 1989), at successive crop growth stages (Rabbinge and Mantel, 1981; Rossing, 1991; Fig. 17.2). Although including viruses in the system makes it even more complex, similar relationships could also be derived as evidenced for the damage due to BYDV (Banks *et al*., 1995; Perry *et al*., 2000; Fabre *et al*., 2003). In any case, extensive data sets are required to characterize properly these relationships in a wide range of production situations.

Making an Aphid DSS: Some Basic Mathematical Constraints of Decision Making

Estimating the accuracy of DSSs and their associated financial benefits over existing practices is important for determining the likelihood of DSS adoption (e.g. Watt, 1983; Hughes *et al*., 1999; Fabre *et al*., 2007; McRoberts *et al*., 2011). We briefly describe here how the financial benefits provided by decision rules (DRs), a simple class of DSS giving binary advice ('Yes, a treatment is needed

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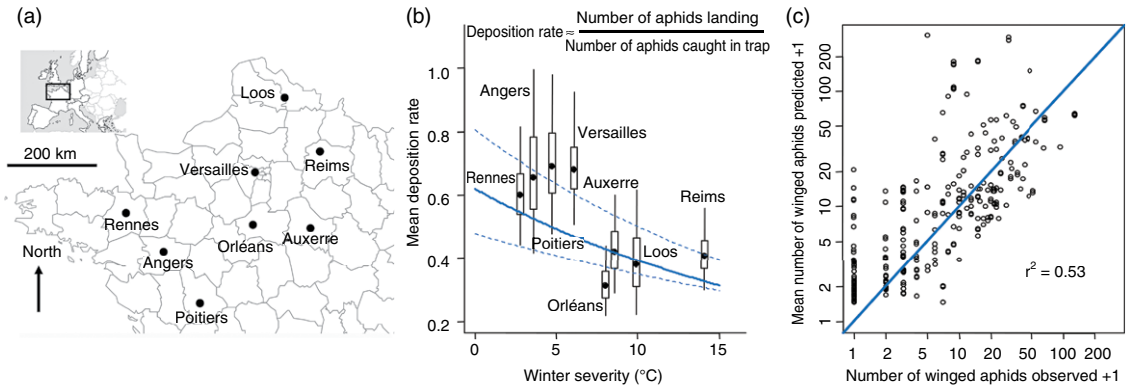

Fig. 17.1. Prediction of the colonization of cereal fields by winged aphids from suction-trap catches (Fabre *et al*. (2010). (a) The daily catches of the bird cherry–oat aphid, *Rhopalosiphum padi*, in eight suction traps (similar to the Rothamsted Insect Survey traps) were used to predict the densities of aphids colonizing cereal fields. Apart from the suction-trap data, this study relies on a long-term and multi-site survey of the number of winged aphids landing in cereal fields. A data set with 387 such field counts obtained from surveys realized from 1989 to 2002 in 15 locations all over the northern part of France was gathered. These 387 counts were associated to the closest suction-trap data set available (the mean distance being 46 km). The data and model are detailed in Fabre *et al*. (2010). (b) Box plot of mean deposition rates as a function of suction-trap location and winter severity. The deposition rates estimate the number of aphids deposited per unit area of crop for one winged *R. padi* caught in a suction trap. The full blue line represents the relationship between winter severity and deposition rate and the broken lines the extent of a 95% confident interval. (c) Predictive performance of the model estimated with cross-validation. The plot represents the correlation between the number of winged *R. padi* observed in the fields and their mean values predicted by the model. Cross-validation is a general method for assessing how accurately a predictive model will perform in practice. This study evidences at a large spatio-temporal scale that suction trapping can offer an efficient alternative to crop sampling.

now' or 'No, it's not worth the trouble'). DRs discriminate the fields where a treatment is actually necessary (the 'cases' T^+) from the fields where it is not (the 'controls' T^-) by comparing the value of a risk indicator variable (I), estimated in a given field, and a preset decision threshold (I_s): a treatment is recommended if $I \geq I_s$. The framework of analysis is the same for risk indicators I obtained from simple aphid sampling schemes or derived from complex simulation models. It relies on receiver operating characteristic (ROC) curves and cost–benefit analysis, and requires taking into account the probability of an aphid outbreak.

The accuracy of a given DR (I, I_s) is measured by its sensitivity

$Se = p\left(I \geq I_s | T^+\right)$, the probability that the DR advises a treatment when it is actually needed, and by its specificity

$Sp = p\left(I < I_s | T^-\right)$, the probability that the DR does not recommend a treatment when it is actually not necessary (Metz, 1978). Ideally, a single threshold I_s should separate the distribution of I in the controls (I^-) and in the cases (I^+): this indicator is perfect (Se = 1 and Sp = 1). But most often, the distributions I^+ and I^- partially overlap. Choosing a low I_s defines a DR with a high Se but a low Sp: useless spray will mostly be applied (Box 17.1a). A high I_s defines a DR with a high Sp but a low Se: useful spray will mostly be missed (Box 17.1b). Clearly, neither of these alternatives is desirable. ROC curves allow navigation between these pitfalls. They describe the compromise between Se and Sp by plotting Se against 1 – Sp for all possible values of I_s (Box 17.1c) (Metz, 1978; Swets, 1988). Moreover, the areas under ROC curves (AUC) are measures on a common scale of the accuracy of several indicators (Box 17.1c). The AUC of indicators used in crop protection often range from 0.7 to 0.9 (Fabre *et al*., 2007).

ROC curves can be combined with cost–benefit analysis to estimate the financial benefit obtained with DSSs over naïve strategies (NS: 'never spray' or AS: 'always spray'). The frequency of outbreaks where a treatment is necessary, also called prevalence (P_{rev}), must be taken into account. Assuming no overhead cost to DSS use (e.g. scouting for aphids is time-consuming), DR strategies are always financially beneficial, but the gains are not

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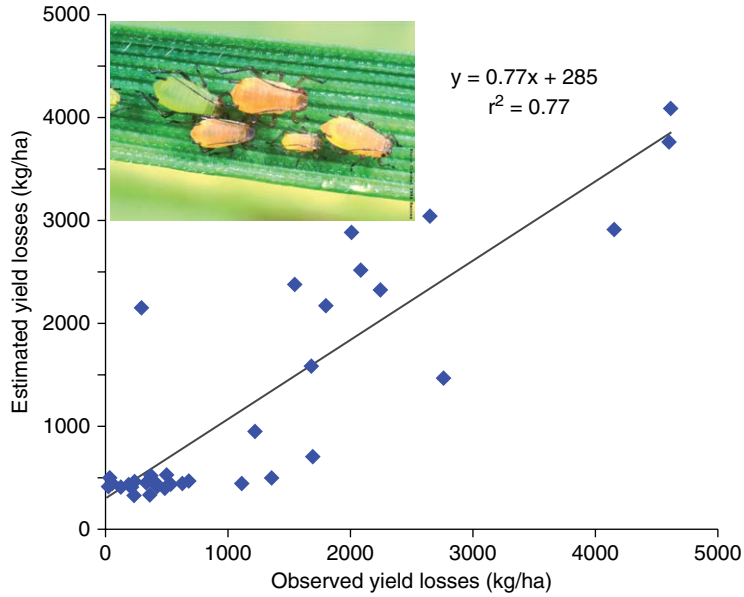

Fig. 17.2. Damage function for *Sitobion avenae* on wheat. The model estimates the yield losses (*YL*) due to the aphid *Sitobion avenae* in spring on wheat from the aphid densities IR_i at four key growth stages (1: heading; 2: flowering; 3: milky ripening; 4: doughy ripening). The model is $YL = \alpha_1.IR_1 + \alpha_2.IR_2 + \alpha_3.IR_3 + \alpha_4.IR_4$ where α_i are damage coefficients at growth stage *i*. The plot represents the correlation between the yield losses observed in 13 field trials located in three regions in France and their mean values estimated by the model. (From Vialatte *et al*., 2005. Photograph of *Sitobion avenae* courtesy of Bernard Chaubet.)

always substantial, particularly in intensive crops where the cost of a treatment is about 5% of the potential yield loss imposed by uncontrolled outbreaks (e.g. tomato in greenhouses; Shtienberg, 2013). Compared to the prophylactic strategy (AS), the cost of managing aphids with optimal DRs are reduced, for example, by more than 20% only for very low prevalence in the range [0, 0.05] for a moderately accurate indicator (AUC = 0.7) and in the range [0, 0.22] for a highly accurate indicator (AUC = 0.9) (Box 17.1d). These ranges can be interpreted as ranges of possible production situations where DSSs are beneficial. In intensive crops, only highly accurate indicators (AUC = 0.95) provide substantial benefits over many production situations.

In extensive crops (Box 17.1e), the cost of a treatment is up to 50% of the yield loss imposed by uncontrolled outbreaks (e.g. wheat in the Middle East; Shtienberg, 2013). The gains obtained with most DSSs over AS strategies are higher, more frequent and less sensitive to indicator accuracy. Even moderately accurate indicators (AUC = 0.7) are advantageous over a wide range of production situations: the costs are reduced by more than 20% for prevalence in the range [0, 0.42]. The picture is quite different when comparing optimal DRs with the best naïve strategy (instead of solely the AS strategy) (Box 17.1f). For a treatment cost equal to 50% of the yield loss imposed by uncontrolled outbreaks, the best naïve strategy is indeed to never spray (NS) if the prevalence is ≤0.5, and to always spray (AS) otherwise. Costs are never reduced by more than 20% for moderately or averagely accurate indicators (AUC ≤ 0.8). Highly accurate indicators are thus needed if the objective is improving crop protection practices instead of only decreasing the number of unnecessary treatments. The reader is referred to Fabre *et al*. (2007) for further analysis.

Aphi.net: a DSS for Managing Aphids Spreading Virus on Cereals

The principles of a binary DR developed to manage Barley yellow dwarf disease (BYDD), one of the most severe autumn diseases affecting straw cereals (barley, wheat and oats) are now illustrated. BYDD is caused by a complex of viruses (BYDV) transmitted by cereal aphids (Chapter 15 and Chapter 24,

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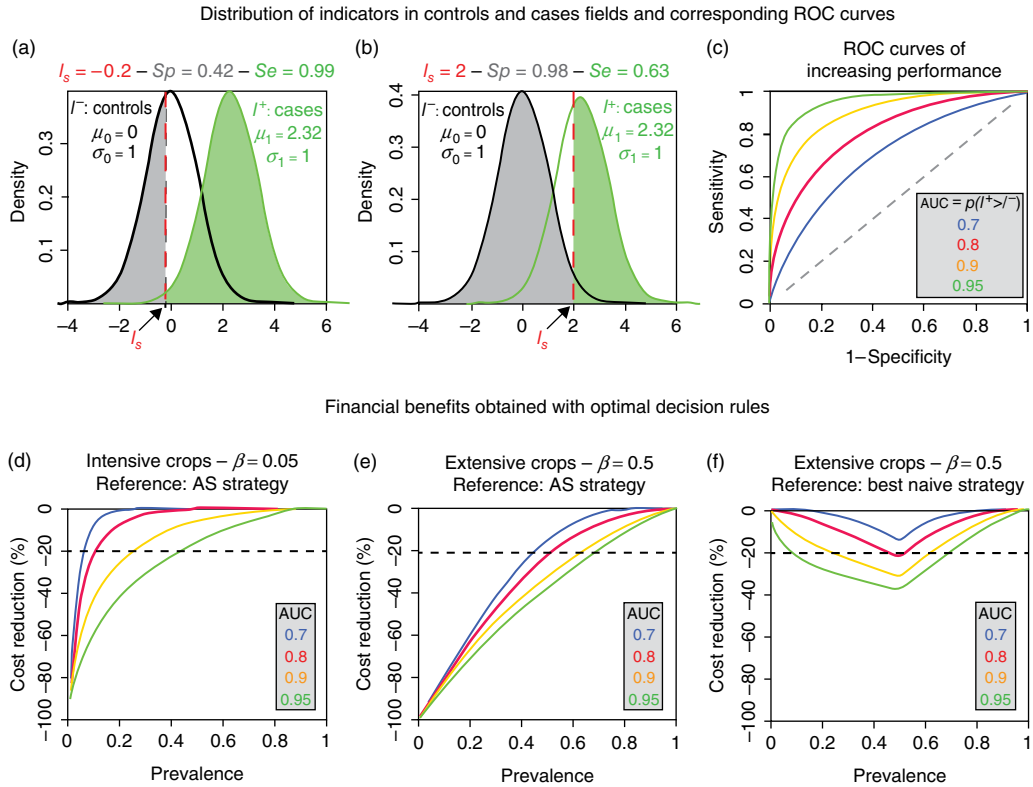
Box 17.1. The financial benefit of binary decision rules (from Fabre *et al.*, 2007)



(a–c) The mathematics of binary decision rules

(a) The accuracy of a binary decision rule (DR) is measured by its sensitivity and its specificity. Here, the values of a hypothetical indicator I in the controls T^- 'fields where a treatment is not required' is assumed to follow a normal distribution $I^- \sim N(\mu_0 = 0, \sigma_0 = 1)$ while it follows $I^+ \sim N(\mu_1 = 2.32, \sigma_1 = 1)$ in the cases T^+ 'fields where a treatment is necessary'. The value of the threshold I_s is set to –0.2. The specificity $Sp = p(I < I_s | T^-)$ of the DR (I, I_s) is the probability that the DR does not recommend a treatment when it is actually not necessary. Its value, 0.42, is figured by the grey area under I^-. Its sensibility $Se = p(I \geq I_s | T^+)$ is the probability that the DR recommends a treatment when it is actually needed. Its value, 0.99, is figured by the green area under I^+.

(b) The sensitivity and the specificity of a DR depend on the decision threshold I_s. The same indicator as in (a) is used, but I_s is now set to 2. The specificity of the DR (I, I_s) is now much better, 0.98, but its sensitivity drops to 0.63.

(c) The receiver operating characteristic (ROC) curve of an indicator I plot $Se = f(1 - Sp)$ for all possible values of the threshold I_s. ROC curves are independent of the proportion of the fields where a treatment is necessary (prevalence of the cases T^+) and of I_s. The accuracy of a set of indicators can be measured, and compared, by the area under the ROC curve (AUC), which is $p(I^+ > I^-)$. The AUCs vary from 0.5 (no discrimination) to 1 (for perfect discrimination). Here, four ROC curves of increasing accuracy (AUC of 0.7, 0.8, 0.9 and 0.95) are plotted. They are obtained by assuming that the underlying distribution of the indicator I in the controls is $I^- \sim N(\mu_0 = 0, \sigma_0 = 1)$, while the means of the distributions of I in the cases increase from 0.74 to 2.32: $I^+ \sim N(\mu_1 = 0.74, \sigma_1 = 1)$ for AUC = 0.7, $I^+ \sim N(\mu_1 = 1.19, \sigma_1 = 1)$ for AUC = 0.8, $I^+ \sim N(\mu_1 = 1.81, \sigma_1 = 1)$ for AUC = 0.9 and $I^+ \sim N(\mu_1 = 2.32, \sigma_1 = 1)$ for AUC = 0.95. ROC curves were obtained by fitting a binormal ROC

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Box 17.1. Continued.

model to data sets consisting of 10^4 values sampled in the normal distributions of the controls and the cases (package 'pROC' of the R software, http://cran.r-project.org/, functions ploc.roc and smooth with method 'binormal').

(d–f) The financial benefit of using decision rule strategies over naïve strategies

The average cost of the 'never spray' strategy (C_{NS}) depends on the prevalence of the cases (*i.e.* P_{rev}: proportion of the fields where a treatment is necessary) and on the average costs of the yield losses in the controls (C_{min}) and in the cases (C_{maj}): $C_{NS} = P_{rev}.C_{maj} + (1 - P_{rev}).C_{min}$. The average cost of the 'always spray' strategy (C_{AS}) is the cost of the treatment C_{trt}. It can be expressed as a fraction ($0 \leq \beta \leq 1$) of the potential yield loss imposed by uncontrolled outbreaks in the cases: $C_{trt} = \beta.C_{maj}$. The parameter β ranges from 0.05 in intensive high-value crops to 0.5 in extensive low-value crops (Shtienberg, 2013). For the average cost of a DR strategy (C_{DR}), the accuracy of the DR (I, I_s) must additionally be considered. It is measured by its sensitivity and specificity $C_{DR} = P_{rev}.[C_{trt}.Se + C_{maj}.(1 - Se)] + (1 - P_{rev}).[C_{min}.Sp + C_{trt}.(1 - Sp)]$. There are as many decision rules (I, I_s) as possible I_s, but generally a single one I_s^* minimizes C_{DR}. (I, I_s^*) is the optimal decision rule with cost C_{DR}^*, sensitivity Se^* and specificity Sp^*.

Assuming $C_{min} = 0$, the cost reduction obtained with optimal DR strategy (I, I_s^*) over a naïve strategy depends solely on the three parameters P_{rev}, β and the accuracy (AUC) of the indicator I considered (panel (c)). The percentage of cost reduction compared to the NS (respectively, to the AS) strategy is $CR_{NS}^* = 100.[(C_{DR}^* - C_{NS})/C_{NS}]$ (respectively, $CR_{AS}^* = 100.[(C_{DR}^* - C_{AS})/C_{AS}]$). The percentage of cost reduction compared to the best naïve strategy CR_{BS}^* is CR_{NS}^* if $P_{rev} \leq \beta$ (as $C_{NS} \leq C_{AS}$) and CR_{AS}^* otherwise.

(d) The percentage of cost reduction obtained with optimal DR strategy (I, I_s^*) over the AS strategy (CR_{AS}^*) as a function of the prevalence (P_{rev}) of the cases for four indicator accuracies (AUC) for a typical intensive crop ($\beta = 0.05$). The ROC curves of the four indicators considered are plotted in panel (c). Below the horizontal dashed line, using an optimal DR reduces the cost of aphid management by more than 20% compared to the AS strategy.

(e) Same as (d) for a typical extensive crop ($\beta = 0.5$).

(f) Same as (e) for the percentage of cost reduction obtained with optimal DR strategy (I, I_s^*) over the best naïve strategy (CR_{BS}^*).

this volume). *Rhopalosiphum padi* is the main vector of BYDV in winter cereals during autumn in Europe. In the early 2000s, INRA researchers, in collaboration with Bayer CropScience France, developed a DSS that was operated until 2010, potentially allowing to decrease by 33% any unnecessary spray in crops without seed treatment. The main cause of its demise was the generalization of seed insecticide dressing in French barley and wheat fields.

The DSS is presented in Box 17.2. A BYDD risk indicator is assessed with a thermo-dependent population dynamics model of *R. padi* (Box 17.2a). Farmers must estimate the proportion of barley plants infested by aphids early after crop emergence, at one or two leaves growth stage, when the decision to spray a foliar insecticide can still be taken. This achieves the best trade-off between the reliability of the decision at field scale and sampling ease (estimating a percentage of infestation is easier than counting aphid densities).

The ROC curve of the BYDD risk indicator is plotted in Box 17.2b. Its AUC, 0.88, is statistically significantly higher than the AUC of the ROC curve of a simpler BYDD indicator (0.81) evaluating the need to spray only according to the value of field sampling, without using the model of population dynamics. It emphasized the added value of the model proposed.

The annual cost of BYDD management according to the DR proposed depends on disease prevalence (Box 17.2c). The prevalence is the frequency of the fields where an insecticide spray is necessary. It is 0.6 in our data set (32 fields out of the 53 used for validation). The sensitivity of the optimal DR for this prevalence is 0.97 and its specificity 0.33.

In a large range of prevalence [0.02–0.78], using the model decreases the cost of BYDD management compared to naïve strategies. Outside, the model is as costly (but no more) as the NS strategy ($P_{rev} < 0.02$) or the AS strategy ($P_{rev} > 0.78$). Compared to the prophylactic strategy, the decrease of the annual cost of BYDD management is at least 20% (i.e. 100 kg/ha) for $P_{rev} \leq 0.34$ and the specificities of the corresponding optimal DR are ≥0.63, meaning that at least 63% of the unnecessary treatments are avoided.

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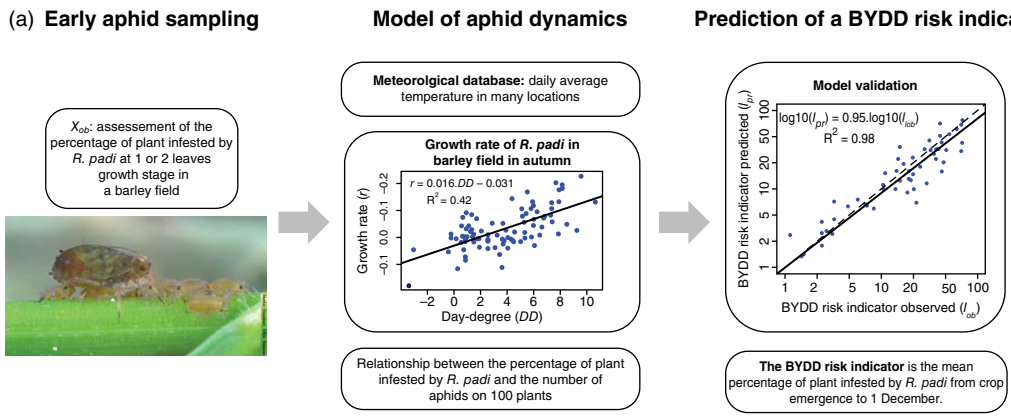
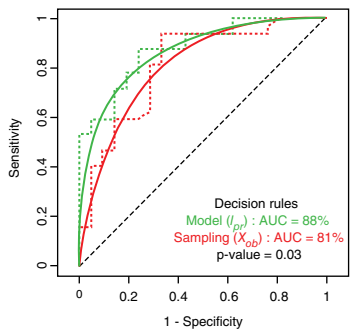
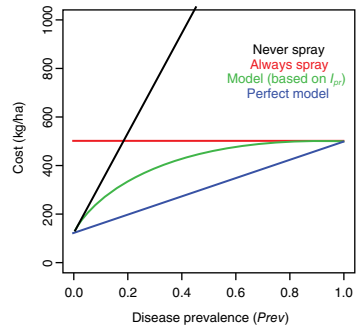
Box 17.2. Aphi.net®, a DSS for BYDD management (from Fabre *et al*., 2003, 2006)







(a) The model of aphid population dynamics

The model requires an assessment of the percentage of barley plants infested by *Rhopalosiphum padi* (X_{ob}). It simulates the population dynamics of *R. padi* using mainly a relationship between average daily temperatures (*DD*) and aphid growth rates (*r*) fitted on a field data set accounting for a wide range of the factors impacting aphid dynamics in autumn (R^2 = 0.42). The model explicitly integrates the uncertainty in this relationship using a Bayesian framework and estimates the mean percentage of plants infested by *R. padi* from crop emergence to 1 December (*I*). This variable *I* is an indicator of the need for insecticide sprays against BYDD vectors (Fabre *et al*., 2003). The model was validated on 53 field trials collected from 1995 to 2002 in the main French small grain production areas using 20-year average daily temperatures as close as possible to the field trials location. This data set was independent of the experiments used to fit the population dynamic model. The model predicts accurately the values of *I* (R^2 = 0.98). The model is fully described in Fabre *et al*. (2006). A validation on a larger data set (53 field trials instead of 25) is presented in this chapter. The variable used by Fabre *et al*. (2006), the area under the curve of the percentage of plants infested by *R. padi*, is equivalent to *I*.

(b) Receiver operating characteristic (ROC) curves comparing the performance of two indicators of BYDD risk management

With the 'model-based' indicator, the decision to spray an insecticide relies on the prediction of the indicator of BYDD risk (I_{pr}) with the model of *R. padi* dynamics (panel (a)). Its ROC curve is compared to the ROC curve of an alternative indicator 'sampling based', for which the decision to spray simply relies on the value of the early assessment of the proportion of plants

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Box 17.2. Continued.

infested by aphids (X_{ob}). The AUC of the 'model-based' indicator (0.88) is significantly higher than the AUC of the 'sampling-based' indicator (0.81) (p-value = 0.03). ROC curves were fitted with the 53 field experiments used for model validation. Among these 53 experiments, 32 were classified as 'cases'. In these fields, the yield losses due to BYDD were higher than the cost of an insecticide spray (estimated to be equivalent to 500 kg/ha). The 21 remaining fields were classified as 'controls' (yield losses <500 kg/ha). ROC curves and AUC were computed using the package 'pROC' of the R software (http://cran.r-project.org). Empirical ROC curves (dotted line, function ploc.roc of the package 'pROC') and smooth ROC curves (full line) fitted with the function smooth (method = 'binormal') are shown. A bootstrap method was used to compare the AUC.

(c) Mean annual cost of BYDD management as a function of disease prevalence

Mean costs are estimated as in Box 17.1, with C_{min} = 120 kg/ha, C_{maj} = 2160 kg/ha and C_{trt} = 500 kg/ha. The two naïve strategies consist of 'never spray' or 'always spray'. The third strategy is to spray according to the recommendation of the optimal binary DR (I_{pr},I_{opt}) relying on the indicator I_{pr} (predicted by the model of aphid population dynamics in (a) in the figure above) and on the decision threshold I_{opt} (determined with the binormal ROC curve fitted in (b) in the figure above). The last strategy is to spray according to a perfect DR (sensitivity = 1, specificity = 1). Costs are expressed in yield loss equivalents. Disease prevalence is the frequency of BYDD outbreak leading to yield losses higher than the cost of an insecticide spray.

The difference between the cost paid to manage BYDD with the actual model and those costs paid with a hypothetical perfect model (for which Se = 1 and Sp = 1) estimates the financial benefit of developing improved indicators (Box 17.2c). On one hand, improved indicators will be more widely adopted due to their better financial performance. On the other hand, they are likely to require more work (e.g. sampling more plants, acquiring more data such as the proportion of migrant winged aphids that carry virus), which, in turn, could be dissuasive.

Past and Present Aphid DSSs

Tracking aphid DSSs and their genealogy is not so easy. EPIPRE (Rabbinge and Rijsdijk, 1983) is sometimes considered as one of the earliest DSSs, although economic thresholds (Pedigo *et al*., 1986) used since the 1960s constitute, in a sense, DSSs. EPIPRE was developed in the early 1980s as a cooperative project for the supervised control of main cereal aphids (*S. avenae*, *R. padi* and *Metopolophium dirhodum* (rose–grain aphid)) in wheat, as well as several fungal diseases. Farmers assessed the proportion of infested tillers in their fields according to predetermined sampling schemes, and this information was introduced into a central computer that produced recommendations for treatments on the basis of simulation models. Rabbinge and Rijsdijk (1983) indicate that 'communications with the farmers is through the mail (the time between a farmer sending a postcard and receiving a computer-written response is never more than 4 days), and by telephone line in case a rapid response is needed'. Since then, several 'aphid' DSSs have been developed. Estimating their real number is nearly impossible as: (i) some DSSs have not been published (e.g. most DSSs are developed by private companies); and (ii) it is sometimes difficult to conclude from the scientific literature if the models have really been used in practice. The characteristics of 23 aphid DSSs are given in Table 17.1. Some were freely accessible online in 2016, but most are nowadays abandoned after several years of use. The development of aphid DSSs in the world since 1980 remains low whatever the period (Fig. 17.3), considering the number of scientists and extension agents working on aphids. The small peak during the 2000s looks particularly tiny, considering the extraordinary development of informatics, computational statistics and web-based applications ('Web 2.0') during this period.

Two-thirds of the DSSs in Table 17.1 concern cereal aphids. Eighteen DSSs (78%) apply to intensive crop production in seven European countries. Only five DSSs from three non-European countries (Australia, New Zealand and the USA) were clearly identified. They apply to extensive or semi-intensive crop production.

Half of the selected DSSs (11) used initial field infestation data as input from the user (aphid counts or percentage of infested plants), sometimes in addition to data on the localization of the field, its shape and/or on cropping practices (sowing date, cultivar and crop density). In four cases only,

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Table 17.1. Tentative review of DSSs for aphid and virus control published since the 1980s.

Crop	Aphids/virus targeted	Country	References	User inputs	Main model features	Outputs
Cereals (winter wheat)	*Sitobion avenae*, *Metopolophium dirhodum*, *Rhopalosiphum padi*	The Netherlands	Zadoks (1981); Rabbinge and Rijsdijk (1983); Reinink (1986)	Percentage of infested tillers	Mechanistic model of aphid population dynamics EPIPRE package	Advice to spray
Cereals (winter wheat)	*S. avenae*, *M. dirhodum*	England	Mann *et al*. (1986); Mann and Wratten (1991)	Percentage of infested tillers	Mechanistic model of aphid population dynamics	Advice to spray, not to spray or to wait
Cereals	*S. avenae*, *M. dirhodum*, *R. padi*	Denmark Baltic countries	Hagelskjaer and Jørgensen (2003)	Percentage of infested tillers	Comparison with thresholds depending on crop growth stage and cultivar Crop Protection Online package	Advice to spray based on thresholds Insecticides and dosages proposal
Cereals	*S. avenae*, *M. dirhodum*, *R. padi*	Switzerland	Derron and Forrer (1989)	Percentage of infested tillers Wheat growth stage Expected yield	Mechanistic model for aphid population dynamics Statistical model for crop loss	Yield loss forecast Advice to spray
Cereals (winter wheat)	*S. avenae*	Sweden	Larsson (2005)	Number aphid/tiller (peak value) Wheat growth stage	Statistical model for crop loss	Economic thresholds at several growth stages
Cereals (winter barley)	*R. padi*/*Barley yellow dwarf virus*	France	Fabre *et al*. (2003, 2006)	Field location Percentage of infested seedlings in autumn (at 1–2 leaves)	Statistical models of aphid population dynamics and BYDV yield losses Aphi.net package	Advice to spray
Cereals (winter wheat)	*S. avenae*	France	Plantegenest *et al*. (1999, 2001)	Number of aphids/tiller at heading growth stage Expected temperature scenario (cold, medium, hot) Expected yield and cereal price	Mechanistic model of aphid population dynamics COLIBRI package	Simulation of aphid population dynamics and estimation of associated yield loss Advice to spray
Cereals (wheat)	*R. padi*/*Barley yellow dwarf virus*	Australia	Thackray *et al*. (2009)	Field location Cereal sowing date	Statistical and mechanistic models of aphid population dynamics and BYDV epidemiology BYDV PREDICTOR package	Date of aphid first arrival Aphid population dynamics and BYDV progress curves BYDV yield loss Advice to spray and optimal date to do so

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Cereals (wheat)	*R. padi*/*Barley yellow dwarf virus*	New Zealand	Knight and Thackray (2007)	Number of aphids caught in suction traps in April and May (for early-sown fields prediction) or in June and July (for late-sown fields prediction)	Statistical relationships between aphid captures and percentage of fields with >5% BYDV incidence (historical database) AphidWatch.com package	BYDV risk forecast
Cereals (winter wheat and barley)	*R. padi*/*Barley yellow dwarf virus*	UK	Foster *et al*. (2004); Northing *et al*. (2004)	Suction-trap catches Field location Sowing date	Weather-driven statistical model of BYDV spread	Percentage of plants infected by BYDV Regional and field BYDV risk forecast
Cereals (winter wheat)	*S. avenae*	France	Pierre and Dedryver (1984)	Number of aphids/tiller at heading growth stage Sum of February daily mean temperatures	Statistical model	Peak of the number of aphids/tiller
Cereals (winter wheat)	*S. avenae*	France	Vialatte et al. (2005)	Occurrence of minimal temperatures <3°C (in days) in February Mean temperatures accumulation in April and May	Statistical models of aphid population dynamics and crop loss	Probability distribution of yield losses
Cereals (winter wheat)	*S. avenae*	France	Ciss *et al*. (2014)	Daily maximum temperatures >14°C Mean daily temperatures	Mechanistic model of aphid population dynamics	Daily maps of aphid population dynamics at large scale (France)
Cereals (wheat)	*Schizaphis graminum*, *Diuraphis noxia*	USA	Elliott *et al*. (2004)	Weather data Aphid field sampling	Statistical model	Economic threshold for a region Advice to spray
Cereals	All cereal aphids	Denmark	Murali *et al*. (1999)	Percentage of infested plants Cultivar and growth stage Previous crop	Comparison with thresholds PC-Plant Protection package	Control recommendations
Sugar beet	*Myzus persicae*/*Beet yellows virus*, *Beet mild yellowing virus* and *Beet chlorosis virus*	UK	Harrington *et al*. (1989) (see Werker *et al*. (1998) and Qi *et al*. (2004) for modified versions)	Previous year's virus incidence Temperature in January and February	Statistical model	Regional virus incidence Advice to apply aphicidal granules at drilling
Potato seeds	*Brachycaudus helichrysi*, *Phorodon humuli*/*Potato virus Y*	Switzerland	Steinger *et al*. (2015)	Cumulative abundance of aphids in the suction trap until mid-June	Statistical model	Average virus incidence

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Table 17.1. Continued.

Crop	Aphids/virus targeted	Country	References	User inputs	Main model features	Outputs
Hops	*Phorodon humuli*	Czech Republic	Mozny *et al*. (1993)	Mean daily air temperature Mean daily relative humidity Daily rain	Weather-driven statistical model CORAC package	Beginning of 'attacks' by the first and second aphid generation
Spring beans	*Aphis fabae*	UK	Knight and Cammell (1994)	Spring suction-trap catches or egg counts on spindle trees Field topography, size and shape Sowing date and plant density Expected price and yield of beans	Decision tree and statistical model of crop loss FLYPAST package	Probability of infestation of a field (three categories of risk) Advice to spray
Lupins	Several aphid species/*Cucumber mosaic virus*	Australia	Thackray *et al*. (2004)	Rainfall summer and early autumn Lupin cultivar, anticipated emergence date, percentage of CMV infection in seed sown, plant density and location	Statistical and mechanistic models of aphid population dynamics and CMV epidemiology Accessible via Internet	Dates of first aphid arrival and personalized risk forecast (CMV spread, yield loss due to infection)
Orchards	*Dysaphis plantaginea*	Switzerland	Samietz *et al*. (2013)	Field location (defining of a climatic area)	Mechanistic model using regional temperature data SOPRA package	Local population levels and age structure Advice to monitor the pest and to spray
Vegetables	*M. persicae*, *Brevicoryne brassicae* and four other species	UK	Collier (2011)	No user input	Statistical model using winter temperatures Web pages and bulletins	Number of aphids trapped until 1 July Risk forecast
Cotton	*Aphis gossypii*	Australia	Hearn and Bange (2002); Bange *et al*. (2004)	Climatic data Presence of beneficial and pest insects, their stage of development and quantity	Statistical model CottonLOGIC package	Date when pest numbers are over defined economic thresholds

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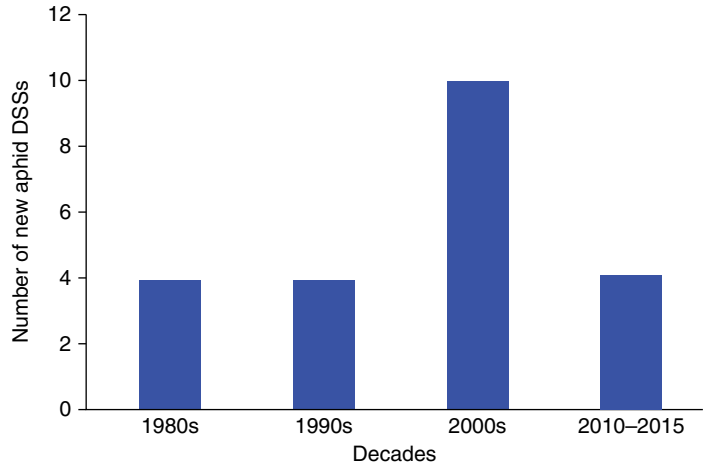

Fig. 17.3. Trends in the numbers of new aphid DSSs published per decade. We first searched for articles in CABI's 1973–2015 bibliographical databases with the formula: (aphid AND DSS) OR (aphid AND forecast) OR (aphid AND population AND modelling). This first step identified 1279 articles. The summary and keywords of each article were then read carefully to select those articles dealing with the use of mathematical models in order to forecast aphid populations in the field. This second step identified 85 articles. In the third step, each of them was read, excepting those that were written in non-Latin characters. Those in which (i) the modelling content was described and (ii) a step of validation and of use by farmers was described or explicitly evoked were considered as DSSs. Finally, articles dealing with the same DSS were grouped, to obtain a final number of 23 DSSs.

suction-trap data are used as input (in the UK, in Switzerland and New Zealand). Almost all DSSs use temperatures (mostly mean daily temperatures) extracted from historical weather databases. A few rely on other climatic variables such as rainfall or relative humidity. Thackray *et al.* (2004) predicted, for example, the timing of aphid immigration into lupin crops in Australia as a function of rainfall during summer and early autumn.

Conclusion

Are aphid DSSs really short-lived and underused?

Is the practice of DSSs a pallid picture of their promise? This is a long-standing question recently explored by Gent *et al.* (2013): 'The general view of limited implementation seems to be inferred from observations that a minority of farmers directly utilize DSSs or that their use is not sustained over time.' Aphid DSSs seem to follow this general rule. This could be due to several additive causes.

First, producers and other practitioners make subjective assessments regarding the risk of yield losses based on factors beyond the classical view of the disease triangle. The sociological aspects of risk assessment and risk aversion are important considerations (Gent *et al.*, 2011). Risk aversion is in some cases so strong that even DSSs with excellent performances could be considered as insufficient. In extensive crop production (e.g. northern America), fear of false-positive advice increasing the cost of crop protection limits the use of DSSs. In the intensive cereal production of Europe, the fear of false-negative advice encourages the use of systemic insecticide-treated seeds or of systematic foliar sprays (Shtienberg, 2013). However, it is important to point out that the framework described to estimate the financial benefit of DRs can be fitted to the personal objectives of the user. One may, for example, avoid risk associated with major outbreaks: the decision threshold (I_s) should then be set to control the sensitivity of the DR instead of minimizing the cost of aphid management. McRoberts *et al.* (2011) advocated use of the concept of subjective probability (which expresses an individual's strength of belief in a particular state of affairs) to better integrate social science considerations and plant disease management.

Moreover, due to the relative scarcity of aphid outbreaks, farmers and extension agents are interested in aphid forecasting the year after each outbreak,

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but their interest decreases rapidly after 1 year without aphid problems, and may disappear completely after 2–4 years. The sporadic occurrence of major aphid outbreaks, which we noted in the Introduction as favouring DSS adoption, is also a double-edged sword.

The necessity for more than half of DSSs to provide an assessment of initial aphid populations in fields is another constraint. Farmers lack time to scout fields during some busy periods (spring), and many of them consider that detecting aphids is particularly difficult. This is not popular and probably generates many errors, and ultimately prediction failures. Using suction-trap catches instead seemed promising (Fabre *et al*., 2010), but obviously required a suction trap reasonably nearby. Several countries have developed such traps (NJF, 2013; Chapter 16, this volume), and the extent of their use in decision support varies. In South Africa, for example, the network of 13 traps is funded by Potatoes South Africa (the growers' association), with matched funding from the Department of Trade and Industry, and the data are used in support of the control of aphid vectors of potatoes and cereals. A growing network of traps in China is used to provide aphid warnings in soybean and wheat. Decision support from suction-trap data is usually through information bulletins that compare aphid population trends in the current season with past seasons, rather than DSS models. There is much further potential for the use of suction-trap data in decision support.

The pessimistic view that DSSs are a pallid picture of their promises should be nuanced in several ways. First, the timescale to assess DSS adoption is typically much longer (a decade) than the lifespan of research grants. Moreover, criteria often used to assess adoption, such as 'direct use', overlook the fact that DSS information is often made available indirectly through other people (e.g. extension advisers, consultants) in farmers' decision networks. Finally, farmers learn from DSSs and internalize the effects of the underlying factors. This is an explanation of the natural life cycle of a DSS: development, verification, application and, in many cases, atrophy (Gent *et al*., 2011). Dutch farmers indicated, for example, that one of the main reasons for stopping the use of EPIPRE was that they had learned how the system led to its recommendation (Zadoks, 1989). In fact, what we really need are data to measure properly the long-term socio-economic impact of DSSs on aphid protection practices. Gent *et al*. (2011) suggest asking, 'Are growers making correct management decisions more often than before the DSS was developed?', rather than basically, 'Are growers directly using the DSS?'.

How to improve aphid DSS adoption and usefulness?

Involving farmers and extension agents early in the development of a DSS is essential. Extending the lifespan of the typical life cycle of DSSs ('development, verification, application and atrophy') requires adding a continuous 'verification' step on a set of reference fields. The data collected could be used at the same time to refine model validation and to polish parameter estimation. It will also help to adapt the model to changing biological contexts (e.g. the effects of global change on the structure of aphid communities) and to changing economic contexts (e.g. the variation of the price of pesticide, of fuel or of crops leads to the need to modify the value of C_{min}, C_{maj} and C_{trt} continuously; Box 17.1). These points show the need to address the funding and management of projects involving DSS development.

Undoubtedly, increasing DSS accuracy is important to favour their adoption (Box 17.1, d–f). This is the only way to relax the trade-off between the sensitivity and specificity of DSSs and thus to improve the benefit associated with their use. The FAO suggests that the adoption of an innovation is unlikely unless it offers a cost reduction of 50% over existing practices. Such a benefit, hopefully likely somewhat overestimated, requires highly accurate predictive systems that are very difficult to achieve, in particular for intensive crops (Box 17.1d,e). The situation is worse when considering the benefit obtained over the best naïve strategy: costs are rarely reduced by more than 20%, even in extensive crops (Box 17.1f). More pedagogy on this applied issue of simple probability consideration is needed to avoid expecting unrealistic financial benefit from DSS adoption. Improving DSS accuracy is challenging. On one hand, progress in basic knowledge concerning aphid population dynamics, virus epidemiology and the physiology of crop damage will help. But what is unavoidable is the need to collect extensive field data sets on these topics in a wide range of production situations. Such a requirement is not always sustained, as DSSs go through

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cycles of interest/disinterest in many scientific institutions and extension services. On the other hand, DSSs being based on time-forward simulation, unavoidable uncertainty limiting *de facto* DSS accuracy occurs as soon as, for example, weather inputs are used (Pfender *et al*., 2011). Finally, keeping the best compromise between simple use and accuracy is certainly even more challenging than increasing DSS accuracy.

Another way to involve farmers and extension agents in DSS development is to formalize their theoretical and empirical knowledge using an elicitation approach (Choy *et al*., 2009). An elicitation approach is interesting when basic knowledge is lacking or when observed data are limited in sample size or representativeness. An elicitation approach, involving a network of scientists and technical experts in France, has been used recently to obtain a DSS of the risk of BYDD before sowing, when farmers can still decide to use foliar spray or seed treatment against cereal aphids (Thébaud *et al*., 2015). However, although its development process is different, this model needs also to be validated *in fine* with field data sets.

Upcoming opportunities for the revival of DSSs

In Europe, the status of many insecticides is currently changing: in particular, the possible limitation of insecticide-treated cereal seeds will contribute strongly to the decrease of systematic insecticide protection of cereals. Thus, the use of DSSs in those crops for decisions on the control of aphids and viruses will probably increase significantly.

In many developed countries, IPM is popular among fruit and vegetable growers, who are especially concerned with lowering insecticide use, and many DSSs exist, especially for fungal diseases. There is certainly a place for aphid DSSs in IPM plans for these crops, but again this requires the collection of extensive data sets in a wide range of production situations.

Finally recent developments in information systems and mobile communication technology (e.g. smartphones or tablets and their 'mobile apps') can now bring DSSs into fields while being connected to Internet databases (e.g. meteorological data and, why not one day, suction-trap data) through information system platforms. Information systems allow the display of times series of pest observations and model output in maps, thus promoting the exchange of pest data among agricultural professionals. Never before has information delivery been more rapid or readily available. This is, in our view, a great opportunity for the revival of DSSs.

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18 Chemical Control

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Introduction

As serious crop pests, aphids are major targets for insecticides and help drive a continuing quest for new compounds with novel modes of action and favourable environmental profiles. The first edition of this chapter (Dewar, 2007) noted a progressive change from a market dominated by organophosphates (OPs) and carbamates (Schepers, 1989; Jeschke *et al*., 2002) towards increasing reliance on pyrethroids and, latterly, neonicotinoids. Over the past 10 years, these changes have continued apace. In many countries, most OPs and carbamates have become obsolete or are being phased out as a consequence of their toxicological profile. Neonicotinoids, as a result of their exceptional efficacy and versatility, have continued to increase in popularity and have been joined by a suite of new molecules with distinct properties and/or modes of action. The carbamoyltriazole, triazamate, an excellent aphicide due to its systemicity and downward translocation in plants (Dewar *et al*., 1994), had a brief period of use prior to its withdrawal due to environmental concerns.

This chapter reviews the availability, characteristics and uses of aphicides, introducing novel products and comparing their potential with that of the older, established products. It is intended to complement the IPM Case Studies (Chapters 24–33, this volume) that focus on chemical control practices and the use of economic thresholds in a variety of specific crop-pest scenarios. These IPM Case Studies tend to give details for particular regions of the world, and the use of insecticides may well differ in practices, regulations and status of insecticide resistance from those described for the same crops in this chapter. Readers are invited to make the comparison.

Like other important crop pests, several species of aphid have evolved resistance to one or more chemical classes, and resistance (Chapter 19, this volume) has also become a major factor influencing the choice of insecticides and the design of control strategies. At the time of writing, debates over a possible impact of neonicotinoids on pollinators (e.g. Copping, 2013) has led to a temporary EU-wide ban on the use of neonicotinoid seed treatments for certain flowering crops, and the implications of this for aphid control are under evaluation (Dewar and Evans, 2014; Dewar, 2017).

Availability and Choice of Aphicides

Table 18.1 lists all the insecticides approved for use against aphids in at least one crop in the UK in 2014 (Lainsbury, 2014). This list will necessarily differ between countries around the world, most notably Africa and the Far East, but it exemplifies the diversity of chemistry available to growers within and between chemical classes. The listing adopts a scheme developed by the agrochemical industry's Insecticide Resistance Action Committee (IRAC) for classifying compounds into groups and subgroups on the basis of their mode of action, primarily to promote the alternation of such groups to combat the spread of insecticide resistance (Sparks and Nauen, 2016). Although use of carbamates and OPs continues to decline, pirimicarb, by virtue of its species specificity, remains widely used. Pyrethroids continue to be a mainstay of aphid control in many crops, with a wide choice available.

UK growers now have access to five of the seven commercialized neonicotinoids (Nauen and Denholm, 2005; Bass *et al*., 2015). These are available as seed treatments (imidacloprid, clothianidin

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Table 18.1. List of approved aphicides in the UK as notified in the 2014 *UK Pesticide Guide*. (From Lainsbury, 2014.)

Insecticide	Class	MoA group[a]
Oxamyl	Carbamate	1A
Pirimicarb	Carbamate	1A
Chlorpyriphos	OP	1B
Dimethoate	OP	1B
Pyrethrins	Pyrethrins	3A
Alpha-cypermethrin	Pyrethroid	3A
Cypermethrin	Pyrethroid	3A
Deltamethrin	Pyrethroid	3A
Esfenvalerate	Pyrethroid	3A
Lambda-cyhalothrin	Pyrethroid	3A
Tau-fluvalinate	Pyrethroid	3A
Zeta-cypermethrin	Pyrethroid	3A
Beta-cyfluthrin	Pyrethroid	3A
Imidacloprid	Neonicotinoid	4A
Clothianidin	Neonicotinoid	4A
Clothianidin + beta-cyfluthrin	Neonicotinoid + pyrethroid	4A+3A
Thiacloprid	Neonicotinoid	4A
Thiamethoxam	Neonicotinoid	4A
Acetamiprid	Neonicotinoid	4A
Pymetrozine	Pyridine	9B
Flonicamid	Pyridine	9C
Others		
Tebufenpyrad	Pyrazole METI	21A
Spirotetramat	Tetramic acid derivative	23
Fatty acids		–

Note: [a]Based on the IRAC mode of action classification (Sparks and Nauen, 2016). See also http://www.irac-online.org/modes-of-action/. MoA = mode of action; METI = mitochondrial electron transport inhibitor.

and thiamethoxam), as well as foliar sprays. This chemical class was first used in agriculture in 1991, when imidacloprid (Elbert *et al*., 1990; Altmann and Elbert, 1992; Shiokawa *et al*., 1994) was introduced to the market as the first commercialized neonicotinoid (Jeschke *et al*., 2002). Its combination of photostability, systemicity, insecticidal activity and residual persistence has led to it becoming one of the largest selling insecticides worldwide for crop protection and animal health. Globally, the other neonicotinoids are acetamiprid (Takahashi *et al*., 1992), clothianidin (Ohkawara *et al*., 2002; Jeschke *et al*., 2003), dinotefuran (Wakita *et al*., 2005), nitenpyram (Kashiwada, 1996), thiacloprid (Elbert *et al*., 2000; Jeschke *et al*., 2001) and thiamethoxam (Senn *et al*., 1998; Hofer *et al*., 2001; Maienfisch *et al*., 2001). All have aphicidal properties, but some are more active than others.

Pymetrozine (Flückiger *et al*., 1992a) and flonicamid (Morita *et al*., 2007) act as feeding blockers. Both are highly effective against aphids and are capable of causing a rapid cessation of feeding that is irreversible and leads to death by starvation. Spirotetramat is the first commercialized molecule in a novel class – the tetronic and tetramic acid derivatives – to show exploitable activity against aphids (Bruck *et al*., 2009), unlike its forerunners spirodiclofen and spiromezifen, which are used primarily against spider mites and whiteflies.

Modes of Action of Aphicides

This section reviews the modes of action of existing classes of aphicide, with reference to the IRAC classification scheme (Sparks and Nauen, 2016).

Carbamates (Group 1A) and organophosphates (1B)

Carbamate and organophosphate insecticides are both acetylcholinesterase (AchE) inhibitors, interfering with the transmission of nerve impulses across the synaptic gap between two nerve cells by preventing the breakdown of the predominant neurotransmitter, acetylcholine (Tomizawa and Casida, 2003). This results in tetanic paralysis that destroys the ability of insects and other organisms to respond to external stimuli.

Pyrethroids (3A)

Pyrethroids are synthetic analogues of the naturally occurring pyrethrins, acting on the voltage-gated sodium channel that governs the movement of sodium ions into the nerve cell and enables impulses to travel along the nerve axon. These insecticides have low mammalian toxicity but high toxicity to fish. Pyrethroids frequently have repellent activity against colonizing aphids, which makes them potentially valuable in controlling non-persistent viruses (Foster *et al*., 1994; Bedford *et al*., 1998). However, to take maximum advantage of this repellency effect, they need to be applied before the aphids arrive, and it is very difficult to forecast the arrival of aphids with the required precision (Chapter 16, this volume).

Neonicotinoids (4A)

Neonicotinoids mimic the mode of action of nicotine, acting on the post-synaptic nicotinic

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acetylcholine receptors (nAChRs) in the central and peripheral nervous systems, resulting in excitation and paralysis, followed by death (Ishaaya and Horowitz, 1998; Nauen *et al*., 2001, 2003; Tomizawa and Casida, 2003). Many of these compounds are sufficiently xylem mobile to be suitable for seed treatment and soil application. They have low mammalian toxicity due to fundamental differences between the nAChRs of insects and those of mammals (Tomizawa and Casida, 2003).

The properties of neonicotinoids and their effects on aphids have been studied in considerable detail. Imidacloprid and acetamiprid, applied topically to the upper surface of leaves, showed translaminar and acropetal (movement towards leaf margins) activity against *Myzus persicae* (peach–potato aphid) and *Aphis gossypii* (cotton or melon aphid) on cabbage and cotton, respectively (Buchholz and Nauen, 2002). Imidacloprid suppressed honeydew production by *M. persicae* feeding on cabbage leaves treated with low sublethal concentrations, suggesting that feeding was interrupted even though the aphids were not killed (Nauen, 1995). In studies on wheat seedlings with radioactive (^{14}C) imidacloprid, high toxicity to aphids persisted 195 days after sowing; a concentration gradient from the oldest to the youngest leaves implicated apoplastic translocation (Stein-Dönecke *et al*., 1994). Imidacloprid strongly reduced the sucking activity of *Rhopalosiphum padi* (bird cherry–oat aphid), as measured by electrical penetration graphs (EPG) in laboratory studies on maize (Jaschewski, 1997; Abraham and Epperlein, 1999); transmission of *Barley yellow dwarf virus* (BYDV) was also reduced by 65% in the latter study. However, imidacloprid did not affect probing behaviour or transmission of the non-persistent *Potato virus Y* (PVY) (Collar *et al*., 1997). *Macrosiphum euphorbiae* (potato aphid), feeding on terminal potato leaflets placed in solutions of imidacloprid, showed a significant reduction in speed of movement, distance moved and then propensity to fly compared to aphids feeding on untreated plants; however, no repellence was detected in colonization behaviour (Boiteau *et al*., 1997). Radioactive imidacloprid, when applied topically to pelleted sugar beet seeds, generated several metabolites, of which the olefinic fraction was the most important (Westwood *et al*., 1998) as it had greater aphicidal activity than the parent compound (Nauen *et al*., 1998). This perhaps explains the long persistence of this insecticide. In the former study, most of the parent compound was metabolized within 97 days. Little was then present in the roots, but 23% was still in the soil, and most (44.5% of the metabolites plus 4.5% of the parent compound) in the leaves.

Thiamethoxam has lower binding affinities with insect nAChRs than the other nicotinoids, but as it is likely to be a nicotinoid precursor for clothianidin, to which it can be metabolized rapidly (Nauen *et al*., 2003), this does not appear to be a disadvantage. Thiamethoxam is transported in the xylem to cotyledons and leaves acropetally when applied as a seed treatment to maize, oilseed rape and other plants (Senn *et al*., 1998; Fischer and Widmer, 2001). The ability of *M. persicae* to penetrate the phloem of potato leaves was reduced by this insecticide in EPG studies (Harrewijn *et al*., 1998). Its presence on the leaf surface did not affect probing behaviour, thus discounting a repellent effect, but very often stylets were withdrawn, and feeding not resumed, after penetration of the mesophyll cells. After drench applications, a large number of electric potential drops (pds) were observed on the EPGs on treated plants. This showed that increased xylem penetration, and thus exposure to higher concentrations of the insecticide, had occurred. Once feeding was terminated, there was no recovery and death by starvation followed.

Clothianidin has very low vapour pressure and volatility, and does not dissociate under acidic to slightly basic conditions (Jeschke *et al*., 2003). It has specific activity against insect nervous systems, and very low toxicity to vertebrates (Ohkawara *et al*., 2002). Clothianidin demonstrated translaminar activity against *A. gossypii* on cucumbers and excellent translocation from the roots to the leaves, and also between adjacent leaves. Such translocation makes it suitable as a seed and soil treatment (Ohkawara *et al*., 2002). It is distributed more evenly over the whole leaf lamina than the other neonicotinoids, which tend to accumulate in the leaf margins (Jeschke *et al*., 2002).

Thiacloprid is an acute contact and stomach poison with systemic properties. It has a short half-life with a good safety margin for bees (Elbert *et al*., 2000, 2002), making it ideal for spray application. The mode of action is similar to that of the other neonicotinoids.

The long persistence of neonicotinoids (especially when applied as seed treatments) implies that pests will often be exposed to sublethal concentrations that can have varied effects on behaviour and demography. The treatment of wheat plants with

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sublethal amounts of four neonicotinoids led to a reduction in population growth and feeding behaviour of the English grain aphid, *Sitobion avenae* (Miao *et al*., 2014).

All seven neonicotinoids are placed in the same IRAC group (4A) due to structural similarity and a shared binding site. Two other compounds targeting nAChRs with high efficacy against aphids have recently been developed. The sulfoximine, sulfoxaflor (Zhu *et al*., 2011), and the butenolide, flupyradifurone (Nauen *et al*., 2015), are unquestionably nAChR agonists but are structurally distinct from neonicotinoids and are therefore placed in new subgroups (4C and 4D, respectively). This distinction is supported by data showing that aphids and whiteflies with metabolic resistance to imidacloprid and other conventional neonicotinoids remain almost fully susceptible to sulfoxaflor and flupyradifurone (Zhu *et al*., 2011; Longhurst *et al*., 2013; Nauen *et al*., 2015).

Pymetrozine (9B) and flonicamid (9C)

Pymetrozine and flonicamid exert similar effects to each other against aphids, causing irreversible cessation of feeding within a few hours of application, followed eventually by starvation and death (Schwinger *et al*., 1994; Morita *et al*., 2007). Pymetrozine is the older molecule and has been studied in more detail. It inhibits feeding in aphids immediately after application, without producing visible neurotoxic effects, and acts via a novel mechanism that is linked to the signalling pathway of serotonin (Kaufmann *et al*., 2004). Pymetrozine has systemic and translaminar activity, ideal for use in soil and foliar application; however, it can take time for the aphids to die (Flückiger *et al*., 1992a,b; Kayser *et al*., 1994; Harrewijn and Kayser, 1997). Low concentrations of pymetrozine and imidacloprid on wheat had antifeedant effects on *Diuraphis noxia* (Russian wheat aphid); aphids on treated plants spent significantly longer in non-probing activities, but nevertheless penetrated the leaf more frequently, because each penetration was followed by a shorter period of phloem ingestion (Burd *et al*., 1996). Electronic monitoring of aphid feeding behaviour following exposure to flonicamid showed that, although treated aphids attached their proboscises to the leaf surface, salivation and sap feeding were strongly inhibited (Morita *et al*., 2007).

The modes of action of pymetrozine and flonicamid are still under investigation. However, pymetrozine has been shown to modulate chordotonal receptor organs that detect alterations in the tension of insect muscles (Ausborn *et al*., 2005).

Diafenthiuron (12A)

Diafenthiuron is a thiourea derivative that affects respiration in insects (Ishaaya *et al*., 2001) by inhibiting mitochondrial ATPase through its reactive intermediate metabolite and photoproduct, the corresponding carbodiimide (Casida and Quistad, 1998).

Tebufenpyrad (21)

Tebufenpyrad is a member of the METI (mitochondrial electron transport inhibitor) group of acaricides and insecticides (Kyomura *et al*., 1990). It acts by inhibiting complex I of the mitochondrial respiratory pathway. Its uses against aphids relate mainly to hops and stone fruit.

Spirotetramat (23)

The tetramic acid derivative, spirotetramat, is a potent inhibitor of lipid biosynthesis (Bruck *et al*., 2009). Due to this mode of action, juvenile stages of sucking pests are especially affected. After foliar application, the compound penetrates the leaf cuticle and is translocated up to growing shoots and down to roots via xylem and phloem. This ambimobility renders it well suited for a wide range of crops, including ones (e.g. top fruit, hops) that are often difficult to target with conventional applications.

Cyantraniliprole (28)

Cyantraniliprole is currently the only member of the anthranilic diamide class of insecticides targeting the control of aphid species such as *M. persicae* and *A. gossypii* (Foster *et al*., 2012; Selby *et al*., 2013). Diamides act by activation of ryanodine receptors, which leads to uncontrolled calcium release in muscle (Lahm *et al*., 2009). The initial effect on aphids appears to be a substantial reduction in probing and feeding, with implications for lower transmission of plant viruses as well as aphid control per se (Jacobson and Kennedy, 2014).

Combination products

As well as being applied singly, insecticides can also be applied as combinations of active ingredients

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either through user-prepared tank mixes or preformulated products. Combinations may be inspired by the need to increase efficacy against a single pest, but more commonly are aimed at increasing the spectrum of control. One example of the latter is a combination of clothianidin and beta-cyfluthrin (Table 18.1), sold to control a wide range of soil-borne and foliar pests (including aphids) on sugar beet in the UK.

Adjuvants and synergists

The efficacy of some insecticides can be enhanced by the use of adjuvants in the mix. For example, ethyl fatty acid ester adjuvant (EOP) enhanced the efficacy of methomyl and endosulfan against aphids on maize, and of imidacloprid against aphids on cotton (Killick and Schulteis, 1998). This was attributed to a slowing of the recrystallization of the active ingredients in spray droplets, thus maintaining for longer a liquid state for increased contact. It was also suggested that the addition of EOP softened the cuticle of the insects, allowing increased uptake of the active ingredients.

The synergist MB-599 (proposed common name 'verbutin') was reported to enhance the activity of some aphicides, including pirimicarb, triazamate and imidacloprid, 2- to 4-fold against *A. gossypii*, *Acyrthosiphum pisum* (pea aphid) and *R. padi* (Szekely *et al*., 1996). The well-known synergist, piperonyl butoxide (PBO), has been shown to enhance the toxicity of pirimicarb and neonicotinoids against *M. persicae* and reduce the potency of resistance to these compounds, provided there is a time gap between exposure to the synergist and the insecticide (Bingham *et al*., 2008).

Application

Most aphicides in the 1980s were applied as sprays (Fig. 18.1), often in response to spray thresholds (e.g. Hull, 1968; George and Gair, 1979; Oakley and Walters, 1994), but sometimes according to prescribed programmes; for example, in potatoes for control of viruliferous aphids (Foster *et al*., 1994). Some insecticides, particularly formulations of carbamates, were applied as granules to the soil

Fig. 18.1. Spray application to sugar beet. (Photograph courtesy of Broom's Barn Research Centre, UK.)

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(e.g. aldicarb for control of *M. persicae* in sugar beet and potatoes). This was often done prophylactically at sowing (Fig. 18.2), before the need for insecticides can be assessed.

However, forecasting schemes are sometimes available to guide such usage (Harrington *et al*., 1989; Werker *et al*., 1998; Qi *et al*., 2004; Chapter 16, this volume). It is difficult to judge how much use farmers have made of these, as the usage of insecticides has tended to remain constant from year to year, irrespective of the forecast level of disease (Dewar and Smith, 1999). The advent of the xylem-mobile neonicotinoids has allowed these to be considered as seed treatments (Fig. 18.3) to replace the older chemicals, albeit also on a prophylactic basis.

Seed treatment of crops has a long history, but there have been major technological innovations over recent decades (Hairston, 2013). Crops that are protected with seed treatments include temperate cereals such as wheat and barley (Schmeer *et al*., 1990; Hofer *et al*., 2001), sugar beet (Dewar and Read, 1990; Proft *et al*., 1999; Dewar *et al*., 2002), oilseed rape (Birch and Nicholson, 2001; Coutts *et al*., 2010), lettuce (Ester and Brantjes, 1999; Parker *et al*., 2002), cotton (Zang *et al*., 1999; Leite *et al*., 2001), maize (Proft *et al*., 1999; Hofer *et al*., 2001) and sorghum (Krauter *et al*., 2001). The insecticides may be applied in several ways (Brandl, 2001): directly to the seed, either as a dressing or a film coat (as with oilseed rape and cereals); partially encrusted (as with sugar beet in Turkey); or to the outside of pelleted seed (as with sugar beet in most of Western Europe). When applied in this last manner, usually as a film coat (Halmer, 1994), the quantities of active ingredient applied to the land are much reduced. For example, the recommended rate of application of imidacloprid to sugar beet in the UK is 60 g a.i. per unit of seeds (1 unit = 100,000 seeds), which equates to just under 70 g a.i./ha, much less than the rate of aldicarb granules (760 g a.i./ha for aphid control) or sprays (e.g. pirimicarb at 140 g a.i./ha). In addition, with seed treatments the insecticide is placed only round the seed, whereas granules are applied along the whole furrow, and sprays over the whole soil and plant surface, thus potentially endangering more non-target organisms.

Fig. 18.2. Granule applicator for applying granules subsurface at the same time as sowing crop with systemic insecticide to protect young seedlings. (Photograph courtesy of G.A. Matthews.)

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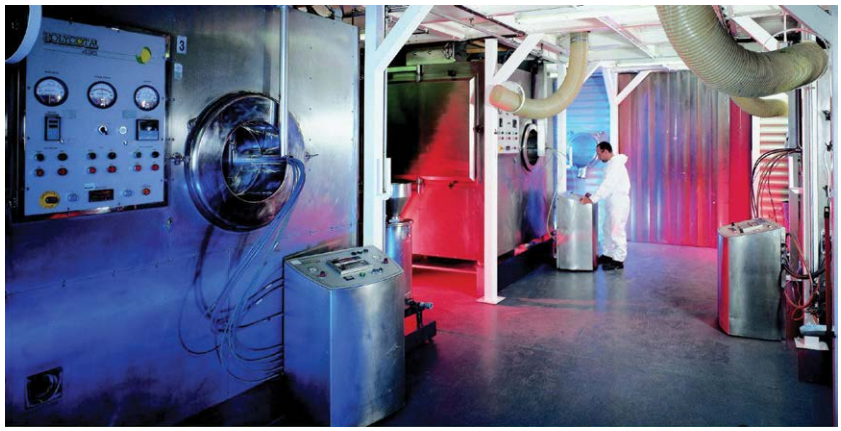

Fig. 18.3. A production plant for insecticide-treated seeds. (Copyright photograph courtesy of Germain's Technology Group, UK).

On the other hand, with seed treatments, the insecticides have to be applied when the seed is being prepared, often months before aphid attack, and this leads to prophylaxis and the potential for unnecessary exposure.

With cereal seed treatments, the same principles apply, but with less clear benefits to the environment. Imidacloprid is applied to wheat and barley at 0.7–1.5 g a.i./kg seed. When seed is sown at 50–150 kg/ha, this is 17–52 g a.i./ha (Ahmed *et al*., 2001; Miles *et al*., 2001). The alternative control for BYDV is well-timed pyrethroid sprays (Miles *et al*., 2001), applied at very low rates (*c*.7.5 g a.i./ha). However, pyrethroids are very active compounds that have to be applied overall, thus potentially affecting any non-target organisms as well as target pest(s).

Soil drench or granule treatments are an alternative for ensuring that the neonicotinoid active ingredients are transported to the most appropriate plant organs – the stems and leaves. Imidacloprid was applied as a soil drench to hops for control of *Phorodon humuli* (damson–hop aphid) (Martin *et al*., 1992), and was included in compost for controlling vine weevils (*Otiorhynchus* spp.) and, by default, also aphids on ornamentals in glasshouses (Pasian *et al*., 1997). Soil drenches of imidacloprid to transplanted tabasco pepper (*Capsicum annuum*) gave complete control of *M. persicae* 96 h after application and persisted for 5 weeks, covering the most susceptible stage (Diaz and McLeod, 2005).

Application can also be via irrigation systems (Fig. 18.4); for example, for aphid control in vegetables in Spain (Hernandez *et al*., 1999). However, by far the most commonly used method is foliar spraying, which can be timed for maximum efficacy, in relation to need rather than as a prophylactic.

There may be occasions when spatially restricted applications can yield adequate aphid control as well as reducing treatment costs. Limiting the application of insecticide to the borders of potato fields in the USA provided excellent control of colonizing *M. persicae*, with a 95% reduction in area treated compared to spraying entire fields (Carroll *et al*., 2009).

Injection of imidacloprid into the trunk of apple trees has been shown to be highly effective in controlling sucking pests such as leafhoppers and aphids (Van Woerkom *et al*., 2014). Another potential innovation, especially in protected cropping environments, is to deploy nets treated with a slow release insecticide formulation to provide a combined physical and chemical barrier to invading pest insects. Preliminary trials have shown this to be effective in restricting colonization by *A. gossypii* and reducing the incidence of aphid-transmitted viruses on cucumber (Dader *et al*., 2014).

Thresholds for Control (see also the IPM section of this volume)

Thresholds for control of aphids are useful to encourage rational use of pesticides and discourage prophylaxis. However, the use of thresholds requires a reasonably comprehensive monitoring scheme.

Wheat and barley

In these cereals, there has been a long-standing threshold in the UK of five aphids per ear prior to

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Fig. 18.4. Drip irrigation – systemic insecticide is metered into the flow line of the drip irrigation system to deliver water close to plants to optimize uptake through the roots. (Photograph courtesy of G.A. Matthews.)

flowering (Growth Stage [GS] 61) for control of *S. avenae* (George and Gair, 1979). This threshold still applies, but has been converted to the proportion of tillers infested (75%) (Oakley and Walters, 1994), which is more likely to be adopted by growers because it is quicker to assess than counting aphids on individual tillers. A similar system called EPIPRE was set up in The Netherlands in the late 1970s (reviewed by Ankersmit, 1989; Chapter 24, this volume), and is still operational (Bouma, 2003).

Significant increases in the use of pyrethroid sprays to control the vectors of BYDV in the autumn (usually *R. padi* and/or *S. avenae* in the UK) occurred after an epidemic of the disease in England following the mild winter of 1988/89 (Oakley and Young, 2000). Prior to this, control was often instigated in response to an 'Infectivity Index' (Plumb and Lennon, 1982), which took account of the number of aphid vectors caught in Rothamsted Insect Survey suction traps and the proportion of them carrying virus. The latter was measured by collecting live aphids in the autumn and testing them for virus transmission on indicator test plants (oats), and subsequently by ELISA (see also Chapter 16, this volume). Unfortunately, in the mild winter of 1998/89, significant spread of virus occurred following a low forecast (Harrington *et al*., 1994), and the ensuing loss of confidence in the forecasting system resulted in a much greater prophylactic approach to aphid control in winter cereals, encouraged by the low cost of pyrethroids (Oakley and Young, 2000). More recently, the Infectivity Index has been linked to winter weather records in an attempt to model overwintering spread of the virus (Foster *et al*., 2004)

Pea

Trials in combine peas conducted between 1985 and 1989 suggested that economic yield responses to aphicides could be obtained when control was applied, if 20% or more plants were infested with *A. pisum* and populations were increasing, at any time between flowering and when the pods were fully formed at the fourth truss growth stage (Lane and Walters, 1991). This entailed quite complicated monitoring, and required crop inspection at least twice to determine whether or not aphid numbers were increasing. Thus, it is not surprising that in 30% of sites examined by Walters *et al*. (1994), this threshold was not used. At these sites, aphid populations crashed dramatically even in the absence of insecticides. It was suggested that data on the timing of both the colonization of crops and the start of rapid increase of infestation were needed to forecast the need for and timing of insecticide applications.

For vining peas, the growing season is much shorter, and prior to 1994, no specific threshold

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had been determined. Control was applied routinely, irrespective of growth stage or infestation level (Biddle *et al*., 1994). Subsequent trials showed that a single spray of pirimicarb at either the visible bud stage or at first flower, when the proportion of plants infested was over 50%, could give economic yield responses; later sprays at first pod did not produce significant responses.

Field bean

Current guidelines for the control of *Aphis fabae* (black bean aphid) in field beans in the UK, based on the work of Way *et al*. (1977), suggest that control would be economically justified if more than 5% of plants were infested. However, more recent varieties may be more tolerant of aphid colonization, as single or multiple applications of pirimicarb at a range of growth stages and infestations did not produce significant yield increases (Parker and Biddle, 1998).

Brassicas

Routine spraying of brassica vegetable crops to control *Brevicoryne brassicae* (cabbage aphid) is widespread in Europe because there are no established thresholds (Blood-Smyth *et al*., 1992). Supervised treatments (i.e. applied according to need rather than in a programme), in this case a tank mix of pirimicarb and deltamethrin, were applied when more than 10% of plants were infested. Although the number of treatments was reduced from an average of 6.1 on the routinely sprayed plots to 1.6 on the supervised plots, the percentage of marketable produce also declined at four of the seven supervised sites. Most of the damage was caused by various caterpillars, which were controlled by the routine sprays.

By contrast, action thresholds have been developed for control of *B. brassicae* on spring and winter oilseed rape (Ellis *et al*., 1999). These authors suggest that when more than 10% of the racemes in a field are infested, control may be worthwhile. However, it is stressed that the cabbage aphid is a sporadic pest and rarely reaches such levels in rape crops.

Cotton

Thresholds of 100 aphids/plant have been implemented for carbofuran against mid-season epidemics of cotton aphids in Oklahoma, USA (Karner *et al*., 1997).

Sugar beet

The threshold for control of the vectors of virus yellows symptoms in sugar beet in the UK was established as one green wingless aphid per four plants when a spray-warning scheme was introduced in 1958 (Hull, 1968). The threshold has remained at that level since, although it has been modified to take account of the reduced susceptibility of plants to both aphids and virus infection with plant maturity (Dewar and Smith, 1999). After the 12- to 14-leaf stage, the threshold reduces to one aphid per plant. After the 16-leaf stage, usually achieved by early July, no further control measures are necessary because the plants become unpalatable to green aphids (Kift *et al*., 1997). At this stage, *A. fabae* usually becomes more prominent, but does not transmit the most abundant virus, *Beet mild yellowing virus* (BMYV), and is often controlled by the large number of predators and parasitoids at that time of year. Control measures are therefore not usually recommended.

Top fruit

Few control thresholds exist for aphids, with the multitude of other pests that can occur on fruit trees. However, the threshold for *Dysaphis plantaginea* (rosy apple aphid) on apples in Nova Scotia in Canada is 1.5 colonies/m of tree height (Hardman, 1992), though the paper does not make it clear what this sampling unit actually is.

Lettuce

Economic thresholds for *Nasonovia ribisnigri* (currant–lettuce aphid) in Spain were calculated from field trials to range from 0.06 to 0.13 aphids/plant, highlighting the very low pest densities at which sprays were needed in order to avoid the cosmetic damage that could reduce substantially the marketability of the crop (Morales *et al*., 2013).

Soybean

The recent colonization of soybean by *Aphis glycines* (soybean aphid) in the northern USA and Canada prompted large-scale experiments to investigate potential yield losses and decision-making thresholds. An economic threshold of 273 aphids/plant provided a 7-day lead time before aphids were expected to exceed an economic injury level of *c*.670 insects/plant (Ragsdale *et al*., 2007).

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Efficacy

The reasons for controlling aphids are twofold – to prevent direct feeding damage and/or to prevent or reduce the transmission of plant pathogenic viruses. Virus diseases can be spread by relatively few aphids, and control measures to prevent this often need to be applied early. If viruses are not of concern, control to prevent feeding damage is often best applied when a threshold for damage has been exceeded, rather than when aphids are first detected.

Poaceae (cereal crops)

Wheat and barley

Aphid control in cereals has two main targets – aphids carrying strains of BYDV and those causing direct feeding damage. The most important aphids carrying BYDV are *R. padi* and *S. avenae*. Control of the former is the focus of attention in many countries. Direct feeding damage is caused mostly by S. *avenae*, *Rhopalosiphum maidis* (corn leaf aphid), *Metopolophium dirhodum* (rose–grain aphid), *Schizaphis graminum* (greenbug) and *D. noxia*.

CONTROL OF BYDV. BYDV is most devastating when crops are infected as seedlings. Treatments applied when plants are very young are therefore likely to give the greatest economic return. However, sprays applied to growing crops are often not very persistent, and further sprays may be necessary to give sufficient protection when crops are most vulnerable, especially in spring-sown crops but less so in autumn-sown crops. Treatments in the autumn just need to be active until the autumn migrations of aphids cease, usually in late autumn.

The advent of seed treatments with enough persistence to cover the susceptible period has offered excellent alternative control strategies, particularly in autumn-sown wheat and barley crops in Europe. Although primary colonization by *S. avenae* or *R. padi* is not prevented, secondary spread of the viruses they may be carrying is reduced significantly by seed treatments such as imidacloprid (Knaust and Poehling, 1992, 1995; Gourmet *et al*., 1996; Hofer *et al*., 2001; Royer *et al*., 2005), thiamethoxam (Senn *et al*., 1998; Hofer *et al*., 2001; Stoetzer *et al*., 2014), or clothianidin (Meredith *et al*., 2002), often with consequent increases in yield. It is only the relative cost of such treatments compared to pyrethroid sprays that has limited their use by growers, although there may still be circumstances under which pyrethroids are as or more effective than seed treatments for virus suppression (Kennedy and Connery, 2012).

Even when aphids are active throughout the year, these seed treatments can be effective and replace some early sprays in the growing season. For example, in Kenya, the incidence of BYDV was reduced significantly in plots of barley sown with imidacloprid-treated seed and subsequently sprayed with cypermethrin; the main aphids controlled were *M. dirhodum* and *R. padi*, but *R. maidis*, *S. avenae*, *S. graminum* and *Hysteroneura setariae* were also present (Wangai *et al*., 2000). Imidacloprid seed dressing, followed by foliar sprays of the pyrethroid, alpha-cypermethrin, reduced the incidence of BYDV and increased yields of autumn-sown wheat in Western Australia, largely by controlling *R. padi* (McKirdy and Jones, 1996, 1997), and imidacloprid seed dressings to wheat and oats gave significant control of *R. maidis* and *R. padi* in trials in New York State, USA, reducing the incidence of some strains of BYDV in some years (Gray *et al*., 1996).

CONTROL OF FEEDING DAMAGE. Prevention of feeding damage in the early growth stages is particularly important in warmer climates, where rapid increases in aphid populations are possible in a very short time. Seed treatments again can offer more persistent protection than short-lived sprays. For example, imidacloprid applied as a seed treatment gave excellent control of both *R. maidis* and *S. graminum* for 6–8 weeks after sowing barley in the Sudan (Ahmed *et al*., 2001), for up to 100 days on barley in India (Singh and Venkateswarlu, 2000) and for 27–85 days after planting wheat and barley in the USA (Pike *et al*., 1993), the latter against *D. noxia*. Indeed, imidacloprid gave best control of *D. noxia* in many countries in Africa, where this aphid was especially prominent (Westhuizen *et al*., 1994; Tolmay *et al*., 1997), and protection often covered the whole season. The seed treatments were regarded as environmentally safer than broad-spectrum foliar sprays of the OPs, monocrotophos and dimethoate (Liu *et al*., 1999). Cold weather can influence the efficacy of OPs and pyrethroids applied to control *S. graminum* on winter wheat in the USA (Royer *et al*., 2011). It was concluded that producers could expect reasonable control so long as temperatures exceeded 13°C for 14 days following treatment.

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Maize

Maize is colonized mostly by *M. dirhodum* at an early growth stage, or by *R. padi* or *R. maidis* when plants are more mature. Again, the neonicotinoid seed treatments, imidacloprid, thiamethoxam, or clothianidin, gave significant improvements in yield by reducing feeding damage and/or BYDV infection in Belgium (Haesaert *et al*., 1998; Proft *et al*., 1999), Germany (Epperlein *et al*., 1997), France (Naibo, 1994), and the USA (Ohkawara *et al*., 2002; Andersch and Schwarz, 2003). However, the long persistence of imidacloprid when applied to maize and sunflowers has been blamed by French and Italian beekeepers for the sharp decline in honey production, especially in the south of the country (Schmuck, 1999; Schnier *et al*., 2003), and the insecticide has since been banned in these crops.

Sorghum

The same early control by imidacloprid seed treatments of infestations of *S. graminum* on sorghum, and in some cases reductions in virus infection with *Sugarcane mosaic virus* (SCMV), was demonstrated in several experiments in the USA (Harvey *et al*., 1996; Sloderbeck *et al*., 1996; Wilde *et al*., 1999).

Soft fruit

The main pest aphids in soft fruits are *Chaetosiphon fragaefolii* (strawberry aphid) in strawberries and *Amphorophora rubi* (Rubus aphid) in European red raspberries and blackberries. Very little research has been done with the newer insecticides against these aphids. Most control relies on encouraging natural enemies or developing resistant varieties (Easterbrook *et al*., 1997; Gordon *et al*., 1997; Meesters *et al*., 1998; Birch *et al*., 2003), although neem seed oil has been reported to give some control of *C. fragaefolii* on strawberries (Lowery *et al*., 1993). More recently, sprays of thiacloprid have given very good control of *Hyperomyzus lactucae* (blackcurrant–sowthistle aphid) and *Aphis schneideri* on blackcurrants in Poland, comparable to that given by acetamiprid (Labanowska, 2004).

Top fruit

Apple and pear

The most important aphids colonizing apples are *D. plantaginea* and *Aphis pomi* (green apple aphid). These two species can occur together, but the former causes greater damage to fruit and branch development (Brown and Mathews, 2007). *Eriosoma lanigerum* (woolly apple aphid) can cause problems in some countries.

Only foliar applications of insecticides (Fig. 18.5), and sometimes topical applications to tree trunks, are available for aphid control in fruit trees. The relative efficacy and persistence of products is determined by the timing of application in relation to petal fall and development of the fruit. Timing is limited by the need to protect pollinators from potential adverse effects.

In most studies, imidacloprid sprays gave better control of the target aphids than the OPs and pirimicarb that preceded them (Barbieri and Cavallini, 1997; Civolani *et al*., 2000), especially when the target aphids were resistant to the older insecticides (Delorme *et al*., 1997; de Fanti, 1997; Bylemans, 2000). Other neonicotinoids, such as acetamiprid and thiacloprid, have also been investigated, giving good control of *A. pomi* or *D. plantaginea* in Spain, France and Germany (Elbert *et al*., 2000).

The systemic properties of triazamate were exploited in many studies on fruit trees. For example, triazamate gave good control of *D. plantaginea* on apples and *Dysaphis pyri* (pear–bedstraw aphid) on pears in studies in France (Capou and Renou, 1999) and Switzerland (Schaub *et al*., 1999). However, this insecticide has since been withdrawn from use.

Imidacloprid as a drench (1 ml a.i./tree) to the roots of 'Granny Smith' apple trees in South Africa gave good control of subterranean populations of *E. lanigerum*, and also resulted in reduced aerial populations (Pringle, 1998). This method of application has least effect non-target organisms such as pollinators, but is probably not as fast-acting as sprays when pest populations develop quickly.

Citrus fruits

Aphis (Toxoptera) citricidus (tropical citrus aphid) was well controlled by foliar applications of imidacloprid to oranges in China (Zhong and Gan, 2000), but applications of this insecticide or acetamiprid to the trunks of citrus trees gave best control of this aphid in Brazil (Yamamoto *et al*., 2000) and Spain (Mansanet *et al*., 1999).

Other aphid species, such as those attacking Japanese apricot (*Prunus mume*), or *Aphis spiraecola* (green citrus aphid), *A. gossypii* and *Aphis (Toxoptera) aurantii* (black citrus aphid) on clementines

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Fig. 18.5. High-volume pesticide application to top fruit in Australia. (Photograph courtesy of H.F. van Emden.)

in the Pignataro Maggiore area of Italy, were also well controlled by imidacloprid sprays, which generally performed better than pirimicarb (de Biase and Russo, 1996; Xue, 2000). Pymetrozine gave as good control of *M. persicae* on peaches as pirimicarb, but was much more persistent, giving over 90% control for 21 days compared to only 7 days for pirimicarb (Flückiger *et al*., 1992a).

Plum (Prunus domestica)

The three most important aphid species attacking plums are *Brachycaudus helichrysi* (leaf-curling plum aphid), *Hyalopterus pruni* (mealy plum aphid) and *P. humuli*. Pirimicarb gave effective control of spring populations of *B. helichrysi* on plums and showed no damaging effects on natural enemies; as a result, the surviving predators kept mid- to late-season populations of *P. humuli* below economic thresholds (Hartfield and Campbell, 1996).

Solanaceae

Potato

The most important aphid pests of potatoes are *M. persicae*, *M. euphorbiae*, *Aphis nasturtii* (buckthorn–potato aphid), *Aulacorthum solani* (glasshouse and potato aphid) and *Rhopalosiphoninus latysiphon* (bulb and potato aphid). In some countries, other aphids such as *A. gossypii* and *A. fabae* can also cause problems in this crop (Rongai *et al*., 1998), although this is relatively rare. Most use of insecticides to control aphids on potatoes is to reduce infection by viruses such as PVY or *Potato leaf roll virus* (PLRV); direct feeding damage is relatively rare. Control of PVY is difficult with systemic products because the vector aphids (of which there are many species – see Chapter 29, this volume) can transmit the virus very quickly (Collar *et al*., 1997) before this type of insecticide can exert an effect; rapid-action insecticides such as pyrethroids, or oils that interfere with probing behaviour, are more effective in preventing PVY spread (Foster *et al*., 1994; Powell and Hardie, 1994).

Reduction in PLRV incidence is more achievable with the newer neonicotinoids, as only feeding aphids, which then become exposed to toxic doses, persistently transmit this virus. Transmission of PLRV was reduced substantially on plants treated with imidacloprid in the field (Woodford, 1992), and in a separate laboratory study, imidacloprid, thiamethoxam and pymetrozine gave greater reductions in PLRV

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transmission than older insecticides such as esfenvalerate, methamidophos, or oxamyl (Mowry, 2005). Pymetrozine also substantially reduced the acquisition of virus from infected plants. In field trials, granular or spray applications gave control of the aphid vectors of PLRV better than or equivalent to that by aldicarb granules (Meredith and Heatherington, 1992; Woodford and Mann, 1992; Turska and Pawińska, 1995; Boiteau *et al*., 1997; Boiteau and Singh, 1999).

Resistance to insecticides is a constant threat in the potato crop, particularly with *M. persicae*, so treatments that have different modes of action are likely to be most effective (Parker *et al*., 2006). Lambda-cyhalothrin and imidacloprid sprays gave very effective control of *A. gossypii* and *M. persicae* that were resistant to pirimicarb in laboratory studies on seed potatoes (Rongai *et al*., 1998), but pymetrozine gave over 90% control for 14 days of mixed populations of *M. persicae* and *M. euphorbiae* on potatoes in Italy. By comparison, the persistence of pirimicarb was less than 8 days (Flückiger *et al*., 1992a). An oil-dispersion formulation of thiacloprid improved control of *M. persicae* and *M. euphorbiae*, including clones that were resistant to other classes of insecticides (Bardsley and Lankford, 2005).

Tobacco

Control of virus diseases such as *Tobacco mosaic virus* (TMV) is the main objective of aphid control in tobacco, since aphids can open the plant to infection when they break the cuticular hairs as they move about (Harris and Bradley, 1973). Although TMV is not transmitted by aphids when probing, wounding allows the virus to enter. However, as with potatoes, there are problems with resistance in *M. persicae* (including subspecies *nicotianae*) to OPs and carbamates. Consequently, the neonicotinoids provide alternative control.

In India, an imidacloprid spray gave more persistent control (16 days) of *M. persicae nicotianae* on tobacco than acetamiprid (14 days), pymetrozine (12 days) and the OPs, acephate and oxydemeton-methyl (only 8 days) (Sreedhar *et al*., 1999). Plant hole treatments with imidacloprid or acephate also gave excellent control of this species (Patil *et al*., 1999), sometimes season long (Ramaprasad *et al*., 1998). In contrast, oxydemeton methyl sprays gave only 8 days effective control. In Italy, the most effective aphicides controlling *M. persicae* on tobacco were foliar applications of pirimicarb plus endosulfan and imidacloprid; granular formulations of benfuracarb and liquid formulations of azadirachtin gave inadequate control (Sannino, 1997). In Greece, a combination of methamidophos (OP) and imidacloprid provided substantial yield benefits through control of *M. persicae* and coexisting pests of tobacco (Deligeorgidis *et al*., 2007). Pymetrozine was shown to have significant effects on PVY transmission on tobacco by *M. persicae* (Margaritopoulos *et al*., 2010).

Tomato

Triazamate, used experimentally, gave good control of *M. euphorbiae* on glasshouse tomatoes in North Carolina, USA (Walgenbach, 1997). Pymetrozine gave poor control of *M. persicae* on beet but good control on tomatoes, due to the different distribution of this insecticide in chenopodiaceous plants compared to solanaceous ones (Wyss and Bolsinger, 1997). Systemic treatments of imidacloprid, thiamethoxam or flonicamid gave excellent and long-lasting suppression of aphid-borne *Cucumber mosaic virus* (CMV) and PVY on tomatoes in Italy (Fanigliulo *et al*., 2011).

Aubergine (Solanum melongena)

The neonicotinoids have proved to be more reliable than the older chemicals for controlling aphid pests of aubergines, as with other Solanaceae. Imidacloprid reduced aphid numbers on aubergines in India, increasing seedling height and total leaf chlorophyll (Jarande and Dethe, 1994), while clothianidin sprays gave control of both *A. gossypii* and *M. persicae* for more than 3 weeks without any phytoxicity (Ohkawara *et al*., 2002). Even longer persistence (56 days) was given by granules applied to the planting hole. As an alternative, pymetrozine gave as good control of *M. persicae* as pirimicarb for up to 20 days on aubergines in Spain (Flückiger *et al*., 1992a).

Chenopodiaceae (sugar beet)

The most important aphids in the various beet crops (*Beta vulgaris*) are *A. fabae*, *M. persicae*, *M. euphorbiae* and, in some countries (e.g. the USA), *Pemphigus fuscicornis*, a root aphid. Aphid control in beet aims primarily to reduce the spread of virus yellows caused by *Beet yellows virus* (BYV) or

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BMYV (Smith and Hallsworth, 1990). Aphids feeding, rather than just probing, spread both of these viruses; therefore, insecticides with systemic activity are likely to give the best control. However, not all these aphids (e.g. *A. fabae*) can transmit BMYV (San Román *et al*., 1995), so it is important to determine the most important vectors before devising control measures.

Imidacloprid applied as a seed treatment gives excellent control of aphids for up to 10 weeks after sowing, resulting in significant reductions in virus yellows infection and in consequent increases in sugar yield (Dewar and Read, 1990; Schmeer *et al*., 1990; Muchembled, 1991; Schaufele, 1991; Courbon, 1992; Dewar, 1992; Dewar *et al*., 1992; Heatherington and Meredith, 1992; Tossens *et al*., 1992; Wauters, 1993; Ayala *et al*., 1996; Wauters and Dewar, 1996; Proft *et al*., 1999; Cioni *et al*., 2001). In trials comparing control strategies, seed treatment with imidacloprid reduced virus infection to just 7%, compared to 12% with two spray applications of pirimicarb or triazamate and 25% with aldicarb granules; infection in untreated plots was 70% (Dewar *et al*., 1996). The persistence of the seed treatment was the main factor in such good control. More recent trials showed that clothianidin and thiamethoxam gave as good or better control of aphids and virus yellows than imidacloprid, reflecting their reported greater activity (Dewar *et al*., 2001, 2002; Meredith *et al*., 2002; Meredith and Morris, 2003).

As a spray treatment, triazamate gave good control of aphids compared to pirimicarb alone or mixed with deltamethrin (Dewar *et al*., 1996; Dewar and Haylock, 1997). The persistence of triazamate (at least 6 days) was much greater than pirimicarb against both *M. persicae* and *A. fabae* (Westwood *et al*., 1997). However, only imidacloprid as a seed treatment gave effective control of triazamate-resistant *M. persicae* (Dewar *et al*., 1998).

Although *A. fabae* transmits only one of the two yellowing viruses – the relatively uncommon BYV (San Román *et al*., 1995) – populations can become quite high in beet crops in some years, causing substantial direct damage. Often, the crops can compensate once the aphid populations have crashed due to predation, parasitization and disease in late July/early August (in the northern hemisphere), so control measures are often unnecessary. However, some yield losses from this species have been recorded in Sweden and in glasshouse trials in The Netherlands (Hurej and van der Werf, 1993a,b), illustrating the potential for damage. The neonicotinoid seed treatments do not give good control of *A. fabae*, as their effect has usually worn off when the main migrations to beet occur in early July (Dewar *et al*., 2002). Control then, if necessary, must rely on sprays, of which pirimicarb gives the best control while also preserving some natural enemies. In Spain, chlorpyriphos-methyl plus cypermethrin, oxydemeton-methyl, imidacloprid and thiometon were the most efficient at controlling very high populations of *A. fabae* (Ayala *et al*., 1996).

Control of root aphids is particularly difficult with conventional insecticides. However, triazamate was translocated downwardly and so, prior to its withdrawal, resulted in good control of *P. fuscicornis* on sugar beet roots in Greece (Ioannidis, 1996).

Fabaceae

Aphis fabae and *A. pisum* are the most important aphid pests of beans and peas. Unfortunately, because these legumes are regarded as minor crops in a world context, there is the problem in vegetable crops in general that the aphicides approved for use tend to be the older OPs, carbamates and pyrethroids, and newer insecticides have been slow to be introduced on any significant scale, despite demonstrations of their potential. Imidacloprid applied as a seed dressing protected broad bean plants throughout the whole season against *A. fabae* in Poland (Narkiewicz-Jodko and Rogowska, 1999). In contrast, *Macrosiphum albifrons* (lupin aphid), *Acyrthosiphon kondoi* (blue-green alfalfa aphid) and *Aphis craccivora* (cowpea aphid) on narrow-leaved lupin (*Lupinus angustifolius*) in Western Australia were controlled most effectively by alpha-cypermethrin, while *M. persicae* was best controlled by imidacloprid sprays (Thackray *et al*., 2000). The greatest reduction of the non-persistent CMV in lupins was given by the contact activity of alpha-cypermethrin; the systemic insecticides tested, including imidacloprid, methamidophos and triazamate, were ineffective.

In India, a foliar spray of imidacloprid gave better control of *A. craccivora* and thrips on groundnuts than the OP insecticides, dimethoate and demeton-S-methyl (Babu and Santharam, 2001).

In Korea, *A. solani* and *A. glycines* were well controlled by imidacloprid applied as granules for 52 days after sowing of soybean crops, with consequent reductions in the incidence of *Soybean*

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mosaic virus (SMV). Benfuracarb and acephate also gave good control (Kim *et al*., 2000). In the USA, the feeding behaviour and incidence of *A. glycines* was reduced significantly on soybean seed treated with thiamethoxam (Magalhaes *et al*., 2009; McCarville and O'Neal, 2013; Stamm *et al*., 2013), but other work has questioned the benefit offered by neonicotinoid seed treatments for controlling *A. glycines* under field conditions (Seagraves and Lundgren, 2012).

Brassicas

The main aphid species that damage vegetable brassicas are *M. persicae*, *B. brassicae* and *Lipaphis pseudobrassicae* (mustard aphid). As with the legumes, newer insecticides are gradually becoming available following studies on their control potential using different formulations and application methods.

Thiacloprid sprayed on cabbage foliage at 50 mg a.i./l gave complete control of *M. persicae* for 18 days in glasshouse trials (Elbert *et al*., 2000). Two applications of various doses of triazamate, lambda-cyhalothrin, imidacloprid and thiamethoxam suppressed populations of *L. pseudobrassicae* on cabbage crops for the entire season in Texas, USA (Liu *et al*., 2001). In India, one spray of imidacloprid was sufficient to give 99% control, although root dips of both imidacloprid and diafenthiuron were ineffective (Zhu *et al*., 1996; Sreekanth and Babu, 2001). Acetamiprid gave the highest mortality of *L. pseudobrassicae* in trials on mustard in India (Chinnabbai *et al*., 1999), and imidacloprid and pirimicarb sprays gave at least 90% control of *M. persicae* and *L. pseudobrassicae* on cabbage for up to 17 days in Chinese trials (Zhu *et al*., 1996). Pymetrozine applied at half field rate (0.0106 g a.i./ha) gave 99.8% control of *B. brassicae* on broccoli in laboratory studies, prompting a recommendation to reduce the rate even further to allow integrated management, including that given by natural enemies (Acheampong and Stark, 2004).

With other application methods, granules of imidacloprid controlled *M. persicae* and *B. brassicae* on Brussels sprout plants for 12 weeks after sowing (Schoonejans *et al*., 1991), while drenches to cauliflower root plugs gave as good control of *M. persicae* and *B. brassicae* as in-furrow applications in Californian trials (Natwick *et al*., 1996). Granules of 2% acetamiprid in the planting hole gave excellent control of *M. persicae* on cabbage (Takahashi *et al*., 1992), and imidacloprid, applied as a seed treatment in a formulated mix with beta-cyfluthrin to control flea beetles in oilseed rape, also controlled virus-carrying aphids (probably *M. persicae*), reduced the incidence of *Turnip yellows virus* (TYV) and increased yield by up to 16% (Birch and Nicholson, 2001).

Lettuce (*Lactuca sativa*)

Aphids are the most serious pest of outdoor lettuce in Europe (Ester *et al*., 1993; Ellis *et al*., 1996; Martin *et al*., 1996) and North America (Alleyne and Morrison, 1977; Forbes and Mackenzie, 1982; Toscano *et al*., 1990). The presence of any aphid on this high-value crop is not tolerated in today's supermarket culture, even though small numbers have no effect on yield. The public's aversion to insect presence has resulted in very rigorous control measures (Parker *et al*., 2002). In addition, lettuce is subject to several yield-reducing aphid-transmitted virus diseases such as *Lettuce mosaic virus* (see Chapter 26, this volume).

The aphid species that colonize lettuce include *Pemphigus bursarius* (lettuce root aphid), *N. ribisnigri*, *M. euphorbiae* and the ubiquitous *M. persicae* (Reinink and Dieleman, 1993; Collier *et al*., 1999). The latter three species can be controlled by foliar sprays of aphicides such as pirimicarb, demeton-S-methyl, pymetrozine and triazamate (Parker and Blood-Smyth, 1996), although *N. ribisnigri* is particularly difficult to control as it resides in the heartleaves. *Pemphigus bursarius* is also difficult to control as it lives on the roots, and none of the approved sprays are translocated downwards.

Applied as seed treatments, neonicotinoids (especially imidacloprid or thiamethoxam) have given aphid control for more than 7 weeks after sowing (Martin *et al*., 1996; Ester and Brantjes, 1998, 1999). Imidacloprid, applied in the seed furrow 7.6 cm below the seed, provided control of aphids on lettuce in Arizona, USA, for up to 100 days after sowing, resulting in 90% marketable heads compared to just 20% from untreated plots (Palumbo and Kerns, 1994). Foliar sprays of acetamiprid, imidacloprid, pymetrozine and pirimicarb gave good control 5 days after application against *N. ribisnigri* in Italy, but only a mixture of imidacloprid and cyfluthrin gave longer persistence (up to 19 days) (Gengotti, 2001).

Imidacloprid has given effective control of light infestations of *P. bursarius* (Parker and Blood-Smyth,

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1996). However, trials have shown downwardly translocated triazamate sprays gave better control (Parker *et al*., 2002). In the absence of either seed treatments or triazamate sprays, as many as 16 pirimicarb sprays were necessary to reduce infestation of plants by both foliar- and root-infesting aphids to commercially acceptable levels in these trials.

Other vegetables

The registration of novel insecticides in many countries these days is so expensive that many small-area vegetable crops are not target crops for major manufacturers. The use of new insecticides on these crops is often undertaken under an 'off-label' approval, the cost of which is borne by the users (the growers or trade organizations) rather than by the manufacturers. Nevertheless, the novel insecticides often give superior control of target pests than the older alternatives, and, due to ever more stringent safety requirements, are often much safer for the consumer. In this economic climate, studies on the efficacy of novel insecticides are relatively rare; a few are mentioned here.

Cavariella aegopodii (willow–carrot aphid) was controlled better and more rapidly by lambda-cyhalothrin than imidacloprid in laboratory studies in The Netherlands (Vercruysse *et al*., 2000). However, imidacloprid and a formulated mixture of lambda-cyhalothrin with pirimicarb gave adequate control of all aphid vectors of carrot motley dwarf (a joint infection by *Carrot mottle virus* (CMoV) and *Carrot red leaf virus* (CtRLV)) in parsley in field trials. The root aphid *Pemphigus phenax* was well controlled by imidacloprid, either as a seed treatment or foliar spray to carrots in Poland (Szwejda, 1997). Imidacloprid as a spray or via a drip irrigation system gave 'outstanding' control of aphids in vegetable crops in Spain (Hernandez *et al*., 1999). The latter application method had no effect on bees and other beneficial insects present in the crops. Imidacloprid, applied to glasshouse sweet and sharp pepper plants as a spray or via a hydroponic system, eradicated *M. persicae* for at least 8 weeks, depending on dose rate (Vantornhout *et al*., 1999). Thiacloprid gave best control of aphids on seedlings of chilli for up to 14 days after each spray (Walunj and Pawar, 2004). Another neonicotinoid, acetamiprid, showed residual activity against *A. gossypii* on glasshouse cucumbers for 2 weeks, compared to only 7 days for acephate (Takahashi *et al*., 1992).

Malvaceae

Cotton

The main pest aphid on cotton is *A. gossypii*. In many countries, imidacloprid, thiamethoxam and diafenthiuron have shown good efficacy against cotton aphids as either a seed treatment (Almand, 1996; Careme *et al*., 1996; Zang *et al*., 1999) or sprays (Almand, 1996; Furr and Harris, 1996; Hopkins and Donaldson, 1996; Layton *et al*., 1996; Wright *et al*., 1997; Koenig *et al*., 2000), especially when mixed with a pyrethroid (Hopkins *et al*., 2000). Some discrepancies in the reported efficacy of imidacloprid against *A. gossypii* were attributed to its feeding behaviour; it can avoid the internal glands of the cotton plants when it penetrates the leaf in its search for phloem. This means that it sometimes avoids lethal doses of insecticide and is not controlled quickly enough (Nauen and Elbert, 1994). Of the other neonicotinoids, thiacloprid gave much better control than methamidophos of *A. gossypii* on cotton in US trials (Elbert *et al*., 2000).

Pymetrozine has also been tested for its potential against cotton aphids, especially in the USA (Koenig *et al*., 2000). Pymetrozine sprays followed by cyhalothrin effectively reduced aphid numbers in non-irrigated or early irrigated cotton in Texas, but was less effective in late irrigated plots (Slosser *et al*., 2001). Over 80% of *A. craccivora* were controlled by pymetrozine in cotton trials in Egypt (Flückiger *et al*., 1992a).

Some evidence of phenotypic variability in aphid susceptibility to insecticides was reported in California. Here, *A. gossypii* reared on cotton under early-season temperature and photoperiod conditions was less susceptible to bifenthrin, chlorpyriphos and triazamate than those reared under late-season conditions (Godfrey and Fuson, 2001). The same species reared on melon plants was more susceptible to bifenthrin and chlorpyrifos than genetically identical clones reared on cotton. However, in leaf dip bioassays, diafenthiuron gave slower control of *A. gossypii* than conventional OPs and pyrethroids, but there was no evidence of cross-resistance in strains that were resistant to the latter (Denholm *et al*., 1995).

The widespread adoption of cotton varieties genetically modified to express toxins derived from the bacterium *Bacillus thuringiensis* (Bt) has transformed control of lepidopteran pests (the primary targets of Bt cotton). However, current Bt toxins

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have no activity against sucking pests such as aphids, so there is growing interest in potential interactions between transgenic plants and the continued application of conventional insecticides (e.g. Kaur *et al*., 2011).

Okra (Abelmoschus esculentus)

Imidacloprid seed treatment of okra increased plant height, leaf area and yield by giving effective control of aphids and jassids (Sreelatha Divakar, 1997). It was also the most effective spray treatment against *A. gossypii* in India when applied twice at 0.006% at a 15-day interval (Sunitha *et al*., 2005).

Other crops

Various methods of applying insecticides have shown good efficacy in some very minor crops, and especially against *P. humuli* on its secondary host, hop. Imidacloprid applied to hops through a drip system gave control of *P. humuli* for up to 2 years, compared to only 1 year with the OP disulfoton (Wright and Cone, 1999). In another study (in Poland), brushing imidacloprid on to plants at a low dose was as effective as spraying against *P. humuli* at higher doses (Solarska and Jastrzebski, 1998). Imidacloprid sprays in the Czech Republic gave 100% control of *P. humuli* compared to only 81% with cyfluthrin, due to the development of resistance (Vostřel, 1998). Surface granule applications to the plant crowns in April successfully controlled *P. humuli* in England; also, a spray to the base of the bines in May was as effective as the standard mephosfolan (Martin *et al*., 1992).

Good control of *Adelges (Adelges) laricis* (larch adelgid) and *Adelges (Sacchiphantes) abietis* (spruce pineapple-gall aphid) on trees was achieved in laboratory tests in Poland using sprays of acetamiprid, imidacloprid and other older insecticides (Labanowski and Soika, 1999). Imidacloprid gave as good control as autumn treatments of insecticidal soap or horticultural oil of *Adelges (Annandina) tsugae* (hemlock woolly aphid) on *Tsuga canadensis* and *Tsuga caroliniana* in eastern USA; the effects lasted for at least 1 year (Rhea, 1996). In later experiments, microinjections of imidacloprid into the active sapwood gave good control (Doccola *et al*., 2003). Injection (Fig. 18.6), implantation, or stem painting of amenity and forest trees with imidacloprid and methamidophos gave worthwhile control of some insect pests, including *Aphis grossulariae* (gooseberry aphid) (Scholz and Wulf, 1998). Of the range of insecticides tested, foliar applications of omethoate, dimethoate plus chlorpyriphos, vamidothion, imidacloprid and soil applications of disulfoton gave the best control of *Myzocallis coryli* (hazel aphid) on hazel (*Corylus avellana*) in Chile (Aquilera *et al*., 1996). In preliminary tests on pecan trees (*Carya illinoinensis*) in Cyprus, imidacloprid showed promising results against *Monellia caryella* (black-margined yellow pecan aphid) (Krambias, 1994). Best control of *Phyllaphis fagi* (woolly beech aphid) was given by imidacloprid sprays in German trials comparing 48 insecticides in a tree nursery (Losing, 1993). Monocrotophos, imidacloprid and dimethoate continued to give complete control of *Pentalonia nigronervosa* (banana aphid) for 40 days in New South Wales, Australia (Treverrow, 1996). *Tinocallis kahawaluokalani* (crape myrtle aphid) was prevented from causing serious damage to crape myrtle (*Lagerstroemia indica* – a landscape and nursery plant) by acephate, imidacloprid and thiamethoxam in studies in the USA (Pettis *et al*., 2005).

Fig. 18.6. Delivering systemic insecticide to mature plants by injection into the tree trunk and subsequent uptake to foliage. (Photograph courtesy of G.A. Matthews.)

Conclusions

The battle to control aphids will continue as long as these pests compete with humans for food resources. A new generation of insecticides with novel modes of action is adding resilience to aphid control and helping to compensate for the loss of older products through obsolescence or insecticide

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resistance. More targeted delivery systems are contributing to ensuring less exposure to potentially hazardous chemicals of non-target organisms and operators than in the past. Certainly, it is now possible to devise useful integrated pest management protocols for aphid problems. However, such protocols may often increase prophylactic use of insecticides, because their application as seed treatments or at sowing has to come before an assessment of risk can be made. In future, it is likely that the genetic modification of plants to resist pests, including aphids, will provide yet more options for control.

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19 Insecticide Resistance

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Introduction

Insecticide resistance is an example of a dynamic evolutionary process in which chance mutations conferring protection against insecticides are selected in treated populations. Over the past 30 years, great advances have been made in the characterization and understanding of such adaptations. These have provided valuable insights into the origin and nature of selection and microevolution in agricultural and horticultural environments.

In practical terms, the evolution of insecticide resistance has undoubtedly contributed to overall increases in the application of chemicals to crops. According to the USDA, in 2007, about 440,000 US tons of insecticide active ingredients were applied in the USA alone at a cost of roughly US$7.7 billion, with significant implications for both human health and the environment. Despite this, resistant insects, such as aphids, continue to affect our food and resource productivity. As a result, the phenomenon imposes a huge economic burden on much of the world; for example, an estimated annual cost of US$1.4 billion in crop and forest productivity in the USA alone (Pimentel, 2005). Moreover, it is proving impossible to combat resistance by embarking on a chemical 'arms race'. The development and registration of a new insecticide takes anywhere from 8 to 12 years and is expensive (as much as US$250 million), and the rate of discovery of new insecticidal molecules, unaffected by current resistance mechanisms, appears to be on the wane. Only by monitoring, characterizing and predicting the appearance and spread of resistance can we hope to use existing chemical tools in a sustainable manner.

Of the thousands of aphid species that exist globally, only a few have been reported as having developed insecticide resistance. However, some of these are ranked among the most problematic pests worldwide (Table 19.1). Some species are highly polyphagous, while others are virtually confined to a single plant species. They damage agricultural and horticultural crops through direct feeding, the transmission of plant viruses and by their impact on the aesthetic value of crops (by depositing honeydew or simply by being present). This has resulted in them being subjected to intense selection by aphicides, which has led to the evolution of a variety of resistance mechanisms. This chapter focuses on the diagnosis and characterization of these mechanisms, their impact on insecticide efficacy and, where known, the dynamics of resistance in aphid populations and the selection factors driving them. Emphasis is placed on developments since the publication of previous major reviews of this topic (Devonshire and Rice, 1988; Devonshire, 1989; Foster *et al*., 2007).

Diagnosis of Resistance in Aphids

Although many laboratory bioassay methods have been developed for detecting and characterizing resistance, most of these are limited to defining phenotypes and provide little or no information on the underlying genes or mechanisms. None the less, bioassays remain the indispensable mainstay of most large-scale resistance monitoring programmes, as

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Table 19.1. Insecticide-resistant aphid species (resistant species of primary importance shown in bold).

Species	Resistance first recorded	Compounds resisted[a]	Regions
Myzus persicae	Anthon (1955)	BPU, C, Nic, OC, OP, Py, Neo	Europe Asia USA South America Australia
Aphis gossypii	Ghong *et al*. (1964)	C, OC, OP, Py, Neo	Europe Asia USA Africa Australia
Schizaphis graminum	Peters *et al*. (1975)	OP	Asia USA Africa
Phorodon humuli	Dicker (1965)[b]	C, OP, Py	Europe
Nasonovia ribisnigri	Rufingier *et al*. (1997)	C, OC, OP	Europe
Sitobion avenae	Foster *et al*. (2014)	Py	Europe
Dysaphis plantaginea	Wiesmann (1955)	C, OP, Py	Europe
Macrosiphum euphorbiae	Foster *et al*. (2002d)	C, OP, Py	Europe
Aphis craccivora	Smirnova and Ivanova (1974)[b]	Nic, OC, OP, Py	Asia
Aphis fabae	Boness and Unterstenhofer (1974)	C, OP	Europe
Aphis nasturtii	Laska (1981)	C	Europe
Lipaphis pseudobrassicae	Tang *et al*. (1988)	OP, Py	Asia
Rhopalosiphum padi	Anon. (1974)[b]	OP	Europe Asia
Therioaphis trifolii maculata	Stern and Reynolds (1958)	C, OP	USA Australia

Notes: [a]BPU = benzoylphenyl ureas; C = carbamates; Nic = nicotine; Neo = neonicotinoids; OC = organochlorines; OP = organophosphates; Py = pyrethroids. [b]Communications to FAO cited by Georgiou and Lagunes-Tejeda (1991).

they are often first to be used in response to reports of suspected resistance and are essential prior to the development of alternative diagnostic techniques based on knowledge of the mechanism of resistance. Indeed, molecular techniques diagnose specific mutations, so unknown mutations can be missed when relying on this approach.

The phenotypic expression of resistance is usually assessed initially in small-scale laboratory bioassays by exposing aphids to topical, foliar, or systemic applications of insecticides (Devonshire and Rice, 1988). The response of potentially insecticide-resistant forms is, whenever possible, compared with known insecticide-susceptible standard baselines, allowing resistance factors to be calculated. The only way of being certain that a population is truly susceptible is to find one that previously has not been exposed to any insecticidal selection pressure. Such pest populations may be extremely rare, and therefore, in the majority of instances, susceptibility is a relative, rather than an absolute, concept. Moreover, even the natural, unselected variability between different populations of a species may result in differing responses to insecticides; that is, natural variation in sensitivity to a given compound is present in the insect population prior to selection by that compound. A further subjective distinction may be made, therefore, between 'resistance' as a selected mutation(s) conferring substantial protection against pesticide(s) and 'tolerance' or 'reduced sensitivity' that can exist in the absence of selection pressure. In pests where a susceptible baseline has not been established, resistance can be detected initially using bioassays applying an insecticide at an equivalent field rate, i.e. to challenge individuals to a realistic dose.

In addition to quantifying resistance per se in bioassays, it is important to establish whether such resistance is of practical importance in the field. One way to do this is to apply insecticides in a more realistic manner under field and pseudo-field conditions, e.g. using 'field simulators' (Foster *et al*., 2002a). These larger-scale approaches ensure that bioassays are correlated with potential field control

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problems. By allowing the expression of 'natural' insect behaviour under more realistic conditions (e.g. on whole, intact plants whose architecture can provide insecticide-free refugia), the actual exposure to an insecticide, applied as a foliar spray or seed treatment, is more closely achieved.

Biochemistry and Molecular Basis of Resistance

The information provided by the use of small-scale and field-scale bioassay techniques is essential. However, attention is becoming focused increasingly on the development of more incisive diagnostics that not only offer greater precision and throughput but also identify the specific mechanism(s) present, and even the genotype of the resistant insect (see also Chapter 2, this volume). Such information on the presence of particular mechanisms can help guide the choice of insecticides to control those populations of aphids. This is exemplified by research on *Myzus persicae* (peach–potato aphid), where significant advances have led to rapid and precise methods for the detection of different resistance mechanisms in individual insects.

Resistance mechanisms in *Myzus persicae* (peach–potato aphid)

Several approaches have been adopted for identifying the various resistance mechanisms, including electrophoretic or immunological detection of resistance-causing enzymes, kinetic and end-point assays for quantifying the activity of enzymes or their inhibition by insecticides and, more recently, DNA-based diagnostics for mutant resistance alleles. Besides its importance as a crop pest, one of the advantages of using an aphid species such as *M. persicae* for such research is that it is easy to maintain in pure-breeding, asexual, clonal lines in the laboratory. This facilitates a more incisive analysis of resistance than when dealing with obligate holocyclic species that are therefore predominantly sexual and genetically heterogeneous. However, there is increasing evidence, from karyotype studies using subtelomeric probes (Monti *et al.*, 2011, 2012), for substantial intraclonal variation in this species, especially in those chromosomes (1 and 3) associated with esterase gene amplification (Blackman *et al.*, 1978).

In northern Europe, *M. persicae* possesses at least six known coexisting resistance mechanisms: (i) an overproduced carboxylesterase conferring resistance to organophosphates (OPs) and carbamates (Devonshire and Moores, 1982); (ii) an altered acetylcholinesterase (AChE) conferring MACE (modified acetylcholinesterase) resistance to certain carbamates (Moores *et al.*, 1994a,b); (iii) target site (kdr and super-kdr) resistance to pyrethroids (Martinez-Torres *et al.*, 1997; Eleftherianos *et al.*, 2008); (iv) an overproduced P450 conferring moderate resistance to neonicotinoids (Puinean *et al.*, 2010); (v) target site (Nic-R^{++}) resistance to neonicotinoids (Bass *et al.*, 2011); and (vi) target site (Rdl) resistance to organochlorines (Anthony *et al.*, 1998). These mechanisms collectively confer resistance to most available aphicides (Table 19.1) and are illustrated in Box 19.1. It is now possible to diagnose all these mechanisms in individual aphids using molecular tools. The use of these techniques on field populations provides information on the dynamic occurrence of these mechanisms and can be used to provide up-to-date advice to growers on potential control problems with particular insecticides (Foster *et al.*, 1998, 2000, 2002d). It has also produced valuable insights into factors influencing the development of resistance and its impact on aphid management strategies.

Metabolic mechanisms

Resistance to OP, carbamate and pyrethroid compounds is commonly mediated by the enhanced hydrolysis of ester bonds. Hydrolytic enzymes can often be measured readily in the laboratory by the use of chromogenic compounds in conjunction with ester substrates such as naphthyl acetate and butyrate. An association between resistance in bioassays and enhanced 1-naphthyl acetate esterase activity was established in *M. persicae* by Needham and Sawicki (1970). This discovery proved central to our understanding of this type of resistance in this and other species. Devonshire (1977) confirmed that the enzyme hydrolysing the model substrate was the same as that responsible for resistance. This specific carboxylesterase enzyme shows a very high affinity for binding to the insecticidal esters. It is present in such large molar amounts that it can also sequester (encapsulate) a substantial proportion of a toxic dose, even without hydrolytic cleavage. The most effective and accurate method for high-throughput quantification is an immunoassay trapping the enzyme selectively in microplates with a specific antiserum before assay with 1-naphthyl acetate (Devonshire

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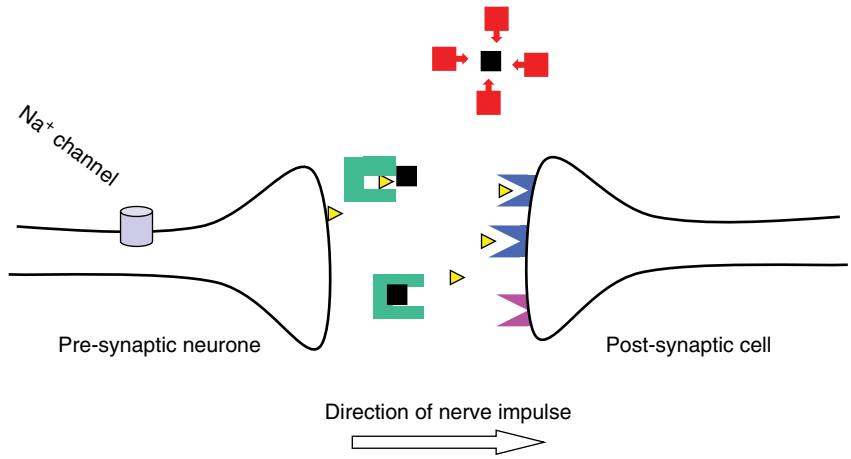
Box 19.1. Schematic diagram of an insect nerve synapse showing examples of insecticide target sites and resistance mechanisms.

Acetylcholine binds with acetylcholine receptors and is broken down by the action of acetylcholinesterase, which can be bound by carbamate and organophosphate insecticides, resulting in continuous firing of the neurone. Target-site resistance causing modified acetylcholinesterase stops these insesticides from binding but still allows the breakdown of acetylcholinesterase. Similar scenarios occur for resistance to other classes of insecticides such as pyrethroids and DDT, whose targets are sodium channels, and cyclodienes, whose targets are gamma amino butyric acid (GABA) receptors.

Metabolic resistance based on quantitative or qualitative changes in various enzymes results in insecticide molecules from a range of classes being sequestered or degraded.



et al., 1986). This technique provides high discrimination by allowing the relevant enzyme to be measured in the absence of contamination by the other esterases present in crude homogenates. In *M. persicae*, these overproduced, closely related carboxylesterases (E4 or FE4) confer strong resistance to OPs and lower resistance to carbamates and pyrethroids (Devonshire and Moores, 1982). Depending on their esterase content and response in laboratory bioassays, individual aphids can be classified broadly into one of four groups; S (susceptible), R_1 (moderately resistant), R_2 (highly resistant), or R_3 (extremely resistant) (Devonshire *et al*., 1986).

Detailed analyses of the underlying molecular genetic changes have implicated gene amplification as the cause of overproduction; that is, the acquisition of multiple copies of the E4 and FE4 esterase structural genes (Devonshire and Sawicki, 1979; Field *et al*., 1988, 1999). These studies have provided a paradigm for the development of resistance by gene amplification, with many subsequent studies of insecticide resistance in a wide variety of pest species drawing on the *M. persicae* model.

The carboxylesterase mechanism has become well established worldwide, with forms of *M. persicae* carrying greater resistance appearing to predominate only when they are under regular insecticide selection pressure. This probably stems primarily from their apparent reduced fitness under certain conditions, discussed below, together with a genetic change that can prevent amplified E4 genes from being expressed (this has not been seen for amplified FE4 genes), a phenomenon associated with methylation levels of the encoding DNA (Field *et al*., 1989). Such 'revertant' aphids retain the capacity to switch their esterase genes back on again when subsequently exposed to insecticide selection (Hick *et al*., 1996), and so constitute potential 'hidden resistance' when analysing populations by bioassay or esterase assays. Their identification requires a diagnostic for DNA

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methylation, which is not suited to high throughput (Field *et al*., 1996), so the incidence of such 'revertant' forms in the field remains unclear.

Myzus persicae has also developed metabolic-based resistance to neonicotinoids. These were introduced in the early 1990s and are now used widely around the world as both foliar and systemic applications. Initially, low-level resistance (<20-fold in topical bioassays) to imidacloprid, the first member of this class to be introduced (known as Nic-R), was found in *M. persicae* clones collected from the UK, mainland Europe, the USA, Zimbabwe and Japan (Devine *et al*., 1996; Nauen *et al*., 1996; Kerns *et al*., 1998; Foster *et al*., 2003a, 2008; see Nauen and Denholm, 2005, for a review of resistance to neonicotinoids in a variety of insect pests). Interestingly, this low neonicotinoid resistance, described as 'natural tolerance', was observed very soon after the introduction of imidacloprid in certain *M. persicae* populations, especially the tobacco-adapted *M. persicae nicotianae* (Devine *et al*., 1996; Nauen *et al*., 1996). In 2007, a clone of *M. persicae nicotianae* showing higher resistance (Nic-R$^+$) was collected from tobacco in Greece. This exhibited 30- to 60-fold resistance to different neonicotinoids (Philippou *et al*., 2009; Puinean *et al*., 2010). Insecticide bioassays using enzyme inhibitors suggested P450-mediated detoxification had a primary role in this resistance (Philippou *et al*., 2009; Puinean et al., 2010). Microarray analysis, using an array of probes representing all known detoxification genes in *M. persicae*, revealed constitutive overexpression (22-fold) of a single P450 gene (*CYP6CY3*) in the Nic-R$^+$ clone. Furthermore, quantitative PCR using genomic DNA as a template showed that this overexpression was due, at least in part, to a ninefold gene amplification (Puinean *et al*., 2010).

Because overexpression of *CYP6CY3* was initially identified in a tobacco-adapted *M. persicae* clone, the possibility that this specific P450 also played a role in providing protection from the plant secondary metabolite, nicotine (as it binds to the same nerve protein as neonicotinoids), was explored (Bass *et al*., 2013). Devine *et al*. (1996) and Nauen *et al*. (1996) had shown that *M. persicae nicotianae* had a reduced sensitivity to nicotine and cross-resistance to neonicotinoids. This was confirmed in artificial feeding assays on clones of *M. persicae nicotianae* (Bass *et al*., 2013). Quantitative PCR showed that *CYP6CY3* was highly overexpressed (10- to 75-fold) and the level of expression was correlated significantly with observed mortality in bioassays using nicotine. Significantly, two *M. persicae nicotianae* clones that were tested had been collected prior to the introduction of neonicotinoids, showing that the use of these insecticides had not initially selected for *CYP6CY3* overexpression. Functional expression of *CYP6CY3* in an insect cell line revealed that it was remarkably efficient at metabolizing nicotine to less toxic metabolites *in vitro* and could also detoxify the neonicotinoids imidacloprid and clothianidin, though at a much lower efficiency. When compared with *CYP2A6*, the main high-affinity metabolizer of nicotine in humans, *CYP6CY3* was found to metabolize both nicotine and neonicotinoids with greater efficiency. This may result from the larger active site of *CYP6CY3* being able to accommodate these substrates more easily. Confirmation that *CYP6CY3* conferred resistance *in vivo* came from transgenic expression in the common fruit fly, *Drosophila melanogaster*, with flies expressing the transgene displaying significant resistance to both nicotine and clothianidin. Together, these findings suggested that overexpression of *CYP6CY3* was a prerequisite for the host shift of *M. persicae* to tobacco and pre-adapted *M. persicae nicotianae* to resist neonicotinoid insecticides (to some extent) when they were introduced.

Target site mechanisms

ACHE. Mutant forms of AChE, showing reduced inhibition by OPs and carbamates, have been demonstrated in several aphid species. These compounds exert their toxicity by inhibiting AChE, thereby impairing the transmission of nerve impulses across the cholinergic synapses. Biochemical and molecular analyses of insecticide-insensitive AChE have shown that pests may possess several different mutant forms of this enzyme with contrasting insensitivity profiles, thereby conferring distinct patterns of resistance to these two insecticide classes.

For many years, increased esterase production was the only mechanism identified in aphids; even though others were known to play a primary role in other species, especially target site insensitivity to insecticides. AChE and the voltage-dependent sodium channel, the targets for OP/carbamate and pyrethroid insecticides, respectively, have been shown to contribute to resistance in aphids. Insensitive AChE in aphids was first identified in *Aphis gossypii* (cotton aphid or melon aphid) in

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1984 (Silver *et al*., 1995) and subsequently in *M. persicae* (Moores *et al*., 1994a) and *Schizaphis graminum* (greenbug) (Zhu and Gao, 1999). This mechanism is genetically dominant, so heterozygotes show resistance. In parthenogenetic populations, such as those common in the UK, the heterozygous genotype persists within clonal lineages, and homozygous resistant genotypes are rare in open field populations, as opposed to protected environments such as glasshouses. This may relate to the latter containing aphids that have probably arrived on imported plant material from more diverse populations abroad.

As with the esterase mechanism, insensitive AChE (also termed MACE) can be identified in individual aphids by using a microplate assay (Moores *et al*., 1994b), or more recently, using a Taqman-based DNA diagnostic (Anstead *et al*., 2008). The AChE target site mechanism confers strong resistance specifically to the dimethyl-carbamates, i.e. pirimicarb and the now unregistered triazamate (Moores *et al*., 1994a; Foster and Devonshire, 1999; Foster *et al*., 2002a). MACE in *M. persicae* was discovered initially in southern Europe, and subsequently in Japan, New Zealand and South America, and for the first time in North America in 2010 in the tobacco-adapted form (Srigiriraju *et al*., 2010). In the early 1990s, it showed a northward expansion in its European distribution, being found for the first time in abundance on UK crops in 1996 (Foster *et al*., 1998). In the UK, *M. persicae* carrying MACE are now very common and widespread, to the extent that aphid control guidelines currently do not recommend the use of pirimicarb against this aphid pest.

The molecular basis of this resistance has been identified in both *M. persicae* (Nabeshima *et al*., 2003; Andrews *et al*., 2004) and *A. gossypii* (Li and Han, 2004; Toda *et al*., 2004). It involves point mutations that alter amino acids close to the catalytic centre of the enzyme. The first mutation in both species changes a serine to phenylalanine (S431F), the latter normally being found at this position in the acyl pocket of the catalytic centre in most AChEs. This raises the possibility that the success of pirimicarb as a specific aphicide arises from its ability to inhibit the enzyme having serine at this position, which so far appears to be unique to aphids. Molecular diagnostics (Bass *et al*., 2014) now play a key role in monitoring the incidence of this and other target site resistance mechanisms (kdr and super-kdr for pyrethroids and Nic-R^{++} for neonicotinoids).

The S431F mutation commonly occurs in tandem with another (A302S), which forms part of the oxyanion hole of the active site. The S431F mutation appears to be primarily responsible for the substantially decreased sensitivity to pirimicarb by obstructing its access either spatially or by aromatic interaction between the enzyme and inhibitor; while the A302S confers a kinetic advantage by increasing the affinity (lower K_m) of the enzyme for its natural substrate, so offsetting the decrease in affinity attributable to the S431F mutation (Andrews *et al*., 2004). However, Toda *et al*. (2004) found aphids carrying only the A302S in field populations of *A. gossypii*, suggesting it carried no substantial fitness disadvantage.

Aphids, in common with some other insect species, carry two AChE genes: *ace1* and *ace2*. The mutations are normally found in *ace1*, which is the paralogue of the *Drosophila* AChE gene that is now referred to as *ace2* (Kim and Lee, 2013). The co-occurrence of the S431F and A302S mutations is not universal (Carletto *et al*., 2010). These authors did not evaluate the effect of the mutations on pirimicarb, but found resistance in another aphid, *A. gossypii*, to some OPs (especially dimethoate) conferred by S431F, which appeared to be enhanced by the presence of the mutation in the oxyanion hole (A302S). Conversely, molecular diagnostic analysis of *A. gossypii* populations has shown the presence of individuals carrying the A302S mutation in the absence of S431F (Toda *et al*., 2008), which is the main mutation in *M. persicae* (Benting and Nauen, 2004); although the enhanced catalytic efficiency of the enzyme conferred by A302S might confer some advantage on those individuals, the toxicological implications have not been determined.

KDR AND SUPER-KDR (KNOCK-DOWN RESISTANCE). Another target site mechanism, involving alleles of the sodium channel gene, termed knock-down resistance (kdr: L1014F) and super-kdr (super-kdr: M918T), has been identified as the main cause of resistance to pyrethroid insecticides (Martinez-Torres *et al*., 1999). Although detected in the late 1990s, kdr, conferred by changes in a voltage-gated sodium channel protein, was found in a number of *M. persicae* clones established in the laboratory over 20 years prior to its discovery, indicating that it had long been present in this species.

There is evidence of linkage disequilibrium between the MACE and kdr mechanisms (Fontaine

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et al., 2011), and the increasing incidence of *M. persicae* carrying multiple resistance genes, e.g. the MACE and super-kdr type that currently dominates in France (Fontaine *et al*., 2011; see below) and the UK. Initial recognition of the kdr mechanism in aphids was dependent on a molecular biological approach in which a highly conserved point mutation in the sodium channel gene was identified based on studies in kdr house flies and other pest species with the same mechanism (Martinez-Torres *et al*., 1997, 1999). Molecular diagnostic methods continue to be essential in understanding the role of this and other mechanisms in resistant aphids (Anstead *et al*., 2004, 2008). The kdr mechanism has been found at high frequency in populations in France reproducing sexually on peaches. It was homozygous in 20–56% of the aphids sampled and heterozygous in most of the remainder, regardless of whether the orchards were sprayed with pyrethroids during the sampling period (Guillemaud *et al*., 2003). However, the frequency increased overall by the end of the winter period, presumably due to pyrethroid usage. Sequencing of the intron regions within the sodium channel gene in *M. persicae* collected from different geographical areas suggests that the kdr and super-kdr target site mutations have multiple independent origins (Anstead *et al*., 2005). In recent years (2009–2015), the frequency of *M. persicae* carrying kdr has fallen dramatically in the UK.

More recently, an alternative super-kdr variant (M918L) has been identified in *M. persicae* (Fontaine *et al*., 2011). In this study, a further polymorphism in the sodium channel at position 932 causing an L932F amino acid substitution, also previously found in the head louse (*Pediculus humanus*), was identified in individuals with the L1014F mutation. Intriguingly, in most insect species, kdr/super-kdr mutations have been shown to be inherited as largely recessive traits; that is, little or no resistance phenotype is observed in heterozygotes. However, this does not appear to be the case in *M. persicae*, where L1014F, M918T and M918L heterozygotes all display a resistant phenotype to a range of pyrethroids (Eleftherianos *et al*., 2008; Fontaine *et al*., 2011); the reasons underlying this unusual expression need further investigation.

Although endosulfan is the only cyclodiene to have been approved for aphid control, molecular biological analysis has shown an association in *M. persicae* between resistance to this compound and the presence of a point mutation for resistance to dieldrin (*rdl*) in the gamma-aminobutyric acid (GABA) receptor found in a broad range of other species. Increased resistance (26-fold) to endosulfan was correlated with the replacement of a single amino acid (alanine 302) with glycine (Anthony *et al*., 1998). Other authors have also documented pronounced endosulfan resistance (Unruh *et al*., 1996; Kerns *et al*., 1998). Molecular diagnosis of French *M. persicae* populations on peaches (Guillemaud *et al*., 2003) showed that the frequency of the *rdl* mechanism decreased over winter, and this has been presumed to be due to a fitness cost (as found in other insect species).

RESISTANCE TO NEONICOTINOIDS. Although enhanced *CYP6CY3* expression confers low resistance to neonicotinoids in *M. persicae*, its practical significance is limited as it does not resist these insecticides when they are applied at the recommended rates for controlling aphids. Indeed, this Nic-R^{+} level of resistance continued to be the highest for two decades following the first use of neonicotinoids (a long time for a chemical class). However, this changed dramatically in 2009 when neonicotinoid spray failures occurred against *M. persicae* on peach trees in southern mainland Europe. Topical bioassays on a clone of *M. persicae* collected from southern France showed strong (>1000-fold) resistance (Nic-R^{++}) to neonicotinoids that would easily compromise their field efficacy (Bass *et al*., 2011; Slater *et al*., 2011). Synergist bioassays implied the presence of two resistance mechanisms in this clone; one based on the known enhanced detoxification by cytochrome P450 and another unaffected by piperonyl butoxide. Microarray and quantitative real-time PCR analyses showed that *CYP6CY3* was overexpressed, but at a level not significantly greater than that exhibited by other (Nic-R^{+}) clones. These findings suggested an additional mechanism conferring strong resistance, with a possible alteration of the neonicotinoid target site, the nicotinic acetylcholine receptor (nAChR). Binding of [^{3}H]-imidacloprid to membrane preparations of aphids from a Nic-R^{++} clone revealed that the high-affinity binding site present in susceptible *M. persicae* was completely lost in the Nic-R^{++} clone, and the remaining lower-affinity site was overexpressed and slightly altered, resulting in a substantial overall reduction in binding affinity. Subsequent sequencing of genes encoding the nAChR, a pentameric ligand-gated ion channel that may be assembled from α and non-α subunits,

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identified a point mutation in the loop D region of the β1 subunit that causes an arginine to threonine substitution (R81T). The importance of R81 in neonicotinoid binding has been highlighted by site-directed mutagenesis and homology modelling studies of vertebrate and insect recombinant receptors (Shimomura *et al*., 2006). Substituting the threonine residue in the chicken β2 subunit at this position with arginine or another basic residue was shown to enhance greatly the affinity of recombinant nAChRs (such as *D. melanogaster* Dα2/chicken β2 hybrids) for imidacloprid. Modelling suggested this resulted from direct interaction of the nitro group of imidacloprid with the introduced basic residue at this position (Shimomura *et al*., 2006). The R81T mutation therefore appears to confer a 'vertebrate-like' quality to the β1 subunit of resistant aphids, resulting in reduced sensitivity of the nAChR to neonicotinoids. Recent work has shown other insecticide classes that act on the nAChR are also affected by the R81T mutation, including the sulfoxamines (sulfoxaflor) (Cutler *et al*., 2013).

In summary, the Nic-R^+ phenotype is conferred by increased P450 production through gene amplification and overexpression, and this same mechanism is enhanced in Nic-R^{++} by insensitivity of the nAChR to various insecticides for which it is the target.

Aphid superclones

The biochemical and molecular genetic diagnostics described above have provided an unparalleled understanding of the incidence and impact of the different resistance mechanisms, especially in *M. persicae*. In particular, it is clear that, as a consequence of prolonged parthenogenesis in field populations, combinations of mechanisms can become 'locked together' in 'superclones' so that they are co-selected, even when the insecticide used is unaffected by some of the mechanisms present (Devonshire *et al*., 1998). This has been demonstrated using microsatellite polymorphisms that have defined a limited number of *M. persicae* clones in the UK population over the years (Fenton *et al*., 2005). Recently, two such superclones (O and P) have come to predominate (Fenton *et al*., 2010) at the apparent expense of aphids with kdr. It is thought that this is because they carry super-kdr (conferred by the M918L mutation) coupled with MACE (both in the heterozygous state), which confers strong resistance to pyrethroids and pirimicarb insecticides, respectively. These mechanisms have been brought together in a genetic background (through sexual reproduction abroad) that is well adapted for survival in the UK, particularly during cold or wet winters such as those seen in 2012/13 and 2013/14, respectively. Fontaine *et al*. (2011) reported strong linkage disequilibrium between these genes in French populations. The discovery of the M918L mutation in the O and P clones was made by serendipity. Prior to this, it was unclear why both clones were common in the UK despite not carrying kdr, or the only super-kdr mutation (M918T) known at that time, while being exposed to pyrethroids in the field. The presence of the M918L mutation was only realized after these clones were used as supposed non-kdr/non-super-kdr standard clones to screen a pyrethroid that then revealed strong resistance (S. Foster, unpublished).

There is evidence for the widespread build-up of aphid 'superclones' around the world (Vorburger *et al*., 2003; Criniti *et al*., 2006; Carletto *et al*., 2010; Fenton *et al*., 2010; Loxdale *et al*., 2010; Chen *et al*., 2013), and it would be worth exploring any association of this phenomenon with resistance gene linkage and insecticide usage. A transcriptome approach (Silva *et al*., 2012) should offer opportunities for such analysis, and in particular for understanding the multiplicity of resistance mechanisms in such populations.

Resistance mechanisms in other aphid species

Aphis gossypii *(cotton aphid or melon aphid)*

Several approaches have been adopted for identifying the various resistance mechanisms. Several studies on *A. gossypii* carried out in the USA (O'Brien *et al*., 1992) and Japan (Saito, 1989; Hosoda *et al*., 1992) have found a link between esterase activity and OP resistance. It has been reported that OP-resistant clones can have 15–35 times more carboxylesterase activity than susceptible clones, and that particular esterase-banding patterns are closely associated with high total enzyme titres and moderate OP resistance (Suzuki and Hama, 1998). Resistance has not, however, been ascribed to a single enzyme but to a group of different isoenzymes. If carboxylesterases confer resistance to OPs in *A. gossypii*, it is clearly through a different mechanism to that in *M. persicae*, where usually only one or the other of two very closely

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related isoenzymes becomes amplified. Furthermore, OP resistance in *A. gossypii* cannot always be ascribed to carboxylesterase-based mechanisms. An association of OP resistance with high oxidase titre has been inferred (Sun *et al*., 1970), and Delorme *et al*. (1997), using synergists, questioned whether oxidases or esterases played a role in OP resistance. Han *et al*. (1998) has concluded that most OP resistance is due to an altered target site.

Shang *et al*. (2012) compared a susceptible and an OP- and carbamate-resistant (10- to 35-fold following 60 generations' selection with omethoate) strain from China and found no involvement of esterases in resistance. Instead, resistance was associated with increased oxidase activity, as judged by the dealkylation of model substrates, which was reflected in a twofold synergism of omethoate toxicity to the resistant strain by piperonyl butoxide. The resistant strain also had a modified AChE with three- to tenfold insensitivity to OPs, and further studies revealed that the insensitivity was associated with mutations in *ace2* and that this gene was duplicated compared to the *ace1* gene, which appeared to offset the inferior catalytic activity of this mutant enzyme (Shang *et al*., 2014).

In vitro studies of OP resistance in *A. gossypii* have shown that it is commonly linked to the presence of insensitive forms of AChE (Gubran *et al*., 1992; Delorme *et al*., 1997). However, the earliest example of this type of resistance mechanism in any aphid species was very specifically to the carbamate, pirimicarb (Gubran *et al*., 1992; Silver *et al*., 1995), a compound introduced in 1969. This form of resistance then became common in the 1970s and proved to be particularly problematic when pirimicarb became a mainstay of many other integrated aphid control programmes, due to its general low toxicity to beneficial insects (Furk *et al*., 1980). The esterase-banding pattern typical of OP resistance is not associated with pirimicarb resistance (Takada and Murakami, 1988; Saito and Hama, 2000).

Mutated AChE in some strains of *A. gossypii* from around the world (e.g. Gubran *et al*., 1992) is very specific, protecting against pirimicarb, but not the monomethyl or oxime carbamates or OPs (Silver *et al*., 1995), while other forms of the enzyme also confer OP resistance (Moores *et al*., 1996; Han *et al*., 1998). Indeed, there is evidence of slight hypersensitivity to bendiocarb conferred by the pirimicarb-insensitive enzyme (Villatte *et al*., 1999), although it is not sufficient for exploitation in an anti-resistance strategy, owing to fitness costs negating practical benefits.

Pyrethroid resistance is common in *A. gossypii* from around the world; for example, in Israel (Ishaaya and Mendelson, 1987), China (Tang, 1992; Guilin *et al*., 1997), Japan (Saito *et al*., 1995), the USA (O'Brien *et al*., 1992) and Australia (Marshall *et al*., 2012). Molecular analysis (PCR-RFLP) of Australian populations identified the 'ubiquitous' kdr mutation (L1014F) in a heterozygous state in a highly resistant strain, but did not find the M918L super-kdr mutation (Marshall *et al*., 2012). However, some resistant individuals have been found unequivocally to have super-kdr-type mutations, in the absence of kdr mutations, in their sodium channel genes (X. Yang and M. Williamson, unpublished). It thus appears that mutation at either position can confer pyrethroid resistance. Resistance to this class of insecticide can be extremely high (>20,000-fold), and it can be affected by the host plant used for the bioassay, although this should have little effect on resistance conferred by target site mutations. Strong resistance to neonicotinoids, conferred by the R81T target site mutation first reported in *M. persicae*, has been found recently in *A. gossypii* (Shi *et al*., 2012).

Schizaphis graminum *(greenbug)*

Clonal *S. graminum* lines established from insects collected from areas of control failure in Kansas, USA, have exhibited 20- to 30-fold resistance to OP insecticides such as parathion (Sloderbeck *et al*., 1991). As in *M. persicae*, these resistant forms displayed enhancement of general esterases based on PAGE and staining with 1-naphthyl acetate.

In subsequent investigations, two different patterns of esterase isozymes with different genetic bases were detected in resistant forms (e.g. Siegfried and Ono, 1995). These have been categorized variously as Type I/Type II patterns or R1/R2 patterns. We will use the former categorization. Type I forms exhibit a single esterase band that is either absent in susceptible insects or expressed at levels below the limits of detection. Type II forms exhibit a different pattern of enhanced esterase isozymes (Ono *et al*., 1994a). After testing over 10,000 individuals, Shufran *et al*. (1996) found that none displayed both Type I and Type II esterase polymorphisms. In addition to marked differences in electrophoretic mobility, the two resistant forms showed striking differences in general esterase activity when measured spectrophotometrically from

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S. graminum homogenates. Both forms were active against a series of 1-naphthol esters, but Type II forms displayed 15-fold higher levels of activity than Type I forms. Type I forms appeared to result from the enhanced production of an esterase enzyme that cross-reacts with an antiserum to E4 from *M. persicae* (Siegfried *et al*., 1997). This similarity between the two species has been reinforced by comparison of the esterase gene sequences and the demonstration that, as in *M. persicae*, the genes are amplified and also methylated (Ono *et al*., 1999). For both esterase forms, activity towards parathion is similar, but strong inhibition by the active metabolite paraoxon has been noted. This suggests that the mechanism of resistance does not involve true enzymatic hydrolysis, but rather that these enzymes have a sequestrating role (Ono *et al*., 1994b). Zhu and He (2000) also suggested that Type II esterases could not utilize paraoxon and chlorpyrifos-oxon efficiently as their substrates and that elevated esterases contributed to OP resistance by sequestration.

Partially purified enzymes from Type I-resistant and -susceptible *S. graminum* strains exhibited similar elution profiles by ion exchange chromatography, although the activity peak from the resistant strains was greater in both height and total area. Kinetic analysis of the resulting activity indicated that the K_m of the esterase was identical for the resistant and susceptible strains. Resistance is therefore associated with the overproduction of isozymes already present in the susceptible strain, rather than the presence of enzymes with altered properties (Siegfried and Zera, 1994).

DNA from Type I forms and a clone derived by crossing Type I and Type II displayed a restriction fragment pattern different from that of Type II and susceptible clones, and an increased hybridization signal compared to susceptible insects. This suggested that the mechanism behind Type I esterase activity might be gene amplification, but that Type II elevated esterase activity resulted from a different genetic mechanism (Rider *et al*., 1998). Shufran *et al*. (1997) found that resistance patterns to a variety of OP and carbamate compounds in Type I and Type II strains differed.

Analyses of *S. graminum* cDNA have resulted in the identification of two AChE DNA fragments. One is closely related to the AChEs found in several insect species, mutant forms of which are now believed to mediate OP and carbamate resistance in a range of insects (Gao and Zhu, 2001, 2002). In studies on OP-resistant clones of *S. graminum*, Zhu *et al*. (2000) examined AChE activity and found it to be slightly less sensitive (2.5-fold) to inhibition by various OP compounds. This is quite different to the very strong insensitivity seen in *M. persicae* and *A. gossypii*. These authors suggested that alterations to AChE were responsible for resistance to OP insecticides. Northern blot analysis (which examines expression levels) did not show overexpression of the AChE gene, and so it is thought that a qualitative, rather than quantitative, change in *S. graminum* confers resistance.

Phorodon humuli *(damson–hop aphid)*

The underlying mechanisms of resistance in *Phorodon humuli* are not well documented, apart, perhaps, from an association between esterases and OP resistance. In *P. humuli* collected from wild and cultivated hop plants in Switzerland, a positive correlation was observed between esterase activity and OP resistance (Beck and Buchi, 1980). In the UK, clones of OP-resistant *P. humuli* had high esterase isoenzyme activity in a complex of bands that was almost absent in susceptible populations (Lewis and Madge, 1984). The antiserum to carboxylesterase E4 from *M. persicae*, which is a closely related species, cross-reacts with homogenates of *P. humuli* (Devonshire *et al*., 1986), showing that increased esterase activity arises from the overproduction of protein(s) homologous to E4. Others have also described methods for measuring esterase activity in *P. humuli* and correlated these with OP resistance (Wachendorff and Zoebelein, 1988). Although the association of esterases with OP and carbamate resistance is established, Buchi (1981) found that pyrethroid resistance in some populations of both *P. humuli* and *M. persicae* did not correlate with high carboxylesterase activity.

Nasonovia ribisnigri *(currant–lettuce aphid)*

In some areas of Europe, a large proportion of the *Nasonovia ribisnigri* population occurs on lettuce during the summer months and the crop is subject to heavy insecticide use. Resistance was first detected in strains collected from southern France and Spain, with resistance factors ranging from 12-fold to acephate (an OP) up to 660-fold to the cyclodiene, endosulfan, in bioassays (Rufingier *et al*., 1997). Maximum resistance to the pyrethroid, deltamethrin, and the carbamate, pirimicarb, was 28-fold and 19-fold, respectively. It was

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speculated that both enhanced detoxification and altered target site(s) were involved.

In the late 1990s, following increasing reports of reduced insecticide success in the field, leaf-dip bioassays were used to compare the activity of several insecticides against suspected resistant *N. ribisnigri* strains from UK lettuce (Barber *et al*., 1999). In comparison to a susceptible strain, these showed widespread low-level resistance to pirimicarb (7- to 11-fold), and very low (two- to fourfold) resistance to pyrethroids and OPs. In some *N. ribisnigri* strains, resistance was associated with a strong esterase band disclosed by staining with naphthyl acetate after PAGE. This might imply a similar overexpression of esterases analogous to that causing resistance in *M. persicae*, but the molecular basis of increased esterase activity has not been investigated.

Rufingier *et al*. (1999) showed that insensitive AChE in *N. ribisnigri* conferred resistance to pirimicarb and propoxur, but was not responsible for methomyl, acephate, or paraoxon resistance. Glutathione transferases were inferred to contribute to endosulfan resistance, based on synergism studies with DEF (S,S,S-tributyl phosphorotrithioate) and enhanced activity with the model substrate DCNB (1,2-dichloro-4-nitrobenzene). However, there was no evidence for the altered target site (GABA receptor) commonly found in other cyclodiene-resistant insects (ffrench-Constant *et al*., 1996), including *M. persicae* (Anthony *et al*., 1998). An altered AChE did not appear to contribute to pirimicarb resistance in UK *N. ribisnigri* strains (Barber *et al*., 1999).

Sitobion avenae *(English grain aphid)*

Although *Sitobion avenae* is one of the most widespread and abundant aphid species, its status as a pest is usually moderate. Pirimicarb resistance has been recorded in Chinese populations and the underlying mechanisms studied in a strain following selection for 20 generations with this compound (Chen *et al*., 2007). This showed 160-fold resistance, together with 33-fold resistance to omethoate and monocrotophos, but with little resistance to deltamethrin or thiodicarb. Enhanced esterase activity appeared to contribute broad but low-level resistance across all compounds tested, complemented by AChE insensitive to pirimicarb and OPs. Sequencing of both AChE genes, *ace1* and *ace2*, revealed one mutation in each consistently found in resistant individuals: L436S in *ace1* and W516R in *ace2*, both of which were novel. However, L436S sits in the same α helix (forming part of the acyl pocket) as the S431L mutation implicated in AChE insensitivity in other aphid species, while W516R is close to the key histidine in the catalytic triad of the enzyme, so both are well placed to influence enzyme-inhibitor interactions. Further work is needed to establish their role unequivocally.

Foster *et al*. (2014) first identified the single classic kdr point mutation (L1014F) in the domain IIS6 segment of the sodium channel in UK *S. avenae* samples collected from cereal crops where there had been reduced pyrethroid spray efficacy. Contact bioassays in glass vials of SR *S. avenae* clones and clones homozygous for the wild-type allele (SS) showed that aphids carrying the mutation had significantly higher resistance (40-fold) to lambda-cyhalothrin. This is consistent with the reported effect of this mutation on pyrethroid sensitivity in other aphid species. Testing of archived aphid samples collected in suction traps showed that kdr *S. avenae* were present in the UK population as early as 2009, with their frequency increasing in subsequent years to levels of over 50% at some trap sites. Interestingly, all kdr aphids tested to date have been heterozygotes (SRs), which may be due to kdr being found in one or a few asexual clones, or to kdr homozygotes suffering a substantial fitness cost.

Macrosiphum euphorbiae *(potato aphid)*

This is a highly polyphagous species occurring on potatoes, lettuce, sugar beet and ornamentals. However, unlike *M. persicae*, with which it shares much of the same host range, this species has never been documented as posing a threat to the efficacy of insecticides. Despite this, many *Macrosiphum euphorbiae* clones isolated from field potatoes in England and Wales since 1998 have produced cross-reactions in an immunoassay designed to measure levels of E4/FE4 carboxylesterase resistance in *M. persicae* (Foster *et al*., 2002c). Mean immunoassay values of each *M. euphorbiae* clone fell within the S–R_2 *M. persicae* range. These values were correlated closely with the response of the *M. euphorbiae* clones to pirimicarb (a dimethylcarbamate), dimethoate (an OP) and lambda-cyhalothrin and deltamethrin (pyrethroids). Furthermore, analysis of esterase levels in *M. euphorbiae* field samples, in comparison with insecticide

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treatment history, and assessments of survival under semi-field conditions against pirimicarb, applied at different rates, produced strong evidence for selection favouring the very high esterase forms. However, a recent survey of *M. euphorbiae* collected from potatoes in England and Scotland in 2013 failed to find any aphids carrying high or very high resistance, suggesting that these forms are not being selected under current insecticide application regimes (S. Foster, unpublished).

Insensitive AChE has been found in a Tunisian *M. euphorbiae* population (Raboudi *et al*., 2012). It was associated with the A302S mutation, common in other resistant aphid species, and with low-level resistance to pirimicarb. However, it is difficult to determine the degree of resistance from the data presented, which were based on the application of multiples of the field rate of pirimicarb, but with no susceptible baseline for a reference. The mutation was not associated with the S431F mutation commonly found in *M. persicae* and *A. gossypii*, illustrating the viability of A302S on its own. It was found by PCR amplification of the AChE gene homologous to *ace1*, the main synaptic AChE modified in resistant aphids, in other species.

Factors Affecting the Dynamics of Insecticide Resistance in the Field

Selection pressures

One of the most intensive studies of resistance dynamics in any pest species involves UK *M. persicae* populations. In the 1970s, R_2 and R_3 OP-resistant esterase forms were documented only in glasshouses. There was then a gradual general increase in their frequency in the field, but annual monitoring of aphids on a range of crops and in aerial trap samples (Muggleton *et al*., 1996; Foster *et al*., 2002d) showed that R_1 and S aphids still tended to predominate. Periodically, however, esterase resistance has escalated, as in 1996 when samples taken from a range of crops contained high proportions of R_2 and R_3 aphids (Foster *et al*., 2002d). Furthermore, many of these individuals also carried the MACE and kdr mechanisms; a combination that led to significant control failures on potatoes and Brussels sprouts (Foster *et al*., 1998). The reasons for this rapid and dramatic upsurge in resistance remain unclear, but probably include early-season applications of pyrethroids aimed at the unusually large influx of the noctuid *Autographa gamma* (silver Y moth) into the UK in that year. This may have inadvertently killed many aphid predators and parasitoids, allowing *M. persicae* to proliferate in the favourable spring and summer conditions. In certain areas, growers were then forced to apply a variety of insecticides, which probably selected heavily for the esterase, MACE and kdr mechanisms. However, in subsequent years up to 2000, field samples taken from various crops showed a progressive decline in the frequencies of high esterase and MACE forms (Foster *et al*., 2002d). This apparent instability most probably reflected selection gradually acting through associated fitness costs (Crow, 1957 – see below), coupled with the response of growers to up-to-date advice on resistance management. In more recent years, MACE forms, also carrying R_1 esterase levels and the newly discovered super-kdr (M918L), have become common in UK field samples (Fig. 19.1).

Ecological factors

Given the breadth and diversity of resistance mechanisms reported to date, it can confidently be assumed that no insecticide, however novel or unconventional in its effect, is immune to the evolution of resistance. The probability of achieving detectable frequencies depends instead on a suite of ecological and genetic factors and how these interact with pesticide usage patterns (reviewed by McKenzie, 1996; Denholm *et al*., 1998). As a consequence, the same product can face very different resistance risks with different species, and even within the same species in different cropping systems.

The prevalence of resistance to the long-established insecticide groups (OPs, carbamates and pyrethroids) among aphid pests of UK agriculture and horticulture provides a case in point. The three aphid species that historically have proved most problematic are *M. persicae*, *A. gossypii* and *P. humuli*. Their capacity to evolve resistance can, to an extent, be rationalized in hindsight in terms of differing life histories and the crop systems they inhabit. During the summer, *P. humuli* is virtually restricted to wild and cultivated hops, on the latter of which insecticides are the predominant means of aphid control. If insecticide resistance in UK populations of *P. humuli* on wild hops and on primary hosts were low (Lewis and Madge, 1984; Furk and Baxter, 1988), immigration of susceptible insects into commercial crops might help to ameliorate selection for resistance. This clearly has not been

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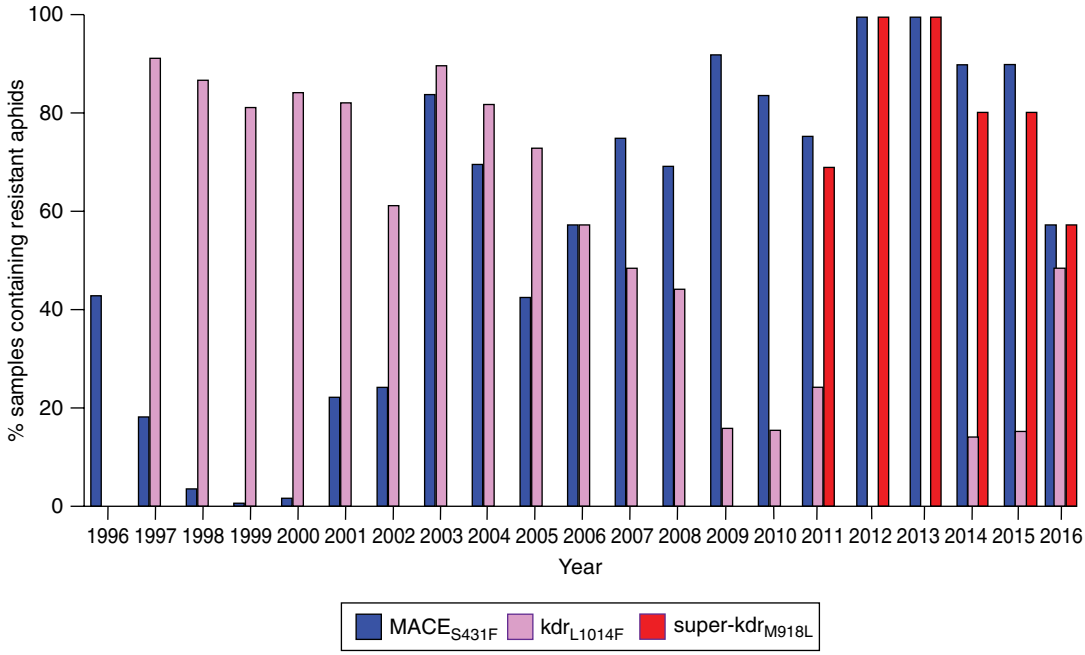

Fig. 19.1. UK *Myzus persicae* field samples containing aphids carrying MACE, kdr and super-kdr. Super-kdr was tested from 2011 onwards.

the case in the UK, nor in the Czech Republic, where *P. humuli* populations from untreated 'wild' hops were found also to be resistant to insecticides (Hrdy, 1975; Hrdy *et al*., 1986). The very different profiles of resistance to OPs, pyrethroids and carbamates exhibited by different *P. humuli* populations indicate that resistance originates in distinct geographical loci and then spreads throughout the extended complexes of hop fields and wild hosts. Loxdale *et al*. (1998) investigated the genetic heterogeneity of the esterases associated with insecticide resistance in *P. humuli* populations collected from primary and secondary hosts and concluded that migration, even within a 30-km region, was restricted. *Phorodon humuli*, therefore, tends to remain relatively localized, and rapid dispersal over wide areas is unlikely in the UK. In this species, untreated 'refugia' appear, at least in practice, to exert a negligible effect on the development of resistance.

Aphis gossypii is restricted mainly to glasshouses in the UK, where selection pressures are generally far more intense than in the open field (Denholm *et al*., 1998). *Myzus persicae* is also a glasshouse pest but, in addition, infests a range of field crops including potatoes, brassicas, lettuce and sugar beet, all treated with insecticides for aphid control. The overall effect of exposing *M. persicae* to the same range of chemicals on glasshouse and field crops has been to select for a number of mechanisms that collectively threaten all available insecticides, except more novel agents such as pymetrozine and flonicamid (Foster *et al*., 2002b, 2003a; S. Foster, unpublished).

Just as one can speculate on the factors that have encouraged the spread and development of resistance in some species, it is also possible to suggest why resistance has not occurred in other species. A good example is *Metopolophium dirhodum* (rose–grain aphid). Despite a long history of control with insecticides, this species has retained susceptibility in laboratory tests (e.g. Furk *et al*., 1983; Stribley *et al*., 1983), and no reductions in field performance have been reported against this pest. Compared with *M. persicae*, *A. gossypii* and *P. humuli*, this cereal aphid appears to present a contrasting situation in which migration between treated crops and extensive areas of wild grass hosts apparently has precluded any increase in the frequency of resistance genes. The failure of this

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species to develop resistance may reflect a lower intensity of insecticide selection, presumably as a result of its ecology and life cycle (many cereal aphids are holocyclic, for example). Having said this, one cereal aphid species, *S. avenae*, has recently evolved resistance to pyrethroids (see above). Further reasons for the apparent lack of resistance in some species might include the absence of population bottlenecks on crops treated with insecticides, or conceivably lower mutation rates or greater fitness costs associated with resistance genes. Despite this speculation, it is clear that resistance risks are not easily predicted. Other species illustrate that the association between ecological factors and the development of resistance is not readily reconciled. For example, the ecology of *M. euphorbiae* has much in common with that of *M. persicae*, which is highly adept at evolving resistance. Both inhabit glasshouses and a range of field crops, and yet only low resistance has been found in the former (Foster *et al*., 2002c).

Pleiotropic effects of resistance

One of the tenets of resistance management is that resistant forms are less fit than the 'normal/wild-type' susceptible genotype/s in the absence of insecticides; otherwise, the former should be present at greater frequencies prior to selection by insecticides. Significant selection pressure from synthetic insecticides dates back only 60 years, but the intensity of usage in some contexts has imposed extremely strong selection. Nevertheless, susceptible forms persist and often increase in frequency within a population when insecticide selection pressures are relaxed. However, the fitness of resistant forms in the absence of insecticides has been studied in only a limited number of aphid species, sometimes with conflicting results, as discussed below (reviewed by Kliot and Ghanim, 2012). Furthermore, detecting what are likely to be subtle fitness deficits can pose substantial hurdles in some species.

Some of the best evidence of the pleiotropic effects of resistance genes comes from work on *M. persicae*, where field and laboratory studies suggest the existence of adverse selection is imposed primarily during times of stress. This illustrates that studies of fitness costs associated with insecticide resistance should focus, at least initially, on situations where insects are under selective pressure, be it from the environment or from predation.

Reduced overwintering ability

The monitoring of UK *M. persicae* populations in the late 1980s showed an apparent fall in the frequencies of high (R_2 and R_3) esterase forms during the winter months (Furk *et al*., 1990), possibly due to counteracting selection in the absence of insecticides. This view was supported by lower levels of high esterase resistance in winged aphids caught in suction traps during the spring/summer migrations of 1993 compared with aphids caught in the previous autumn. Subsequent winter field experiments, using augmented *M. persicae* clones placed on to oilseed rape plants in the open field, showed that aphids carrying higher levels of esterase resistance suffered greater mortality than their lower esterase counterparts during colder, wetter and windier weather conditions (Foster *et al*., 1996). This apparent fitness cost may underlie the dynamics of esterase resistance seen in *M. persicae* in the UK over a number of years (Fig. 19.2), where the phasing out of OPs has led to the loss of a selective advantage for aphids carrying higher esterase levels.

Maladaptive behaviour

The movement of aphids from ageing leaves to younger leaves is an important aspect of aphid fitness, as individuals remaining at the time of leaf abscission risk starvation during the period of relocating a host plant (Harrington and Taylor, 1990). This danger increases dramatically under cold and wet conditions, when movement can be severely restricted. Aphids are therefore under strong selection pressure to recognize the cues associated with leaf senescence and to respond accordingly. Studies of this important aspect of behaviour using UK *M. persicae* clones, performed at low temperatures (around 5°C) in the laboratory and the field during the winter months, have shown that the rate of aphid movement is inversely associated with esterase resistance level (Foster *et al*., 1996, 1997); that is, aphids with greater esterase resistance tended to move at slower rates from deteriorating/senescing oilseed rape leaves. As a result, these forms appear to run greater risks of becoming separated from their host plants after leaf fall.

Another component of aphid fitness is their response to the alarm pheromone, (*E*)-β–farnesene. Any reduction in response could be highly maladaptive, as the dispersal of aphids through this stimulus is considered to be an important behavioural

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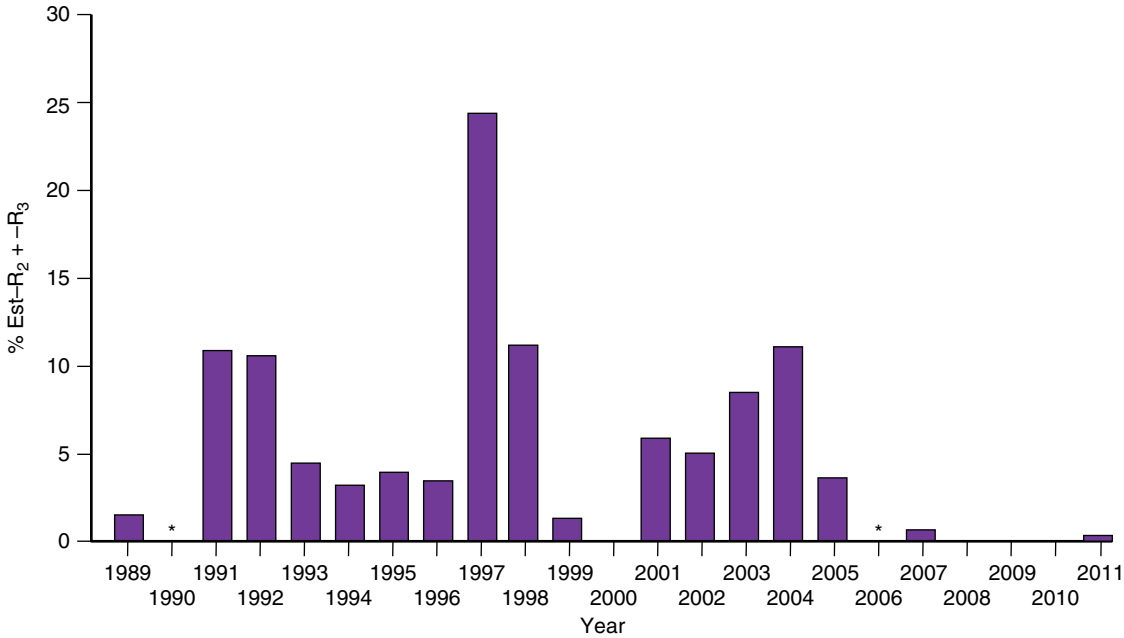

Fig. 19.2. Frequency of *Myzus persicae* carrying esterase R_2 + R_3 resistance, from the suction trap at Rothamsted Research, UK, between 1989 and 2011.
Note: *No data available.

adaptation for avoiding attack by natural enemies (Pickett *et al*., 1992). Response studies using bioassays on *M. persicae* clones carrying different combinations of kdr and esterase resistance have shown a reduced alarm response associated with both mechanisms (Foster *et al*., 1999, 2003b). Homozygous kdr aphids were far less responsive than aphids without kdr, with kdr heterozygotes showing an intermediate response. There was also a significant inverse correlation between esterase resistance level and the response of non-kdr aphids. Insecticide-susceptible and -resistant *M. persicae* provide the ideal biological material for testing the hypothesis that interactions with the third trophic level (predators and parasitoids) can play a significant inhibitory role in the evolution of adaptive traits at the second trophic level, based on a potential fitness trade-off between resistance to insecticides and avoidance of parasitism through alarm defence behaviour. Foster *et al*. (2007) tested this using *M. persicae* clones, representing different esterase and kdr resistance genotypes. Observations of these clones during periods of exposure to adult females of the parasitoid, *Diaeretiella rapae*, were done using small-scale arenas in the presence and absence of measured amounts of synthetic (*E*)-β-farnesene. Clones showing a consistently high alarm response (insecticide-susceptible, wild-type forms) displayed a range of behaviours during and after parasitoid attack that were significantly associated with greater fitness (avoidance of parasitization) compared to aphids showing a low alarm response (insecticide-resistant forms). Furthermore, this culminated in the latter suffering significantly higher levels of mummification. These data not only provide important empirical evidence that a normal (wild-type) high aphid alarm response reduces vulnerability to parasitoid attack but also represent the first example of insecticide-resistance genes having negative pleiotropic effects on fitness by producing maladaptive behaviours in the context of selection imposed by a higher trophic level. This implies that parasitoids, and probably other natural enemies, can influence the evolution and dynamics of insecticide resistance.

Conclusions

In many respects, the continuing battle against insecticide resistance can be equated with co-evolution,

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and is a clear illustration of how such processes generate biological diversity. Researchers have made great progress in monitoring and characterizing pesticide resistance and in understanding some of the genetic, ecological and operational factors that affect the speed of its development. Nowhere has this been more obvious than in the study of aphids. In doing so, we have gained valuable insights into evolutionary biology and genetics; on the origin and nature of adaptations and in understanding genetic responses to changes in the environment. Regardless of the progress that has been made, it is clear that the 'arms race' between insect evolution and human ingenuity will continue to present major challenges, particularly if EU-imposed legislation increases, such as the current restriction on neonicotinoid seed treatments in certain flowering crops, implemented because of the perceived deleterious effects they have on bees. In order to meet these challenges, it will be necessary to gain a greater understanding of the processes that mediate the development of resistance. In particular, there is a need for empirical research on the mechanisms conferring resistance to more novel chemical groups, and an understanding of the breadth of resistance that these mechanisms confer. Additionally, there is a paucity of information on the ecological factors that mediate resistance development, the role and manipulation of untreated refugia for susceptible forms, the value of insect dispersal and migration, and the selection of 'superclones' such as those found in *M. persicae*. Armed with such information, pest specialists will be better able to develop models that realistically assess 'resistance risk' and thereby strengthen future risk-mitigation tactics; the 'Holy Grail' of resistance management.

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20 Biological Control[1]

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Introduction

In recent decades, the development of new concepts in ecology, such as ecosystem services (Losey and Vaughan, 2006), landscape ecology, food web complexity (Gagic *et al*., 2011), apparent competition and mutualism, has changed our concepts of pest control. Consequently, the theoretical bases underlying the biological control of aphids have evolved towards a more integrated approach. The intensification of agriculture has led to an oversimplification of agricultural systems, and therefore also of the associated trophic systems. The extreme case is that of glasshouses, in which crops are increasingly grown hydroponically, without soil and fed with nutrient solutions. These simplified environments are particularly poor in natural enemies and are susceptible to pests.

The concept of a biological control programme is far more complex than the quick solution of an insecticide treatment. Biological control requires the consideration of all the factors that can affect pest populations, including the biology of the pest and its natural enemies, whether introduced or naturally present, tritrophic and intraguild relationships and the persistence of natural enemies. In the glasshouse, one can reconstruct the trophic community to optimize crop protection. For field crops, a biological control approach must consider the pre-existing complexity and functioning of the ecosystem if satisfactory results consistent with the economic requirements are to be obtained. Traditionally, three types of biological control have been recognized (Van Driesche and Bellows, 1996): (i) classical biological control, in which a natural enemy is introduced into a geographic area in which it has not previously occurred and is usually aimed against pests that have themselves been introduced from another region of the world; (ii) augmentative biological control, the objectives of which are the mass rearing and release of native natural enemies that do not naturally occur in sufficient numbers or at the optimum time; and (iii) 'conservation' biological control, which includes the enhancement of naturally occurring populations of natural enemies by habitat management or manipulating their behaviour (Chapter 21, this volume). Though the three approaches still coexist today, current techniques are based much more on the functioning of the agroecosystem and on a holistic consideration of the crop system itself. For instance, Bale *et al*. (2008) defined modern biological control as a restoration of the ecosystem function of pest management. In this chapter, we present the characteristics, advantages and disadvantages of the most commonly used natural enemies. Then, we discuss practical examples of aphid control in protected crops and in various types of field crops.

Natural Enemies

Natural enemies of aphids belong to diverse taxonomic groups, from entomopathogenic fungi to parasitoids, and include generalist and specialist predators. Each type of antagonist can be characterized by functional traits that condition its effectiveness and

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potential use (Snyder and Ives, 2003). For instance, specificity to prey or host is a key character that will influence its efficacy in biological control. Very specific natural enemies are closely linked to their prey, often showing a strong numerical response but also a type 3 functional response that prevents overexploitation of the host population at low density. In addition, specific natural enemies can locate their prey at low density, a capacity often based on specific chemical signals emitted by the prey or on more general cues issued by the plant or induced by the presence of the pest. High specificity entails a reduced risk of any environmental side effects of introduction by inoculation or mass release. Specificity can be defined in several ways. Some natural enemies are habitat specific (e.g. the parasitoid *Aphidius rhopalosiphi* is found mainly in cereal crops, where it parasitizes all aphid species; Stilmant *et al*., 2008). In some cases, strict host specificity is observed (e.g. the parasitoid *Aphelinus mali* to its host *Eriosoma lanigerum* (woolly apple aphid); Mueller *et al*., 1992). The degree of specificity can vary greatly from species to genus or family, and sometimes even more widely (e.g. some coccinellids that can target most aphid species, or chrysopids that feed on various prey species of appropriate size). Specificity may be related to particular behavioural traits such as host/prey recognition, acceptance, suitability and defence mechanisms. Generalism does not exclude the existence of particular food preferences based on the quality of the prey (Desneux *et al*., 2009). Polyphagous predators attack a wide range of often taxonomically unrelated prey. Then the limiting factor is the niche occupied or the range of prey sizes. Polyphagous predators can be divided into those with a short generation time, enabling several generations per year, and thus the development of a numerical response (e.g. the cecidomid *Aphidoletes aphidimyza*), and those with only one generation per year or every 2 years, making them unable to respond to population increases of their prey (e.g. most carabid species; Kindlmann and Dixon, 1999). Some polyphagous predators, however, are capable of numerical responses by aggregation.

Predators have direct effects on the population dynamics of their prey by immediately killing them, thereby physically removing them from the environment. Moreover, predators generally require several prey for their development and oviposition by the adult female, with a relationship between the number of prey killed and fecundity. In contrast to predators, aphid parasitoid larvae only kill the host at the end of their development, and female fecundity correlates with the number of hosts actually killed. Moreover, because the host is not killed immediately, there is a delay between the time of parasitization and the removal of the host from the population, meaning that a female may encounter already parasitized hosts in its environment.

In terms of biological control, natural enemies capable of numerical responses may be used for a curative approach and regarded as 'cleansing' predators, whereas predators without numerical responses are better able to prevent prey outbreaks and are thus preferable in conservation biological control. However, conservation approaches can also encourage specific natural enemies.

Parasitoids

Classical biological control

Parasitoids are widely used in biological control and correspond to 80% of the known successes in classical biological control (van Lenteren, 1986; Boivin *et al*., 2012). Aphid parasitoids are koinobionts, i.e. they keep their hosts alive during larval development (Boivin *et al*., 2012). Because of their way of life and short development time, parasitoids can exert a strong regulatory effect on their host population. However, in field conditions, observed rates of parasitism are relatively low (Langer *et al*., 1997; Thies *et al*., 2005). A single parasitoid female never exploits an aphid colony completely, because it would increase its residence time for a low fitness gain (Charnov, 1976). Moreover, aphid parasitoids tend to maximize their rate of fitness gain rather than fitness gain itself, indicating that they are probably more time than egg limited (Barrette *et al*., 2009).

The Aphidiinae are a subfamily of the Braconidae (Hymenoptera), specialized for aphid parasitism and including over 400 species, some of which being marketed for biological control (Boivin *et al*., 2012). The Aphelinidae (Hymenoptera: Chalcidoidea), also specialized for aphids, include nearly 1000 species (Starý, 1988). In the Diptera, the genus *Endaphis* (Cecidomyiidae) includes six parasitoid species, including *Endaphis fugitiva*, which is an interesting possibility for control of the banana aphid, *Pentalonia nigronervosa* (Muratori *et al*., 2009).

Glasshouse crops

Glasshouse crops occupy approximately 2.4 million ha worldwide, including 45,000 ha under glass

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(van Lenteren, 2006). These are high added value crops, demanding continuing optimization. The glasshouse is a confined space in which the environment is kept optimized for the crop, but may fluctuate depending on sunshine. Aphids are among the major pests in glasshouses (Rabasse and van Steenis, 1999), characterized by an uneven distribution, very rapid population growth and a capacity to colonize ephemeral habitats such as agricultural crops (Dedryver *et al*., 2010; Fig. 20.1).

Although the first attempts to use parasitoids to control aphids in glasshouses date back more than 40 years (Lyon, 1968; Rabasse, 1980), only a limited number of species are currently used and mass-produced (Table 20.1).

Given the high capacity of aphids to increase, parasitoids are typically introduced early in the season, when the aphid population is still very low, to maximize their efficacy and to reduce the number released, and therefore the cost of the treatment (Salin *et al*., 2011). Unsuccessful releases result from intervention when aphid density is already high. A summary of more effective trials is presented in Table 20.2. To control *Myzus persicae* (peach–potato aphid) or *Aphis gossypii* (cotton or melon aphid), insect producers recommend the release of 0.15 *Aphidius colemani*/m^2 for preventive introductions and 1.5 individuals/m^2 for heavily infested areas (Fig. 20.2).

The same density is recommended for *Aphidius ervi* for control of the potato aphid *Macrosiphum euphorbiae* (van Lenteren, 2003). *Aphelinus abdominalis* may also be used in roses at a density of 2.2–9.9 individuals/m^2 to control *M. euphorbiae* (Blümel and Hausdorf, 1996). Releases focused on infested areas are also advised for *A. abdominalis*, which parasitizes *M. euphorbiae* and *Aulacorthum solani*, because this parasitoid does not disperse well and is more expensive (Mölck and Wyss, 2002). As several aphid species may be present simultaneously on a crop, mixed releases of two or even more as a cocktail of parasitoid species are increasingly recommended (Salin *et al*., 2011; Dassonville *et al*., 2013; Thielemans *et al*., 2013). Although there is a potential risk of competition hampering aphid control, in practice such combinations appear to work, possibly because of small differences in niches and preferences. For instance, in strawberry crops, due to the potential presence of several aphid species, three consecutive releases of a cocktail of mummies of several parasitoid species (Fresaprotect®) are advised for a cost per season of around €3000/ha, depending on the price practised by distributors of natural enemies. Finally, combined releases of parasitoids with the gall midge, *A. aphidimyza* or the ladybird *Adalia bipunctata* (Fig. 20.3) may bring heavy infestations under control.

Starý (1993b) proposed the initial introduction into glasshouses of the non-target aphid, *Schizaphis graminum* (greenbug) on cereals, along with its associated parasitoids (*A. colemani*, *Lysiphlebus testaceipes*) to control another target pest, the aphid *M. persicae* on beans. This approach allows the parasitoid population to grow before that of *M. persicae*, the *S. graminum* acting as a parasitoid reservoir. This is a typical case of apparent competition, in which several hosts or prey species share the same natural enemies (Holt and Lawton, 1994; Langer and Hance, 2004). Such a preventive system (the banker plant system) reintroduces complexity into the glasshouse ecosystem. Another example is the introduction of pots of barley infested with bird cherry–oat aphid, *Rhopalosiphum padi*, inoculated with adults of *A. colemani* at the start of the crop for effective control of *A. gossypii* on Marguerite daisies (Van Driesche *et al*., 2008). A recent review of banker-plant systems included 19 natural enemies targeting 11 pest species, the most frequent being *A. gossypii* (Frank, 2010), and analysed the advantages (high efficacy and lower costs than mass release) and drawbacks (need for management of banker plants) of this technique. Commercial biocontrol companies have marketed banker plants for several years. This strategy may be complemented by other means, such as alternative food and sheltered oviposition sites

Fig. 20.1. *Myzus persicae* damage to glasshouse sweet peppers. (Photograph courtesy of Christophe Salin.)

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Table 20.1. Commercial availability of biological control agents for aphid control. (From Wei *et al*., 2003; Copping, 2004; van Lenteren, 2012a,b; Yano, 2010; Boivin *et al*., 2012; Reddy, 2016; www.biobest.be/; www.koppert.com/; www.viridaxis.com/; http://biolineapp.com/; www.appliedbionomics.com/.)

Type	Species	Number of suppliers	Countries with suppliers
Braconid parasitoid	*Aphidius colemani*	13	UK, USA, Belgium, Canada, Germany, The Netherlands, Thailand
Braconid parasitoid	*Aphidius ervi*	7	UK, USA, Belgium, Germany, The Netherlands
Braconid parasitoid	*Aphidius matricariae*	4	USA, Canada
Braconid parasitoid	*Aphidius gifuensis*	1	China
Braconid parasitoid	*Ephedrus cerasicola*	1	Belgium
Braconid parasitoid	*Diaeretiella rapae*	2	USA
Braconid parasitoid	*Lysiphlebus testaceipes*	2	USA, Italy
Braconid parasitoid	*Praon volucre*	1	Belgium
Aphelinid parasitoid	*Aphelinus abdominalis*	9	UK, USA, Belgium, Germany, The Netherlands
Aphelinid parasitoid	*Aphelinus asychis*	?	Asia
Aphelinid parasitoid	*Aphelinus mali*	1	USA
Predatory midge	*Aphidoletes aphidimyza*	18	UK, USA, Belgium, Canada, Germany, The Netherlands
Ladybird	*Adalia bipunctata*	2	UK, Belgium
Ladybird	*Coleomegilla maculata*	3	USA, The Netherlands
Ladybird	*Harmonia axyridis*	5	UK, USA, Belgium, Canada, Finland
Ladybird	*Hippodamia convergens*	14	UK, USA, Belgium, Canada, The Netherlands
Ladybird	*Coelophora (Lemnia) biplagiata*	1	China
Ladybird	*Propylea japonica*	1	China
Lacewing	*Chrysoperla sinica*	1	China
Lacewing	*Chrysoperla carnea*	11	UK, USA, Belgium, Germany
Lacewing	*Micromus variegatus*	1	USA
Lacewing	*Chrysoperla rufilabris*	6	USA
Hover fly	*Episyrphus balteatus*	2	UK, Belgium
Predatory bug	*Anthocoris nemoralis*	3	UK, Belgium, Italy
Predatory bug	*Deraeocoris brevis*	2	UK, Canada
Predatory bug	*Geocoris punctipes*	3	USA
Predatory bug	*Orius* species	19	UK, USA, Canada, China, Belgium, Germany, Italy, Japan, The Netherlands, Poland
Fungal pathogen	*Beauveria bassiana*	5	USA, Colombia, Czech Republic, France, India, Italy, Switzerland, Russia
Fungal pathogen	*Isaria fumosorosea*	1	USA
Fungal pathogen	*Lecanicillium* spp.	9	USA, Belgium, India, Mexico, The Netherlands

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Table 20.2. Some examples of trials involving augmentative release of parasitoids to control aphids on glasshouse crops.

Species	Target	Crop	Banker plants	Country	Effect	References
Aphidius matricariae	*Myzus persicae*	Sweet pepper		France	Significant impact on aphids	Rabasse (1980)
Aphidius matricariae	*Myzus persicae*	Sweet pepper		Former USSR	Good control	Shijko (1989)
Aphidius colemani	*Aphis gossypii*	Cucumber	*Rhopalosiphum padi* on cereals	UK	Good control using banker plants combined with predatory midge	Bennison and Corless (1993)
Aphidius colemani	*Myzus persicae*	Beans	*Schizaphis graminum* on cereals	Czech Republic	Good control using banker plants	Starý (1993b)
Aphidius colemani	*Aphis gossypii*	Cucumber	*Rhopalosiphum padi* on cereals	The Netherlands	Good control using banker plants combined with predatory midge	Mulder *et al*. (1999)
Aphidius colemani	*Myzus persicae nicotianae*	Sweet pepper	*Rhopalosiphum padi* on cereals	The Netherlands	Good control using banker plants	van Schelt (1999)
Aphidius colemani	*Aulacorthum solani*	Sweet pepper	*Rhopalosiphum padi* on cereals	The Netherlands	Good control using banker plants	van Schelt (1999)
Lysiphlebus testaceipes	*Myzus persicae*	Beans	*Schizaphis graminum* on cereals	Czech Republic	Some effect using banker plants	Starý (1993b)
Ephedrus cerasicola	*Aphis gossypii*	Cucumber	*Myzus persicae* on swedes	Norway	Significant effect using banker plants but *Myzus persicae* a potential risk	Hågvar and Hofsvang (1995)
Aphelinus abdominalis	*Macrosiphum euphorbiae*	Cut roses	*Macrosiphum euphorbiae* on potato	Austria	Good control using banker plants combined with selective aphicide	Blümel and Hausdorf (1996)
Aphelinus abdominalis	*Myzus persicae*	Cut roses	*Macrosiphum euphorbiae* on potato	Austria	Good control using banker plants combined with selective aphicide	Blümel and Hausdorf (1996)
Aphelinus asychis	*Macrosiphum euphorbiae*	Cut roses		USA	Significant impact on aphids combined with a ladybird beetle	Snyder *et al*. (2004a)

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Mix of six parasitoid species: *Aphidius colemani*; *Aphidius ervi*; *Aphidius matricariae*; *Ephedrus cerasicola*; *Praon volucre*; *Aphelinus abdominalis*	Mix of raspberry aphids	Raspberry	UK	Significant impact on aphid with a high proportion of *Praon volucre*	Dassonville *et al*. (2013)
Mix of six parasitoid species: *Aphidius colemani*; *Aphidius ervi*; *Aphidius matricariae*; *Ephedrus cerasicola*; *Praon volucre*; *Aphelinus abdominalis*	Mix of strawberry aphids	Strawberry	UK, Belgium	Significant impact on aphid	Dassonville *et al*. (2013); Hance and Salin (2014)

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Fig. 20.2. The braconid parasitoid *Aphidius colemani* ovipositing in a young *Myzus persicae* nymph. (Photograph courtesy of Christophe Salin.)

Fig. 20.3. Larvae of *Adalia bipunctata* eating *Myzus persicae*. (Photograph courtesy of Christophe Salin.)

(Messelink *et al*., 2014), to enable the persistence of the parasitoid population. However, the use of several natural enemies in glasshouses combined with conservation methods results in an increased complexity of the food web in the glasshouse. This may increase the risks of intraguild predation (IGP) and may favour hyperparasitoids, or apparent mutualism (Bloemhard *et al*., 2014; Messelink *et al*., 2014).

Field crops

In field crops, the international transport of agricultural products has unintentionally introduced many aphid species to new countries. Consequently, the classical control approach has been used more frequently in field crops than have augmentative and mass-release interventions.

ORCHARDS. The introduction of *A. mali* to French apple orchards to control *E. lanigerum*, native to North America, was one of the first uses of classical biological control against an aphid (Howard, 1929) (Table 20.3 provides a list of classical control introductions). This was followed by several introductions in Europe, Australia and New Zealand (Howard, 1929). *Aphelinus mali* established, but in several cases did not control the woolly aphid satisfactorily due to climatic conditions, IGP, prey refuges or insecticide treatments (Asante and Danthanarayana, 1992; Stiling, 1993).

Similarly, *Trioxys pallidus* was introduced from France into California in 1959 in an attempt to control *Chromaphis juglandicola* (small walnut aphid) (Brown *et al*., 1992; Edwards and Hoy, 1995). Because this parasitoid became established only in the more humid areas, an Iranian ecotype was introduced in 1969, which established throughout the drier Central Valley of California. However, the two biotypes did not appear to interbreed and occupied distinct climatic niches (van den Bosch *et al*., 1970; Edwards and Hoy, 1995). This observation poses the question of cryptic species, which seem to be common among the Aphidiinae (Derocles *et al*., 2012). The established *T. pallidus* failed to control another known host, *Myzocallis coryli* (hazel aphid); therefore, a further ecotype, originating from *M. coryli* in Europe, was introduced in 1984 and proved successful (Messing and Aliniazee, 1989). Tolerance of high densities of *M. coryli* by filbert trees (*Corylus maxima*) and the retention of fallen leaves in the orchard to provide an overwintering habitat for *T. pallidus* mummies allowed for synchrony between host and parasitoid early the following season, and probably contributed to this success (Messing and Aliniazee, 1989; Aliniazee, 1998). However, biological control of *C. juglandicola* has subsequently been badly affected by the use of insecticides against lepidopteran pests in walnut orchards, frequently leading to secondary outbreaks of the aphid (Edwards and Hoy, 1995). Early field releases of a parasitoid strain resistant to the insecticide were promising; they established successfully, survived applications of azinphos-methyl and spread to nearby orchards (Hoy and Cave, 1989; Hoy *et al*., 1989). However, molecular studies showed that the released, pesticide-resistant parasitoids did

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Table 20.3. Introductions of parasitoids for biological control of aphids (see text for references).

Species	Target	Crop	Origin	Introduced	Year	Established
Aphelinus mali	*Eriosoma lanigerum*	Apple	USA	51 countries	1920 onwards	Y (42 countries)
Trioxys complanatus	*Therioaphis trifolii*	Lucerne	Middle East, Europe	USA	1955–1957	Y
Praon exsoletum	*maculata*	(alfalfa)				Y
Aphelinus asychis						Y
Aphidius smithi	*Acyrthosiphon pisum*	Lucerne;	India, Europe	USA, Canada	1958–1963,	Y
Aphidius ervi		peas			1983–1987	Y
Trioxys pallidus	*Chromaphis juglandicola*	Walnut	France, Iran	USA	1959, 1968	Y
Aphidius matricariae	Range of species		France	Brazil, Chile	1961	Y
Aphidius ervi	*Sitobion avenae*	Cereals	France	Chile	1976–1978	Y
Aphidius rhopalosiphi	*Metopolophium dirhodum*		Europe			Y
Aphidius smithi	*Diuraphis noxia*					Y
Aphidius uzbekistanicus	*Sitobion fragariae*					Y
Ephedrus cerasicola	*Metopolophium festucae*					Y
Ephedrus nacheri	*cerealium*					Y
Ephedrus plagiator						Y
Monoctonus nervosus						Y
Praon gallicum						Y
Praon volucre						Y
Aphidius salicis	*Cavariella aegopodii*	Carrot	USA	Australia	1962	Y
Aphelinus asychis	*Schizaphis graminum*	Sorghum	Eastern and	USA	1968, 1970	Y
Aphelinus varipes			Western			Y
Aphidius matricariae			European			N
Diaeretiella rapae			countries, France,			Y
Ephedrus plagiator			Iran, Pakistan and			?
Praon pakistanum			Chile			N
Eucallipterus tiliae	*Trioxys curvicaudus*		Europe	California, USA	1970s	Y
Tinocallis platani	*Trioxys tenuicaudus*					Y
Aphidius smithi	*Acyrthosiphon pisum*	Legumes	USA	Chile	1971	Y
Aphidius ervi	*Acyrthosiphon pisum*	Legumes	Europe	Argentina	1972, 1978	Y
	Acyrthosiphon kondoi					
Lysiphlebus testaceipes	*Aphis (Toxoptera) aurantii*	Citrus	Cuba	France	1973–1974	Y
Lysiphlebus testaceipes	*Schizaphis graminum*	Cereals	USA	Chile	1974	Y
Monoctonus nervosus	*Sitobion avenae*	Cereals	USA	Chile	1976	N
Aphidius ervi	*Sitobion avenae*	Cereals	France, Iran	Chile	1976–1982	Y
Aphidius rhopalosiphi	*Metopolophium dirhodum*					Y
Aphidius uzbekistanicus						Y
Praon gallicum						Y
Praon volucre						Y

Continued

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Table 20.3. Continued.

Species	Target	Crop	Origin	Introduced	Year	Established
Trioxys complanatus	*Therioaphis trifolii maculata*	Lucerne (alfalfa)	USA, Iran, Cyprus, Pakistan, France	Australia	1977–1979	Y
Praon exsoletum						Y
Aphelinus asychis						Y
Aphidius smithi	*Acyrthosiphon pisum*	Lucerne; peas	USA, Canada	Australia, New Zealand	1977–1979	Tasmania only
Aphidius eadyi						Y
Aphidius pisivorus						?
Aphidius ervi	*Acyrthosiphon kondoi*	Lucerne	Europe	Australia, New Zealand	1978–1982	Y
Ephedrus plagiator						N
Praon barbatum						N
Aphidius rhopalosiphi	*Sitobion avenae* *Metopolophium dirhodum*	Barley	Europe	Australia, New Zealand	1980	Y
Aphidius sonchi	*Hyperomyzus lactucae*	Lettuce	Mediterranean, Japan	Australia	1981	Y
Praon volucre			Mediterranean			Y – Tasmania
Pauesia cedrobii	*Cinara (Cedrobium) laportei*	Cedar trees	Morocco	France	1981	Y
Lysiphlebus testaceipes	*Aphis craccivora*	Beans	USA	Australia	1982	Y
Lysiphlebus fabarum			Mediterranean			N
Pauesia cinaravora	*Cinara cronartii*	Pine trees	Georgia, USA	South Africa	1983	Y
Pauesia bicolor	*Cinara cronartii*	Pine trees	USA	South Africa, Kenya, Malawi	1983	Y
Trioxys pallidus	*Myzocallis coryli*	Hazel (filbert)	Europe	USA	1984	Y
Lysiphlebus testaceipes	*Schizaphis graminum*	Cereals	USA	Argentina	1984	Y
Aphidius rhopalosiphi	*Metopolophium dirhodum*	Cereals	England, France, Chile, New Zealand	New Zealand	1985–1986	Y
	Sitobion avenae			Australia		N
Binodoxys indicus	*Aphis craccivora*	Lupin	India	Australia	1986	Y
Diaeretiella rapae	*Diuraphis noxia*	Cereals	Czech Republic	USA	1989	Y
Aphidius colemani	*Diuraphis noxia*	Cereals	Chile	Czech Republic	1996–1997	Y
Aphelinus albipodus	*Diuraphis noxia*	Cereals	Eurasia, Morocco	USA	1988–1997	Y
Aphelinus asychis				Canada		Y
Aphelinus varipes						Y
Aphidius colemani						Y
Aphidius matricariae						?
Aphidius picipes						?
Diaeretiella rapae						Y
Ephedrus plagiator						?
Praon volucre						?

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Aphidius colemani	*Pentalonia nigronervosa*	Banana	Australia	Tonga	1990–1991	Y
Lysiphlebus testaceipes			Europe			N
Aphelinus varipes	*Diuraphis noxia*	Cereals	Ukraine and Germany	Australia	1990	N
Aphelinus hordei	*Diuraphis noxia*	Cereals		South Africa	1991–1994	Y
Aphidius picipes	*Sitobion avenae*	Cereals	Ukraine	Chile	1991–1992	?
Ephedrus cerasicola	*Metopolophium dirhodum*					?
Ephedrus nacheri	*Diuraphis noxia*					?
Ephedrus plagiator	*Sitobion fragariae*					?
	Metopolophium festucae					
Pauesia juniporum	*Cinara cupressivora*	Pine trees	Europe	Malawi	1994	Y
				Kenya	1994	Y
				Uganda	1995	Y
Lipolexis oregmae	*Aphis (Toxoptera) citricidus*	Citrus	Japan	Florida	1996, 2000–2002	Y
Aphidius transcaspicus	*Hyalopterus pruni*	Plum	Greece	California	2000–2008	N
Binodoxys communis	*Aphis glycines*	Soybean	China	North America	2007	N
Binodoxys communis	*Aphis gossypii*	Cucumber, Taro	China	Hawaii	2013	?
Diaeretus essigelae	*Essigella californica*	Monterey pine	California	Australia	2009	Y

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not replace the wild-type population completely (Edwards and Hoy, 1995). More recently, *Aphidius transcaspicus* was introduced to Californian *Hyalopterus pruni*. Despite repeated releases of more than 50,000 individuals from 2000 to 2008, this species did not become established in Californian orchards (Latham and Mills, 2012). Similarly, the parasitoid *Lipolexis oregmae* (introduced as *Lysiphlebia japonica*) was released in 1996 at 30 locations throughout Florida following the introduction of the tropical citrus aphid *Aphis (Toxoptera) citricidus* in 1995. This parasitoid species did not become established in Florida, and subsequent introductions in Belize and Puerto Rico also failed (Michaud, 2002). However, the species overwintered during the 2000/01 season from new releases conducted from 2000 to 2002 (Hoy and Nguyen, 2011). *Lipolexis oregmae* then became established on a wide variety of hosts, with a parasitism rate of 2–12.9% on *A. (T.) citricidus*. However, the predation of red imported fire ants, *Solenopsis invicta*, on the mummies that are formed at the ground level probably reduces the efficacy of the parasitoid, and its impact on the brown citrus aphid remains to be quantified (Persad *et al*., 2007).

CEREALS. In Chile, in response to the accidental introduction of cereal aphids around 1967, ten parasitoid species were introduced in the late 1970s from France and other parts of Europe. They established successfully, with a satisfactory control of the aphid pests (Starý, 1993a; Starý *et al*., 1993) (Table 20.3). The small size of the crop fields in an ecosystem with high plant and habitat diversity is thought to have contributed to this success (Starý *et al*., 1993). In Argentina, Brazil and Chile, the total cost of the parasitoid introduction was less than US$350,000 for an annual benefit in reduced pesticide applications of approximately US$52 million/year (Zuniga, 1990).

Another success story occurred in the 1980s, in Australia and New Zealand, where *A. rhopalosiphi* was introduced from Europe to control the invasive rose–grain aphid, *Metopolophium dirhodum*, and the English grain aphid, *Sitobion avenae* (Farrell and Stufkens, 1990). Successful establishment resulted in a 10- to 20-fold reduction in *M. dirhodum* populations on barley crops between 1984 and 1989, with parasitism reaching 100% on some spring-sown crops (Farrell and Stufkens, 1990).

In North America, the greenbug, *S. graminum*, was first reported in the early 1900s, with annual losses of US$10–250 million, depending on the year (Brewer and Elliott, 2004). A first programme of classical control in 1968 involved the introduction of 11 species of parasitoid. However, of the six species introduced in Oklahoma and Texas, none were considered permanently established in 2004 (Brewer and Elliott, 2004). For two species, *Diaeretiella rapae* and *Aphelinus varipes* introduced to the Great Plains, it was impossible to assess the efficacy of the release because these species were present before the introduction programme, though Brewer and Elliott (2004) concluded that the introduction of parasitoids contributed little to the control of the greenbug in these regions. In field surveys, the native parasitoid, *L. testaceipes*, was dominant (Archer *et al*., 1974; Carver, 1989). This species is now considered one of the most important biological control agents of *S. graminum* in the USA (Fernandes *et al*., 1998). Later, *L. testaceipes* was introduced into Chile and Argentina against *S. graminum* on sorghum (Botto *et al*., 1991; Starý, 1993a).

Similarly, after *Diuraphis noxia*, the Russian wheat aphid (RWA), was introduced to North America in 1989, the National RWA Integrated Pest Management Program searched for and imported natural enemies from the putative geographical origin of RWA in Eurasia (Tanagoshi *et al*., 1995). By 1997, more than 11.8 million individuals of 11 parasitoid species, comprising over 80 geographical strains from 25 countries, had been released, and many became established (Tanagoshi *et al*., 1995; Prokrym *et al*., 1998; Burd *et al*., 2001; Table 20.3). In Washington and Idaho, *Aphelinus albipodus*, *Aphidius uzbekistanicus* and *Praon gallicum* were recovered 6 years after being released. However, a full economic and biological evaluation of these releases was not practicable because it was impossible to identify positively many of the released or recovered parasitoids, due to limited pre-release surveys (Brewer *et al*., 2001).

Although these classical biological control attempts have had some impact on RWA in the USA, this species remains an important pest. One reason for control failure may be the very large field sizes and monoculture-cropping pattern prevalent in many cereal production areas; therefore, diversification of the cropping system may be the key to improving biological control of cereal aphids (Burd *et al*., 2001; Thies *et al*., 2011), providing refuges for enhancing parasitoid survival during the summer months.

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The precise identification of introduced parasitoids is sometimes difficult. For example, an aphelinid was introduced to South Africa; samples were originally identified as *A. varipes*, later as *Aphelinus hordei* (Prinsloo and Neser, 1994; Prinsloo, 1998) and then as *Aphelinus* sp. nr. *varipes* (Prinsloo, 2000). During initial attempts to establish this parasitoid, the light conditions prevalent during rearing induced a diapause soon after release, but subsequent attempts have been more successful (Prinsloo, 1998). *Aphelinus hordei* recoveries were made several weeks after release, and were identified using molecular markers (Prinsloo *et al*., 2002).

LEGUMES. Many aphid species have also spread throughout regions where legume crops, particularly lucerne (alfalfa), are grown, frequently prompting the importation and release of parasitoids (Table 20.3).

A search for natural enemies of *Therioaphis trifolii maculata* (spotted alfalfa aphid, SAA) in Europe, the Middle East, Africa and Asia led to the importation and release into the USA of *Praon exsoletum*, *Trioxys complanatus* and *Aphelinus asychis* (originally recorded as *Aphelinus semiflavus*) (van den Bosch, 1957; van den Bosch *et al*., 1964). This introduction resulted in reduced aphid abundance and crop damage. All three imported parasitoids established successfully, in spite of variations in their climatic requirements and tolerances. The ability to enter a facultative aestival diapause allowed *T. complanatus* to dominate in the hotter, more arid areas, whereas the non-diapausing *A. asychis* preferred more humid regions with less severe temperature extremes. It is thought that SAA would have escaped control in some regions, such as California, if only one or two of the three parasitoids had been introduced (van den Bosch *et al*., 1964). Gutierrez and Ponti (2013) used a weather-driven, physiologically based demographic system model to decipher the respective roles of three exotic parasitoids (*A. semiflavus*, *P. exsoletum* and *T. complanatus*), a native coccinellid beetle (the convergent lady beetle, *Hippodamia convergens*), a fungal pathogen (*Pandora neoaphidis* (Entomophthorales: Entomophthoraceae)) and host-plant resistance. They showed that control of SAA was only achieved when all factors were included; parasitoids alone or when combined failed to control the aphid. Classical control may also have a negative effect on native parasitoid populations. The decline of the native parasitoid, *Praon pequodorum*, in lucerne was probably caused by competition with the introduced *A. ervi*. Indeed, although *P. pequodorum* was the better competitor at the larval stage, the searching behaviour of *A. ervi* was more efficient, resulting in a higher level of parasitism per unit time. Consequently, regular harvesting of lucerne favours *A. ervi*, because its searching efficiency allows for rapid population growth under disturbed conditions (Schellhorn *et al*., 2002). SAA also invaded Australia, and developed resistance to a broad range of insecticides (Hughes *et al*., 1987; Holtkamp *et al*., 1992). In the 1970s, three parasitoids were introduced to eastern Australia: *T. complanatus* from the USA in 1977 and from Iran in 1978, *P. exsoletum* from Cyprus and Iran in 1978, and *A. asychis* from southern France in late 1978. *Trioxys complanatus* was the only parasitoid to become widely established, representing 85–93% of the parasitoids emerging from SAA mummies. This species is considered as primarily responsible for the subsequent decline of the aphid (Hughes *et al*., 1987), although native arthropod predators and the introduction of more aphid-resistant lucerne cultivars also contributed (Carver, 1989). The success and persistence of the parasitoid was attributed to the patchiness of the irrigated lucerne environment (Hughes *et al*., 1987), and particularly to the lack of synchronization of harvesting lucerne, favouring the movement of parasitoids from harvested fields to nearby standing crops at an earlier growth stage. This reduced the impact of local extinctions of both aphids and parasitoids (Waterhouse and Sands, 2001). The benefit of this introduction was estimated at approximately AUS$1 million/year (Hughes *et al*., 1987). In 1989, a new biotype of *T. trifolii* (Sunnucks *et al*., 1997) began to cause considerable damage to clover pastures in parts of Australia (Milne, 1997). This biotype was parasitized only occasionally by *T. complanatus* (Milne, 1997). However, *A. asychis* from France, which was released in 1978 and 1979 to control the *maculata* form, also attacked the clover biotype (Waterhouse and Sands, 2001). *Aphidius smithi* and *A. ervi*, imported from India and Europe, respectively, were released to control *Acyrthosiphon pisum* (pea aphid) in pea- and lucerne-growing regions of North America between 1958 and 1961 (Hagen and Schlinger, 1960; Mackauer and Kambhampati, 1986). Although the two parasitoid species appeared to occupy different climatic zones, *A. smithi* declined during the 1970s

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and *A. ervi* became dominant. This raised questions about the reliability of laboratory screening before release: screening had suggested that *A. smithi* was the more promising species for legume aphid control (Mackauer and Kambhampati, 1986). In California, *A. smithi* could not survive long periods when aphids were absent from the hotter, drier interior regions during summer, as it did not enter diapause, but it established well in coastal areas (Hagen and Schlinger, 1960). A total of 105,000 *A. smithi* adults were also released in Manitoba from individuals collected in California. Recoveries were made in 2001, but at a density too low to control pea aphid. Climatic conditions and competition with *A. ervi* were probably the cause of this poor result (Wylie *et al*., 2005). A range of parasitoids has been imported into New Zealand and Australia to combat *A. pisum* and *Acyrthosiphon kondoi* (Cameron *et al*., 1981; Carver, 1989; Waterhouse and Sands, 2001). *Aphidius smithi*, *Aphidius pisivorus*, *Ephedrus plagiator* and *Praon barbatum* failed to establish (Carver, 1989), whereas *Aphidius eadyi* and *A. ervi* did establish and have significantly affected *A. pisum* and *A. kondoi*, respectively. *Aphidius ervi* has been particularly effective in the high-rainfall areas of eastern Australia, but is less effective in drier inland areas (Waterhouse and Sands, 2001). *Aphidius eadyi* appears to be specific to *A. pisum*, and in New Zealand is well synchronized with its host, becoming active early in spring when aphid numbers are still low (Cameron *et al*., 1981). *Aphidius ervi* took longer to establish, but the introduction of several different geographic strains over several years eventually paid off (Waterhouse and Sands, 2001). Interestingly, *A. ervi* has since taken over from *A. eadyi* as the dominant species attacking *Acyrthosiphon* spp. in New Zealand, reminiscent of how it replaced *A. smithi* and *P. pequodorum* in North America. Unlike *A. eadyi*, *A. ervi* can utilize a number of other aphid species in the ecosystem, and it has been suggested that it is the more efficient of the two at low aphid densities, partly explaining why it became more dominant when aphid population densities on legume crops declined.

More recently, in 2000, the soybean aphid (SBA), *Aphis glycines*, was introduced to North America and had spread rapidly to 30 states and three Canadian provinces by 2009. This species may produce yield losses of more than 40% (Ragsdale *et al*., 2011). The first release of *Binodoxys communis* from China began in 2007, but it has not yet established successfully, due to the lack of an adequate host for overwintering, ant-attendance in secondary hosts, a genetic bottleneck, or rapid dispersal from the release site (Ragsdale *et al*., 2011). This strain has also probably gradually lost its capacity to enter diapause due to repeated periods of quarantine and laboratory rearing (Gariepy *et al*., 2015). *Binodoxys communis* was also introduced in Hawaii against *A. gossypii* (Acebes and Messing, 2013).

BANANA. The banana aphid, *Pentalonia nigronervosa,* is an important virus vector, and attempts at biological control were initiated on Tonga by introducing *L. testaceipes* and *A. colemani* (Starý and Stechmann, 1990; Table 20.2), but only *A. colemani* became established, principally on *A. gossypii* on cotton and taro crops (*Colocasia esculenta*) (Carver *et al*., 1993; Wellings *et al*., 1994; Stechmann *et al*., 1996). *Aphidius transcaspicus* was introduced to Hawaii, and field cage tests showed that it successfully attacked *P. nigronervosa* (Wang and Messing, 2006). Recently, a new banana aphid parasitoid was discovered in the Hawaiian Islands, *E. fugitiva*, a new species of Cecidomyiidae. This may have potential for biocontrol of the banana aphid, though its search efficiency needs establishing (Muratori *et al*., 2009).

FOREST AND URBAN TREES. *Cinara cronartii* (black pine aphid), an invasive pine forest pest in South Africa since the 1970s, was controlled by introducing in 1983 of the parasitoid, *Pauesia cinaravora* (Kfir and Kirsten, 1991; Marsh, 1991). No outbreak of *C. cronartii* has been recorded since 1994 (Day *et al*., 2003). First identified in Malawi in 1986, *Cinara cupressivora* was estimated to have killed trees in Africa worth US$41 million by 1991. The first releases of *Pauesia juniperorum* were made from Europe in Malawi and Kenya in 1994 and in Uganda in 1995. This species has had a substantial impact on *C. cupressivora,* although the aphid's decline cannot be attributed solely to this introduction (Day *et al*., 2003). Similarly, *Pauesia cedrobii* was introduced to control *Cinara (Cedrobium) laportei* (cedar aphid), invasive in southern France, where it established and spread as far north as Paris within 12 years (Fabre and Rabasse, 1987; Remaudière and Starý, 1993).

In California, *Eucallipterus tiliae* (lime aphid), originally a Palaearctic species, causes a nuisance

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problem on urban lime trees. In 1970, four European parasitoids were released in California; only *Trioxys curvicaudus* became established, contributing to local control of the aphid, aided by the development of aphid resistance in trees (Zuparko and Dahlsten, 1996). Interestingly, *T. curvicaudus* did not spread further than 40 km from the release sites over a 20-year period, possibly due to the patchy distribution of its host and climatic conditions (Zuparko and Dahlsten, 1996).

The Monterey pine aphid (*Essigella californica*) was detected in 1998 in Canberra, Australia, where it caused substantial damage. *Diaeretus essigellae* was selected for introduction because of its high specificity, with the first release in November 2009. The first monitoring in 2010 failed to find establishment, but subsequent observations showed the parasitoid was able to overwinter under forest conditions (Stone *et al*., 2013).

Appraisal of classical biological control using parasitoids

Classical biological control of aphids by the introduction of parasitoids has been widely applied in numerous countries. In some cases, the reduction of the target pest was clearly established, permitting the calculation of the amount of money saved by this approach. For instance, the cost of a 7-year project to release *D. essigellae* to control *E. californica* was recovered in about 6 months because of the increase of pine production (Kimber *et al*., 2013). However, it is not always easy to evaluate the true benefit of exotic parasitoid introductions for aphid control. This challenge stems partly from inadequate data on the community of native natural enemies and on their capacity to control an exotic aphid species. Moreover, it is often difficult to distinguish between the role of the native generalist enemies and that of the introduced parasitoids. Establishment depends on many factors. It has long been known that small differences in biological attributes and thermal thresholds among different strains of imported natural enemy species can affect their success significantly, especially when releases cover a wide geographic area (Bernal and Gonzalez, 1997; Lee and Elliott, 1998). Some Aphidiinae species, such as *D. rapae* and *A. colemani*, appear much better adapted to climatic conditions in some important regions of *D. noxia* infestation (Elliott *et al*., 1995). The importance of laboratory studies of temperature effects on parasitoids to ensue 'climate matching' of the regions of collection and release has been emphasized strongly (Bernal *et al*., 2001). Nevertheless, comparisons between developmental thresholds and day-degree requirements for development of a parasitoid and its host do not necessarily provide an accurate prediction of temporal synchrony (Lee and Elliott, 1998). In the case of *B. communis*, the loss of ability to diapause, probably due to long periods of laboratory rearing, does not allow its establishment and successful overwintering in North America (Gariepy *et al*., 2015). Climate change may also affect the synchrony between host and parasitoid, and thus affect the population dynamics of both species substantially (Hance *et al*., 2007). These points merit further attention.

Biological control by augmentation in field crops

Although the mass release of *Trichogramma* species to control lepidopteran eggs in field crops is increasingly widespread, aphid biocontrol employing inundative releases of parasitoids in outdoor crops remains rare (Dedryver *et al*., 2010; Zhang *et al*., 2010; Razinger *et al*., 2016) (Table 20.4). Inundative releases require close synchronization with the aphid population and should be performed early in aphid development. In open fields, the dispersal of natural enemies is not limited, and the quantities of parasitoids needed for a release are much larger. Cost is also an important factor, because the return that farmers can expect from field crops is substantially lower than from glasshouses, precluding expensive investment in biological control (Boivin *et al*., 2012).

Halfhill and Featherston (1973) used portable field cages with an average temperature 11°C higher than outside, to accelerate the development of lucerne for rearing millions of *A. smithi* on *A. pisum* on fields where their release was intended. This technique enabled the annual release of between 100 and 300 million parasitoids from 1965 to 1969, to prevent the migration of *A. pisum* from lucerne, where they overwintered, to approximately 4000 ha of peas. The aphid populations in the fields receiving the mass releases remained low, whereas they varied widely under chemical control. However, the requirements of parasitoid production were considered too difficult for wide application. Levie *et al*. (2005) came to very similar conclusions. They released 20,000 *A. rhopalosiphi*/

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Table 20.4. Some examples of trials involving augmentative release of parasitoids to control aphids on open field crops.

Species	Target	Crop	Rearing techniques	Country	Effect	References
Aphidius smithi	*Acyrthosiphon pisum*	Lucerne	In cages on the field	USA	Significant impact on aphid but too expensive	Halfhill and Featherston (1973)
Aphidius gifuensis	*Myzus persicae*	Tobacco	In insectaries and small plastic greenhouses, local production	China	Satisfactory aphid control	Wei *et al*. (2003) Yang *et al*. (2009)
Aphidius rhopalosiphi	*Sitobion avenae*	Wheat	In insectaries	Belgium	Significant impact on aphid but too expensive	Levie *et al*. (2005)
Ephedrus persicae *Aphidius matricariae*	*Dysaphis plantaginea*	Apple orchards	Mass production in insectaries (Viridaxis, S.A.)	Belgium	Significant impact on the number of trees with aphid colonies, but variable results among years	Nicolas *et al*. (2013)

ha in two waves at 1-week intervals in experimental wheat plots. The population of *S. avenae* was reduced considerably compared with the control, and there was a higher level of parasitism. However, the cost of €2000/ha, approximately 20 times the price the farmer would accept, remains the major limitation of this technique (Levie *et al*., 2005). In China, Wei *et al*. (2003) developed a mass-rearing procedure for *Aphidius gifuensis* for the control of *M. persicae* on tobacco. Under their conditions, including the labour costs in China (US$0.25/h for a technician), they estimated that 1000 mummies cost approximately US$0.06, and that the total cost of producing 125,000 *A. gifuensis* mummies/day was US$223.69. The researchers released 109,800 parasitoids in 1998, 196,000 in 1999, 780,000 in 2000 and 5,600,000 in 2001, achieving satisfactory control (Wei *et al*., 2005). They recorded a net increase in parasitism, which reached 8.4–52.8, 64–82.3 and 93–93.5% in early, mid- and late season, respectively.

Since 2002, the techniques for mass-rearing *A. gifuensis* in small plastic glasshouses have been popularized in many rural villages in China, allowing augmentative releases on approximately 4000 ha of tobacco (Yang *et al*., 2009). Mass releases of *A. gifuensis* greatly reduced the aphid population and the number of insecticide treatments (Yang *et al*., 2009). In apple orchards, the inundative release of two parasitoid species, *Ephedrus persicae* and *Aphidius matricariae*, against rosy apple aphid, *Dysaphis plantaginea* (rosy apple aphid) resulted in fewer colonies in treated compared with untreated plots (T. Hance, unpublished). However, high variability between plots indicated that the early establishment of the parasitoids after introduction was not homogeneous. This problem remains to be solved (Nicolas *et al*., 2013).

Predators

Because they directly remove their prey, predators exert more direct pressure on the prey population than do parasitoids. Moreover, the development time of predators is generally longer than that of the prey, sometimes with only one generation per year. The shorter the development time, the more closely the numbers of predators may correlate with the development of the prey population. In coccinellids, the development time from egg to adult is several times that of aphids (Hemptinne *et al*., 1993). Consequently, at oviposition, it is not only the quality of the aphid colony that is important for the female choice but also its expected growth potential. Ladybirds therefore lay eggs in young aphid colonies with high growth potential for sustaining larval development. The same behaviour has been demonstrated in hover flies (Hemptinne *et al*., 1993).

Predators of aphids belong to many taxonomic groups (Bell *et al*., 2008), characterized by very different lifestyles and exploiting different niches

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either spatially or temporally. Ladybirds often represent the image of biological control to the public. However, they provide few examples of successful biological control. Several predators are marketed and increasingly used to control aphids, particularly in glasshouses, whereas outdoor utilization remains rare. Here, we will focus on the most widely used predators.

Aphidoletes aphidimyza (predatory gall midge)

Aphdoletes aphidimyza (Diptera; Cecidomyiidae) is the third most important invertebrate used in augmentative biological control worldwide (van Lenteren, 2012b; Fig 20.4). It has been used in more than 20 countries to control aphids since 1989, and numerous studies have confirmed its efficiency (Markkula and Tiittanen, 1985; Nijveldt, 1988), including in field crops and apple orchards (Bouchard *et al*., 1988; Grasswitz and Burts, 1995; Wyss *et al*., 1999). Recent developments concern using banker-plant systems to increase the efficiency of the *A. aphidimyza* releases, as well as improvements in mass rearing and diapause induction (Alotaibi, 2008; Frank, 2010). Examples of the first augmentative release trials of *A. aphidimyza* against aphids in glasshouses are listed in Table 20.5.

Glasshouses

Since the first mass rearing and augmentative release of *A. aphidimyza* in the 1970s, many reports have confirmed the potential of this predator against *M. persicae* and *A. gossypii* in glasshouses (Markkula and Tiittanen, 1985). According to Bondarenko (1989), a ratio of 1:5 to 1:9 *A. aphidimyza* larvae to aphids efficiently reduces the aphid populations on cucumbers. The midge can also significantly control rose aphids and green peach aphids at ratios of 1:10 to 1:15 (Popov and Belousov, 1987). This generalist

Fig. 20.4. Larvae of *Aphidoletes aphidimyza* eating an adult aphid. (Photograph courtesy of Christophe Salin.)

Table 20.5. Examples of the first trials involving augmentative release of the predatory midge *Aphidoletes aphidimyza* to control aphids on glasshouse crops.

Target	Crop	Banker plants	Country	Effect	References
Myzus persicae	Paprika		Norway	Good control early in season Midge entered diapause later in season	Hofsvang and Hågvar (1982)
Myzus persicae	Sweet pepper		USA	Good control with release rate of 1:10 aphids	Gilkeson and Hill (1987)
Myzus persicae	Sweet pepper	*Megoura viciae*, broad bean	Denmark	Good control using banker plants Supplementary releases sometimes needed later in season	Hansen (1983)
Myzus persicae	Sweet pepper		Germany	Good control in 2 years out of 4, combined with lacewing egg releases	Hommes (1992)
Aulacorthum solani	Lettuce		Germany	Failed to control aphids	Quentin *et al*. (1995)
Aphis gossypii	Cucumber	*Rhopalosiphum padi*, cereals	UK	Good control using banker plants, combined with parasitoid releases	Bennison and Corless (1993)

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predator is influenced more by aphid density and location on the plant than by the species of aphid within the patch (Jandricic *et al*., 2013).

Failures have also been reported (Hofsvang and Hågvar, 1982; Quentin *et al*., 1995; van Schelt and Mulder, 2000). In fact, the release rate, the timing of release and the temperature have substantial impacts on aphid control by *A. aphidimyza* (Popov and Belousov, 1987; Bondarenko, 1989; Hommes, 1992). Sometimes, the combination of *A. aphidimyza* with other beneficial insects has shown promising results, such as with lacewing (Hommes, 1992), the parasitoids *A. matricariae*, *A. colemani* and *Ephedrus cerasicola* (Hofsvang and Hågvar, 1982; Elliot *et al*., 1987; Bennison and Corless, 1993) and *H. convergens* (Navratilova, 1999). However, recently, the impact of IGP and antagonistic interactions was highlighted when *A. aphidimyza* was used together with other beneficial insects and nematodes (Lucas *et al*., 1998; Powell and Webster, 2004; Messelink *et al*., 2011; Hatami *et al*., 2012). For instance, *A. aphidimyza* larvae are easy intraguild prey for *Coleomegilla maculata lengi*, *Chrysoperla rufilabris* and *Episyrphus balteatus* because of this species' highly specialized mechanism of predation (Lucas *et al*., 1998). Hatami *et al*. (2012) demonstrated asymmetric IGP between *A. aphidimyza* and *Hippodamia variegata* in the presence or absence of *A. gossypii*. The combination of the pirate bug, *Orius laevigatus* and *A. aphidimyza* exhibited weak asymmetric IGP that depended on N fertilization levels (Hosseini *et al*., 2010); the effectiveness of *A. aphidimyza* was only significant at low levels of N fertilization. The presence of predatory mites can also disrupt the control of aphids by *A. aphidimyza* (Messelink *et al*., 2011). These mites feed on *A. aphidimyza* eggs, even where there is alternative food. The three predatory mites tested reduced *A. aphidimyza* numbers significantly, and the *M. persicae* density increased significantly in the presence of hyperpredation by *Amblyseius swirskii* on the midge. An antagonistic effect can also occur where infective juveniles of entomopathogenic nematodes such as *Heterorhabditis bacteriophora* are present (Powell and Webster, 2004). Indeed, *H. bacteriophora* reduced the emergence rate of *A. aphidimyza* on wheat pots in glasshouse experiments (Powell and Webster, 2004).

Experiments have been conducted to develop banker-plant systems to support *A. aphidimyza* in combination with or as an alternative to parasitoids (Mulder *et al*., 1999). Such systems provide alternative hosts and pupation substrates for the emerging larvae before the target pest invades and enable *A. aphidimyza* to establish early. The efficiency of this method requires further refinement and verification (Frank, 2010). To date, *Megoura viciae* (vetch aphid) on broad beans, cereal aphids on cereal seedlings, *A. gossypii* on barley or wild grasses and wheat, and *M. persicae* on broad beans have provided banker plants for *A. aphidimyza* in glasshouses and outdoor ornamental crops.

Field and orchard crops

Aphidoletes aphidimyza have been reported as the major aphid predator on apple (Adams and Prokopy, 1980; Brown and Lightner, 1997), and there have been many attempts to improve the effectiveness of *A. aphidimyza* releases on apple orchards since the 1980s (Bouchard *et al*., 1988; Grasswitz and Burts, 1995; Wyss *et al*., 1999; Nicolas *et al*., 2013). Although releasing *A. aphidimyza* shows promise against apple aphids in orchards, there can be problems of synchronization between the predator and prey (Morse and Croft, 1987) and the negative effects of low temperatures (Wyss *et al*., 1999). For the rosy apple aphid *D. plantaginea*, *A. aphidimyza* is one of the three most abundant predators in Europe, together with *A. bipunctata* and *E. balteatus* (Solomon *et al*., 2000). However, *A. aphidimyza* appears to occur too late in the development of aphid colonies to regulate *D. plantaginea* populations successfully (Miñarro *et al*., 2005).

Outdoor releases of *A. aphidimyza* controlled the aphids *M. persicae* and *Macrosiphum rosae* (rose aphid) (Nijveldt, 1988), and *A. aphidimyza* was important in reducing the numbers of cabbage aphids (*Brevicoryne brassicae*) in fields in Poland (Jankowska, 2005). To control the damson–hop aphid, *Phorodon humuli*, Solarska (2004) combined the release of the parasitoid *A. colemani* with *A. aphidimyza*. The efficacy of these predators ranged between 60% and 67% for the first release and between 60% and above 70% for the second, reaching 100% at the third, but the latter occurred when the natural mortality of the aphid was already high. Their effectiveness was nearly equal to that of a synthetic pesticide.

Mass rearing

Many attempts have been made to reduce the costs and improve the efficiency of *A. aphidimyza*

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production (Alotaibi, 2008). Storage of *A. aphidimyza* larvae at low temperatures appears promising, even though the results vary with location, laboratory population and methodology used (Kostal and Havelka, 2001). At 3°C, Kostal and Havelka (2001) obtained a survival rate above 50% after 7 months and 12% after 1 year under continuous darkness. Havelka and Zemek (1999) showed significant differences among the demographic characteristics of various *A. aphidimyza* populations that could influence the mass production and application of this predator considerably. The spectacular mating behaviour of *A. aphidimyza* and its requirement for spider webs for mating constitute one of the constraints of rearing, because unmated females do not oviposit (van Schelt and Mulder, 2000; van Lenteren and Schettino, 2003).

Coccinellidae (ladybirds)

Ladybirds have been used in biological control for more than a century. The introduction of *Coccinella undecimpunctata* to New Zealand in 1874 was considered the first known attempt at classical control using coccinellids against aphids (Dumbleton, 1936; Hodek, 1973). However, a recent analysis of historical sources indicated that this was, in fact, a spurious record resulting from cumulative misreporting (Galbreath and Cameron, 2015).

Ladybirds are major predators of aphids, including many species of economic importance (Hodek *et al*., 2012), and there have been frequent attempts to use ladybirds for aphid control (Obrycki and Kring, 1998). The biology of ladybirds and their potential for biological control were reviewed in detail by Majerus (1994), Obrycki and Kring (1998) and Dixon (2000), and most recently by Hodek *et al*. (2012) and Majerus (2016), which includes a detailed chapter on their use in biological control (Michaud, 2012). The success of ladybirds in aphid control is usually considered to be less efficient than that achieved against scale insects (Hodek, 1973; Iperti, 1999; Dixon, 2000). Indeed, the success rate for aphid control reaches only 4.1% on average and differs significantly from the 11.5% recorded for coccids (Hirose, 2006), though this difference stems mainly from just a few specific coccid examples (Hirose, 2006). Several reasons have been proposed for the poor performance of aphidophagous versus coccidophagous ladybirds, including: the much slower development rate of aphidophagous ladybirds in relation to that of their prey; their oviposition strategies that optimize the use of an often ephemeral food resource; and their greater mobility and dispersal abilities as adults (Iperti, 1999; Dixon, 2000). Aphids also have a higher intrinsic rate of increase than coccids (Hirose, 2006). However, in this context, it is interesting that Dixon (2000) has pointed out that ladybirds are primarily (and probably excessively) regarded as a tool for reducing aphid numbers rather than organisms attempting to maximize their fitness. Table 20.6 summarizes the main attempts at classical control and augmentative release of ladybirds.

Since 1900, 179 coccinellid species have been introduced into North America, but only 18 have established, sometimes only after many years and repeated introductions (Wheeler, 1993; Obrycki and Kring, 1998). In addition, several species have established after accidental introduction, including *Coccinella septempunctata* (7-spot ladybird) and *Propylea quatuordecimpunctata* (14-spot ladybird).

Introduced species have been implicated in the decline of some native species of coccinellids in the USA and elsewhere (Wheeler and Hoebeke, 1995; Obrycki and Kring, 1998; Dixon, 2000; Snyder *et al*., 2004b). The first attempt to introduce *Harmonia axyridis* in the USA from Japan dates to 1916. This was followed by 14 introductions in different states from 1964 to 1982. In 1988, this ladybird was considered established only in Louisiana, but subsequently it spread throughout North America. Presently, *H. axyridis* has established in at least 38 countries outside its native range: 3 countries in North America, 6 in South America, 26 in Europe and 3 in Africa, at an estimated dispersal rate of 100–500 km/year (Brown *et al*., 2011).

Glasshouses

Few attempts have been made to control aphids in glasshouses using ladybirds, but trials were already undertaken in the 1970s in Finland using *C. septempunctata* and *A. bipunctata* (2-spot ladybird) against *M. persicae* on sweet peppers and chrysanthemums and *M. rosae* on cut roses (Hämäläinen, 1980). Self-perpetuating populations were not established; repeated releases of larvae were necessary, making their use uneconomic. Establishment in glasshouses is very difficult because adults tend

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Table 20.6. Examples of trials involving classical control and augmentative release of ladybirds to control aphids.

Species	Target	Crop	Country	Effect	References
Glasshouse:					
Coccinella septempunctata	*Myzus persicae*	Sweet pepper	Finland	Control with repeated releases of larvae	Hämäläinen (1980)
Adalia bipunctata	*Macrosiphum rosae*	Chrysanthemum Cut roses		Uneconomic	
Harmonia axyridis flightless form	*Aphis gossypii*	Cucumber	France	For inundative release only due to a reduction of fecundity of the mutant	Ferran *et al*. (1998)
Coccinella septempunctata *Hippodamia variegata*	*Aphis gossypii*	Cucumber	Morocco	Satisfactory control but dependent on timing of release and initial aphid density	El Habi *et al*. (2000)
Coccinella undecimpunctata	*Aphis fabae*	Soybean	Egypt	Successful control at release rate of 200 adults/140 plants	Zaki *et al*. (1999)
Hippodamia convergens	*Aphis gossypii* *Macrosiphum euphorbiae*	Strawberry	Belgium	Effective against *Aphis gossypii* when high densities released together with parasitoids	Sterk and Meesters (1997)
Harmonia axyridis	*Macrosiphum euphorbiae*	Cut roses	USA	Significant impact on aphids Combined with aphelinid parasitoid	Snyder *et al*. (2004a)
Harmonia axyridis	*Aphis gossypii*	Cucumber	Japan	Some effect with release of egg masses and flightless adults	Kuroda and Miura (2003)
Adalia bipunctata flightless form	*Myzus persicae* *Aulacorthum solani*	Sweet pepper	The Netherlands	Satisfactory control on *Myzus persicae* but not on *Aulacorthum solani* due to the dropping behaviour of this species	Lommen *et al*. (2008)
Harmonia axyridis flightless form	*Aulacorthum solani* *Aphis gossypii*	Cucumber	Japan	Satisfactory control when larvae are released	Seko *et al*. (2014)
Field:					
Hippodamia convergens	*Capitophorus elaeagni*	*Elaeagnus* hedge	USA	77% reduction in aphid densities after 15 days	Raupp *et al*. (1994)
Hippodamia convergens	*Monellia caryella* *Monelliopsis pecanis*	Pecan orchard	USA	Good control Released with lacewings	LaRock and Ellington (1996)
Hippodamia convergens	*Diuraphis noxia*	Wheat	USA	Little effect and considered uneconomic Combined with lacewings	Randolph *et al*. (2002)
Harmonia axyridis	*Macrosiphum rosae*	Amenity roses	France	Good control but timing of release critical	Ferran *et al*. (1996)
Harmonia axyridis	*Phorodon humuli*	Hops	France	Early release of 50 larvae/plant reduced aphid populations; resultant adults dispersed quickly	Trouvé *et al*. (1997)

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Coccinella septempunctata *Propylea japonica*	*Aphis gossypii*	Cotton	China	Good control with repeated releases; overwintering adults collected to mass-rear larvae for release	Zhang (1992)
Coccinella septempunctata brucki	*Acyrthosiphon kondoi*	Lucerne (alfalfa)	Japan	Good control; overwintering adults collected to mass-rear larvae for release	Takahashi (1997)
Coccinella septempunctata *Menochilus sexmaculatus*	*Lipaphis pseudobrassicae*	Mustard	India	Successful control when larvae released at a rate of 1000/ha	Shenhmar and Brar (1995)
Coccinella undecimpunctata	*Aphis gossypii*	Okra	Egypt	Successful control when larvae released at rates of 1:50 aphids	Zaki *et al*. (1999)
Adalia bipunctata	*Dysaphis plantaginea*	Apples	Switzerland	Releases in spring limited aphid build-up Releases in autumn reduced overwintering eggs	Wyss *et al*. (1999) Kehrli and Wyss (2001)
Synonycha grandis *Coleophora (Lemnia) biplagiata*	*Ceratovacuna lanigera*	Sugarcane	China	Good control by release of adults collected over winter	Deng *et al*. (1987)

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to escape (Ferran *et al*., 1998; Rabasse and van Steenis, 1999). To prevent this, trials were done with natural flightless morphs. The residence time and proportion of individual *A. bipunctata* on plants are significantly greater for flightless than winged forms, and the former are therefore more effective in controlling *M. persicae*. The results on *A. solani* were less conclusive because equivalent effects on aphid numbers were recorded with both winged and wingless forms, probably because the aphid's mortality was increased by its dropping behaviour (Lommen *et al*., 2008). A chemical mutagen applied to males, followed by selective breeding, has been used to produce a flightless form of *H. axyridis* (Tourniaire *et al*., 1999). The flightless mutant *H. axyridis* and the production method have been patented in Europe (Tourniaire *et al*., 1999). However, the mutation reduces adult reproductive fitness and, although significantly more flightless than normal adults remained on *A. gossypii*-infested glasshouse cucumbers following release, they produced significantly fewer offspring despite a longer oviposition period (Ferran *et al*., 1998). Some success has been achieved in Japan with the release of egg masses and flightless adults of *H. axyridis* against *A. gossypii* on glasshouse cucumbers (Kuroda and Miura, 2003). More recently, control of *A. solani* and *A. gossypii* was obtained by releasing the flightless form of *H. axyridis*, with better success for larvae than adults (Seko *et al*., 2014). With *C. septempunctata* and *H. variegata* against *A. gossypii* on glasshouse cucumbers in Morocco (El Habi *et al*., 2000), both adult and larval releases provided satisfactory control, but efficiency depended on the timing in relation to aphid population levels and on a high predator–aphid ratio. Adults of *C. undecimpunctata* were released into a glasshouse at rates of up to 200/140 plants to control *Aphis fabae* (black bean aphid) on soybeans, with some success (Zaki *et al*., 1999). In strawberry crops, high densities of *H. convergens*, together with the parasitoid *A. colemani*, were effective against *A. gossypii*, although control of *M. euphorbiae* was attributed to another parasitoid, *A. ervi* (Sterk and Meesters, 1997). Trial results have also suggested that *H. axyridis* can be released to complement the control of *M. euphorbiae* on glasshouse-grown roses (Snyder *et al*., 2004a).

Field crops and amenity plants

Some species of aphidophagous ladybirds overwinter in mountainous areas in huge adult aggregations (Hagen, 1966; Dixon, 2000). For many years, *H. convergens* collected from aggregations in the USA have been sold to growers (Fenton and Dahms, 1951; Dreistadt and Flint, 1996), but the released adults usually disperse rapidly (Davidson, 1924; Kieckhefer and Olson, 1974). Obrycki and Kring (1998) emphasized that there was no biological basis for releasing *H. convergens* collected from overwintering aggregations and that the practice might deplete local populations, spread ladybird parasitoids and diseases and increase the vectoring of plant pathogens.

To avoid dispersal of aggregation-collected *H. convergens*, Dreistadt and Flint (1996) preconditioned them by allowing flight in screen cages and by providing water before release. Although these individuals dispersed more slowly than unconditioned ladybirds and reduced the aphid populations, most had still left after 3 days, and the preconditioning process was deemed uneconomic. Inundative releases of aggregation-collected *H. convergens* were tried in nurseries and glasshouses (Flint *et al*., 1995) and were successful on chilli peppers grown in netting cages (Votava and Bosland, 1996). However, huge numbers are needed. For instance, an inundative release of approximately 2300 *H. convergens*/m^2 is required to control high aphid densities on roses, about two orders of magnitude higher than the 11–22 beetles/m^2 usually recommended by beetle suppliers because ladybirds leave the plants on average 2 days after release. However, the price per treatment remains competitive with an imidacloprid application (Flint and Dreistadt, 2005). *Harmonia axyridis* larvae have also been released against aphids on amenity roses in Paris, performing as well as conventional insecticides (Ferran *et al*., 1996). However, if released at low aphid numbers (<30/bush), the ladybirds dispersed quickly.

In China, *C. septempunctata* and *Propylea japonica* were mass-reared from field-collected, overwintered adults and released as larvae (repeated several times) to control *A. gossypii* on cotton (Zhang, 1992). In northern China, *C. septempunctata* is hand collected from wheat crops and translocated to cotton, a strategy enabling a reduction in pesticide use (Zhang, 1992). It is believed that aphid populations in cotton can be suppressed if the ratio of natural enemies to aphids reaches 1:120 very early at the seedling stage. To achieve this, natural enemies can be increased via conservation measures and mass release (Luo *et al*., 2014). Table 20.6 lists other examples.

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Orchard crops

Adalia bipunctata is commonly associated with trees and can be an important natural enemy of aphid pests in orchards. In field cage experiments in Switzerland, *A. bipunctata* releases gave better results against *D. plantaginea* on apples than releases of *A. aphidimyza* and the hover fly, *E. balteatus*, partly because *A. bipunctata* was less affected by early cold temperatures (Wyss *et al.*, 1999). When tested together, *A. bipunctata* and *E. balteatus* showed an additive effect, and reduced aphid densities by 95%. April releases of *A. bipunctata* larvae were effective against the spring population of *D. plantaginea* in apple orchards, and autumn releases significantly reduced the number of fundatrices the following spring, although the high release rate necessary made this approach expensive (Kehrli and Wyss, 2001).

Adult *H. convergens*, together with lacewings, have been released against aphids in pecan orchards in New Mexico, with some success (LaRock and Ellington, 1996), and *H. axyridis* and *Cycloneda sanguinea* have been evaluated for release against citrus aphids (Michaud, 2000).

Chrysopidae (lacewings)

Lacewings are generalist predators that can feed on phylogenetically unrelated prey species of economic importance (Senior and McEwen, 2001) (Fig. 20.5). Lacewings have received considerable attention as potential biological control agents, though usually used in inoculative and augmentative approaches rather than in classical biological control.

Fig. 20.5. Lavae of the green lacewing *Chrysoperla carnea*. (Photograph courtesy of Christophe Salin.)

Improvements in mass-rearing techniques have led to their availability from a growing number of commercial suppliers, principally selling *Chrysoperla* species (Nordlund *et al.*, 2001; Copping, 2004; Table 20.1). Augmentative releases of eggs or young larvae have been used in several experimental or commercial aphid control programmes in orchards, field crops and glasshouses. McEwen *et al.* (2001) discussed the biology and potential of lacewings as biological control agents. Examples of trials involving augmentative releases of lacewings to control aphids on glasshouse and field crops are listed in Table 20.7.

Glasshouses

One of the first successful trials involved releases of *Chrysoperla carnea* (common green lacewing) larvae on potted chrysanthemums. The introduction of 1-day-old larvae at an aphid:chrysopid ratio of up to 50:1 and third-instar larvae at a ratio of 200:1 significantly reduced the numbers of *M. persicae* because of their high voracity (Scopes, 1969). On aubergine, releases of *C. carnea* larvae every 2–5 weeks at ratios of up to 1:20 aphids were required for significant reductions of the *M. persicae* population, but a 1:5 ratio almost completely eliminated the aphid (Hassan, 1978). Trials were also done in the former USSR in the 1970s, but were labour-intensive, often making them uneconomic (Beglyarov and Smetnik, 1977). Simlar conclusions were drawn from releases of *C. carnea* eggs in Scandinavian glasshouses against several aphid pests on green peppers and parsley. Augmentative releases of lacewings would not be economic until mass-rearing methods were improved (Tulisalo *et al.*, 1977). The release of 1000 eggs/200 m^2 is recommended by insect suppliers, corresponding to a ratio of 1 adult of *C. carnea*/5–30 aphids (Reddy, 2016). Low hatch rates and delayed hatching of eggs made the release of young larvae a better option. However, the application of *C. carnea* eggs to glasshouse lettuces provided better aphid control than releases of either the parasitoid *A. matricariae* or the predatory midge, *A. aphidimyza* (Quentin *et al.*, 1995). For strawberry crops in Italy, releasing 18 second-instar larvae/m^2 provided satisfactory control of *M. euphorbiae* and *Chaetosiphon fragaefolii*. In that system, chrysopid egg predation by ants can be a serious problem, requiring the application of ant repellent on the cardboard holding the eggs (Tommasini and Mosti, 2001).

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Table 20.7. Examples of trials involving classical control and augmentative release of lacewings to control aphids.

Species	Target	Crop	Country	Effect	References
Glasshouse:					
Chrysoperla carnea	*Myzus persicae*	Chrysanthemum	UK	Significant reduction in aphids with release of 1–2 larvae/plant	Scopes (1969)
Chrysoperla carnea	*Myzus persicae*	Aubergine	Germany	Good control with release of 1 larva/5 aphids Repeated releases needed with 1 larva/20 aphids	Hassan (1978)
Chrysoperla carnea	Several species	Sweet pepper, parsley	Finland	Effective on pepper with release of 1 egg/3 aphids and on parsley with 1 egg/27 aphids; uneconomic at time of trials	Tulisalo *et al*. (1977)
Chrysoperla carnea	Several species	Lettuce	Germany	Good control when eggs placed on young plants before transplanting, then 25–30 eggs/m^2 weekly	Quentin *et al*. (1995)
Chrysoperla carnea	*Macrosiphum euphorbiae* *Chaetosiphon fragaefolii*	Strawberry	Italy	Good control Release of larvae better than release of eggs	Tommasini and Mosti (2001)
Field:					
Chrysoperla carnea	*Myzus persicae* *Macrosiphum euphorbiae*	Potato	USA	Some effects on *Myzus persicae* when eggs and larvae released	Shands *et al*. (1972)
Chrysoperla carnea	*Acyrthosiphon pisum* *Brevicoryne brassicae* *Myzus persicae* *Aphis craccivora*	Pea, brassicas, tomato, aubergine, sweet pepper	Former USSR	Releases of larvae ineffective on peas and brassicas Effective control with release of 1 larva/5 aphids on tomato, aubergine and sweet pepper	Beglyarov and Smetnik (1977)
Chrysoperla carnea	*Aphis fabae*	Sugar beet	Germany	Good control for 2 weeks with release of 1 egg/5 aphids	Şengonca and Löchte (1997)
Chrysoperla carnea *Chrysoperla rufilabris*	*Aphis fabae*	Sugar beet	USA	Effect difficult to assess because aphids declined naturally on control plots after treatments applied	Ehler *et al*. (1997)
Chrysoperla carnea	*Aphis gossypii*	Okra	Egypt	Good control with two releases of 1 larva/5 aphids	Zaki *et al*. (1999)
Chrysoperla carnea	*Aphis gossypii*	Cotton	Egypt	Good control with repeated releases of eggs and larvae	El Arnaouty and Sewify (1998)
Chrysoperla carnea	*Aphis pomi*	Apple orchard	Canada	Significant reduction in aphids with egg releases	Hagley (1989)
Chrysoperla carnea	*Illinoia liriodendri*	Amenity tulip trees	USA	Release of eggs ineffective due to low egg viability and predation by ants	Dreistadt *et al*. (1986)

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Chrysoperla lucasina	*Aphis gossypii*	Melon	France	Good control with release of 1 larva/20 aphids	Malet *et al*. (1994)
Chrysoperla lucasina	*Aphis fabae*	Artichoke	France	Satisfactory control with repeated releases of larvae	Maisonneuve (2001)
Chrysoperla rufilabris	*Diuraphis noxia*	Wheat	USA	Little effect and considered uneconomic Combined with ladybirds	Randolph *et al*. (2002)
Chrysoperla rufilabris	*Monellia caryella* *Monelliopsis pecanis*	Pecan orchard	USA	Good control when eggs and larvae released with ladybirds	LaRock and Ellington (1996)
Chrysoperla rufilabris	*Mindarus kinseyi*	White fir seedlings	USA	Good control with release of 2 larvae/seedling Combined with insecticidal soap treatments	Ehler and Kinsey (1995)
Chrysoperla rufilabris	*Aphis gossypii*	Cotton	USA	High larval mortality and adult dispersal, expensive method	Knutson and Tedders (2002)
Micromus igorotus	*Ceratovacuna lanigera*	Sugarcane	India	Effective control with 1500 pupae/ha	Vidya *et al*. (2012)
Chrysoperla carnea	*Aphis gossypii* *Myzus persicae*	Cantaloupe	Egypt	Reduction of aphid population by 73.9 and 83.07%	Younes *et al*. (2013)

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Field crops and amenity plants

In potatoes, repeated early-season weekly applications of *C. carnea* eggs produced a marked decline of *M. persicae* corresponding to a total of about 1.25 million hatching *Chrysopa* larvae/acre. *Coccinella septempunctata* was more effective than *Chrysopa* spp. in controlling aphids at high predator densities, whereas the reverse was observed at low densities, probably because lacewing larvae were more mobile. Both species were less effective against *M. euphorbiae* (Shands *et al*., 1972). Releasing *C. carnea* eggs on sugar beet crops in Germany controlled *A. fabae* for 2 weeks (Şengonca and Löchte, 1997), but similar trials in California, using *C. carnea* and *C. rufilabris* eggs were less successful, although aphid populations declined naturally on all plots soon after treatment, hindering an adequate impact assessment (Ehler *et al*., 1997). The efficiency of *Chrysoperla* larvae varies greatly with crop and may be influenced by leaf structure and trichome presence, as well as by the rate of aphid increase, climatic conditions, ground cover and agricultural practices (Daane, 2001). Releases of *Chrysoperla* larvae against aphids on outdoor crops in the former USSR have also produced mixed results, being more effective on sweet peppers, tomatoes and aubergines than on peas and brassicas (Beglyarov and Smetnik, 1977).

In outdoor melon crops, the release of second-instar *Chrysoperla lucasina* larvae at a ratio of 1:20 aphids on to plants previously inoculated with *A. gossypii* kept the aphids below the economic damage threshold, control comparable to an insecticide treatment (Malet *et al*., 1994). However, augmentative releases of *C. rufilabris* and ladybirds against RWA had very limited success and were considered uneconomic (Randolph *et al*., 2002). In India, mass release of *Micromus igorotus* to control the sugarcane woolly aphid, *Ceratovacuna lanigera*, provided effective control at a density of 1500 pupae/ha (Vidya *et al*., 2012).

Improved mass rearing and the field application of lacewings have stimulated an increasing number of trials (Table 20.7). Recently in Egypt, *M. persicae* and *A. gossypii* populations were reduced by 79%, 80% and 89% on cantaloupe 3 weeks after the release of 3, 5 and 7 larvae/plant, respectively (Younes *et al*., 2013). High larval mortality, adult dispersal and high cost are usually cited as major constraints on augmentative releases of chrysopids (Knutson and Tedders, 2002). According to Warner and Getz (2008), the dramatic cuts in production costs for *C. carnea* and *C. rufilabris* have yet to be translated into reduced retail prices. Indeed, the use of artificial diet for lacewing rearing may reduce the production cost to about 85% of the use of factitious prey (Haramboure *et al*., 2016). Similarly, based on an analysis of the efficiency of mass production, Nasreen *et al*. (2011) concluded that the high labour costs were mostly only affordable in countries where wages remained quite low. Availability and cost remain major weaknesses of inundative releases of Chrysopidae.

Adult lacewings are unsuitable for field releases, and are even problematic in the glasshouse because of their dispersal behaviour (Nordlund *et al*., 2001; Tommasini and Mosti, 2001). However, Şengonca and Henze (1992) used lacewing hibernation boxes to collect overwintering adults in arable fields in Germany, subsequently re-releasing them into wheat fields to coincide with the appearance of cereal aphids. With this approach, lacewing eggs were recorded 1 month earlier than in control fields, but without any clear effects on aphids. In China, overwintering adult *Chrysoperla sinica* were collected from fields to produce larvae for inoculative release the following spring against several pests in mixed cropping systems, especially cotton intercropped with wheat (Wang and Nordlund, 1994). From this reservoir in wheat early in the year, the lacewings moved on to adjacent crops as the wheat ripened.

Current problems with augmentative releases of lacewings include natural predation of eggs and young larvae (Dreistadt *et al*., 1986; Daane and Yokota, 1997), poor egg-hatch rates and post-hatch cannibalism (Tommasini and Mosti, 2001), IGP (Rosenheim *et al*., 1993) and competition with other, naturally occurring predators (Maisonneuve, 2001). Concerns have also been expressed about the effects of prolonged commercial culturing on lacewing performance (Ehler *et al*., 1997).

Orchard crops and tree seedlings

Trial releases of *C. carnea* eggs on to apple trees in Canada significantly reduced *Aphis pomi* (green apple aphid) densities, but releasing the eggs from cardboard containers placed manually in the trees was expensive (Hagley, 1989). Although the larvae of *Chrysoperla plorabunda* ate *A.* (*T.) citricidus* and appeared to be effective predators in the laboratory, in orchards the release of newly hatched

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larvae did not control aphid populations and very few larvae were observed feeding on the aphid. The availability of alternative prey may explain this poor result (Michaud, 2001). In early trials in pecan orchards in the USA, eggs or newly hatched *C. rufilabris* larvae were released from aircraft, but this method was later changed to manual placement on selected trees (LaRock and Ellington, 1996). These releases formed part of an IPM programme that included releases of adult ladybirds (*H. convergens*), cultural management strategies and limited insecticide inputs. *Monelliopsis pecanis* (yellow pecan aphid) and *Monellia caryella* (black-margined yellow pecan aphid) were kept below economic damage levels.

Effective control of *Mindarus kinseyi* on white fir seedlings in California was attained with releases of two *C. rufilabris* larvae per seedling in conjunction with insecticidal soap treatments, although both treatments had to be repeated later in the season (Ehler and Kinsey, 1995).

Syrphidae (hover flies)

Like coccinellids, syrphids are characterized by a 'buy futures' tactic whereby females select aphid colony sizes based on future growth potential rather than their immediate value (Kan, 1988; Ambrosino *et al*., 2007). Consequently, there have been few attempts to use hover flies in classical or augmentation biological control. Instead, attempts to enhance their impact on pests have concentrated on manipulating habitats around field crops or glasshouses to provide floral food resources for adults before oviposition, as part of conservation biological control strategies. For instance, in sweet pepper glasshouses, introducing banker plants of barley infested by *Rhopalosiphum maidis* (corn leaf aphid) attracted syrphids into glasshouses from outside but did not arrest *E. balteatus* released into the glasshouses long enough for oviposition. This is mainly because the mean residence time of the released *E. balteatus* in the presence of banker plants was only 5.8 days, compared with the minimum time required for them to become gravid of approximately 7 days (Pineda and Marcos-Gracia, 2008). Biological control by conservation is covered in Chapter 21, this volume.

The potential of *E. balteatus* for augmentative releases against *D. plantaginea* was assessed using laboratory and field cage experiments in Switzerland (Wyss *et al*., 1999). Releases of larvae, together with ladybird larvae, on to apple seedlings reduced aphid densities to 5% of those on control seedlings. Larvae of *E. balteatus*, released in vegetable fields in China at a ratio of 1:180 aphids, reduced aphid populations by over 90% in 3 days (Yang *et al*., 2002). However, techniques for egg mass release need to be improved in the future. Using several semiochemicals and aphid honeydew, Leroy *et al*. (2010) induced *E. balteatus* to oviposit on small plastic sheets (1 × 5 cm). They then used these sheets with eggs for release in cages and in field experiments. In cages, a population of 500 aphids was eliminated in 10 days by the introduction of 15 *E. balteatus* eggs. Such techniques may hold promise for augmenting predator populations at the right time and to the appropriatel level, avoiding the dispersal occurring when adults are released (Leroy *et al*., 2010).

Entomopathogenic Fungal Species

From 700 to 1000 species in approximately 90 genera have been reported as entomopathogenic fungi (St Leger *et al*., 2011; Fang *et al*., 2012; Sandhu *et al*., 2012).

Several species have high potential as biological control agents as mycoinsecticides and mycoacaricides (de Faria and Wraight, 2007; Khan *et al*., 2012a). De Faria and Wraight (2007) have provided an exhaustive review of 171 products, registered and in use (75%) and no longer available or never registered (25%), developed to target primarily Hemiptera, Coleoptera, Lepidoptera, Thysanoptera and Orthoptera.

Certain entomopathogenic fungi attack restricted host ranges, such as *Aschersonia aleyrodis*, which infects only scale insects and whiteflies (Meekes *et al*., 2002). By contrast, other species have a wide host range. For example, specific strains of *Metarhizium anisopliae* and *Beauveria bassiana* are pathogenic to several insects, and are used for the biological control of agricultural pests worldwide (de Faria and Wraight, 2007; Sandhu *et al*., 2012).

A major challenge for biocontrol based on entomopathogenic fungi is their hazard to humans, the environment and non-target organisms, including beneficial insects. However, several studies have demonstrated that such collateral damage is minimal (Goettel *et al*., 2001; Copping, 2004; Pell *et al*., 2010) and is certainly a safer alternative than chemicals in conservation (Wang *et al*., 2012) or augmentation (Chandler *et al*., 2008) strategies.

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Taxonomic revision

The most widely used species attacking aphids are found in the order Hypocreales of the division *Ascomycota*, such as *Lecanicillium* spp., *Beauveria* spp., *Metarhizium* spp. and *Isaria fumosorosea* (formerly *Paecylomyces fumosoroseus*). For the other entomopathogenic species previously identified as Zygomycota, order Entomophthorales, we shall use a recent reclassification (Gryganskyi *et al*., 2013) placing them in a new phylum, Entomophthoromycotina.

Entomopathogenic fungi have evolved to exploit the resources provided by their hosts, ultimately killing them, and numerous species are obligate insect pathogens (including all Entomophthoraceae). Understanding their variable life cycles and their pathogenic features will help to identify new ways to improve the virulence of wild strains and determine the best formulations and application strategies for further commercialization (Pell *et al*., 2010; Khan *et al*., 2012a; Sandhu *et al*., 2012).

Asexual conidia produced by entomopathogenic Hypocreales are transported by the wind, land on the cuticle, germinate and initiate the penetration process. After death of the host, the fungus overwinters as chlamydospores or sclerotes, or emerges from the cadaver, and sporulating conidia are passively dispersed.

Entomophthorales fungi remain in or on insect cadavers to overwinter. Some species may form resting zygospores or azygospores if hosts are not present or the environment becomes unfavourable (Hajek *et al*., 2013). Conidia are actively dispersed under hydrostatic pressure, forming a halo around the cadavers, and then passively by wind or other insects.

Mycoinsecticides and aphid biocontrol

It has been known for decades that isolates of *Lecanicillium* spp., *B. bassiana*, *M. anisopliae* and *I. fumosorosea* are active against aphid species (de Faria and Wraight, 2007; Khan *et al*., 2012a). Most commercial mycopesticides against aphids are manufactured from Hypocreales; their asexual forms are readily mass-produced *in vitro* and the small infective spores can be formulated and sprayed for inundative augmentation (Chapple *et al*., 2000; Hesketh *et al*., 2008).

In contrast, Entomophthoromycotina species are difficult, or even impossible, to mass-produce *in vitro* (Freimoser *et al*., 2001; Shah and Pell, 2003). Therefore, these species have been more successful in small-scale, classical introductions, inoculative augmentation (often using material produced *in vivo*) and, more recently, conservation biocontrol (Shah and Pell, 2003; Ekesi *et al*., 2005; Pell *et al*., 2010).

Hypocreales

The most common commercial products used against aphids are prepared and formulated from *Lecanicillium* spp. (i.e. Vertalec® and Mycotal®, Koppert Biological Systems, The Netherlands), from *B. bassiana* (i.e. BotaniGard® and Mycotrol®, Emerald Bioagriculture, USA; Naturalis®, Troy BioSciences, USA), from *M. anisopliae* (i.e. MET52®, Novozymes, USA), from *I. fumosorosea* (i.e. Preferal®, SePro, USA), or from *Isaria javanica* (i.e. PFR-97®, Certis, USA; Nofly®, Novozymes, USA – labelled *I. fumosorosea*). De Faria and Wraight (2007) recorded 171 common, rarely used, or experimental products: more than 93% contained Hypocreales. Khan *et al*. (2012a) reviewed the side effects of *B. bassiana* (and *Beauveria brongniartii*) strains and formulations on beneficial and non-target organisms.

GLASSHOUSES. *Lecanicillium longisporum* has shown good efficacy against several aphid species, including *M. persicae* (Milner, 1997; Roditakis *et al*., 2008) and *A. gossypii* (Kim *et al*., 2007), and was the first developed as an inundative mycoinsecticide in glasshouses under the name Vertalec® (Fig. 20.6).

Vertalec® (*L. longisporum*) is produced by liquid fermentation as blastospores, and is formulated with a nutrient source as a wettable powder containing 10^9 blastospores/g (Milner, 1997). In Europe, Vertalec® is used exclusively in glasshouses, where optimal conditions for infection, particularly humidity, can be maintained. On green peppers, application together with sublethal doses of imidacloprid improved efficacy against *M. persicae* (Roditakis *et al*., 2008). However, even in glasshouses, temperatures and humidities frequently fall outside the activity range of the Vertalec® isolates (Hall and Papierok, 1982; Yeo *et al*., 2003).

Recent advances have detected, characterized and identified other *Lecanicillium* species or isolates combining aphicidal and other biocidal properties (Goettel, 2008; Goettel *et al*., 2008). Three

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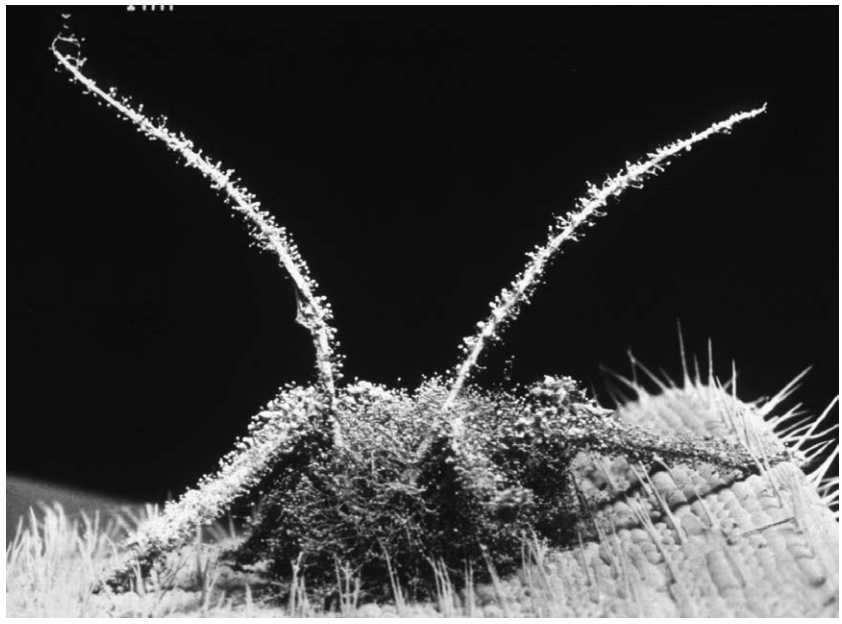

Fig. 20.6. Aphid infected by the entomopathogenic fungus, *Lecanicillium longisporum*, which is available as the commercial mycoinsecticide Vertalec® for use against aphid pests on glasshouse crops. The fungus can be seen emerging from the body of the infected aphid. (Photograph courtesy of D. Chandler.)

species of *Lecanicillium* (*Lecanicillium* spp., *L. attenuatum* and *L. longisporum*), showed dual activity *in vitro* against three aphid species (*M. persicae*, *M. euphorbiae* and *A. solani*) and powdery mildew (*Sphaerotheca fuliginea*) (Kim *et al*., 2007). Vertalec® was then evaluated for the simultaneous control of aphids and powdery mildew on cucumbers in a glasshouse. Experiments demonstrated that applications at 3-day intervals eliminated aphid populations after the third treatment, completely controlling the aphids 16 days after aphid inoculation (Kim *et al*., 2010).

A detrimental side effect of Mycotal® (*Lecanicillium muscarium*) was observed for the parasitoid *A. colemani* on emergence, but the ladybird *H. axyridis* was not affected (Aqueel and Leather, 2013). By contrast, Aiuchi *et al*. (2012) demonstrated that Vertalec® and Mycotal® were both compatible with *A. colemani*.

Commercial products based on *B. bassiana* are also available for aphid control. Under commercial or experimental formulations, *B. bassiana* proved effective against a large range of aphid species found in glasshouses, as reported recently for *Aphis craccivora* (Maketon *et al*., 2013), *A. gossypii* (Vu *et al*., 2007), *A. solani* (Jandricic *et al*., 2014) and *M. persicae* (Vu *et al*., 2007; Khan *et al*., 2012b). Jandricic *et al*. (2014) identified several *Beauveria* and *Metarhizium* spp. isolates equally or even more virulent than the commercial strains of Botanigard®, Naturalis® and MET52®. The results also indicated that nymphs were much more susceptible than adults to commercial and experimental isolates of *Beauveria*, *Metarhizium* and *Isaria*, but they exerted little effect on reproduction.

The potential of *Metarhizium* spp. has been widely studied, with the manufacture of commercial or experimental products against numerous insects, especially in Central and South America (de Faria and Wraight, 2007). However, one of the few reports of their use for aphid control (de Faria and Wraight, 2007) relates to MET52® (Jandricic *et al*., 2014), which was initially recommended against Lepidoptera. Chandler (1997) conducted laboratory bioassays with 25 *M. anisopliae* strains against lettuce root aphid, *Pemphigus bursarius* (lettuce root aphid). Only one out of the 25 isolates consistently killed lettuce root aphids; assays on lettuce in the field have, however, been inconclusive (Parker *et al*., 2002).

OPEN FIELDS. In the laboratory, isolates of *Lecanicillium* spp., *B. bassiana*, *M. anisopliae*

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and *I. fumosorosea* have shown virulence against several aphid species found on field crops (e.g. Zaki, 1998; Poprawski *et al*., 1999; Feng *et al*., 2004; Kim *et al*., 2007; Saranya *et al*., 2010). However, in open fields, only a few commercial products are recommended, of which Mycotrol® and Mycotrol® O are based on the GHA isolate of *B. bassiana*.

There are few publications on the efficiency of mycoinsecticides against aphids under tropical field conditions. Filho *et al*. (2011) assessed *B. bassiana*-based oil dispersions on *M. persicae* on cabbage under cage and field conditions. However, inactivation of *B. bassiana* conidia by UV radiation has been reported (Inglis *et al*., 1995; Fernandes *et al*., 2007; Huang and Feng, 2009), constituting a major constraint for the development of such products for sunny regions. To avoid their degradation, it appears that oil-formulated conidial suspensions are less susceptible to sunlight (Alves *et al*., 1998) and rainfall (Inglis *et al*., 2000), and show enhanced adhesion and deposition on the hydrophobic cuticle of arthropods, leading to a 10–20% increase in efficacy compared with aqueous formulations (Ibrahim *et al*., 1999). However, the rapid aphid reinfestation observed demonstrates that the stand-alone use of mycoinsecticides for aphid control is still not a satisfactory strategy in the tropics and that the utilization of *B. bassiana* in IPM strategies there remains to be explored.

ORCHARDS. Several papers report the efficiency of Hypocreales against aphids in orchards. For instance, Mycotrol® is registered for orchard use, and the laboratory and field efficacy of the GHA isolate has been demonstrated against *A. (T.) citricidus* in the USA (Poprawski *et al*., 1999). Dorschner *et al*. (1991) also demonstrated the efficacy of a different, aphid-derived isolate of *B. bassiana* against hop aphids on potted plants, but not in commercial fields. Two studies have identified the potential of autodissemination or assisted autodissemination by ants of *L. longisporum* to aphids on hops and apples (Hartfield *et al*., 2001; Bird *et al*., 2004). Shapiro-Ilan *et al*. (2008) tested the virulence of *I. fumosorosea* blastospores against three pecan aphids (*Monellia caryella*, *Melanocallis caryaefoliae* and *Monelliopsis pecanis*) under laboratory conditions and demonstrated its potential for commercial use pending further glasshouse and field trials.

LABORATORY AND EXPERIMENTAL DATA. Most of the approved *B. bassiana* products contain aerial conidia produced by either solid-state or diphasic fermentation. Pham *et al*. (2010) optimized solid-state fermentation on polished white rice that tripled conidia production by *B. bassiana*. Lohse *et al*. (2013) recently optimized a large-scale fermentation system for an endophytic strain of *B. bassiana*, resulting in a low-cost culture medium producing very high spore yields (conidia and blastopores). Agroindustrial waste offers an alternative to conventional production via submerged fermentation (De la Cruz Quiroz *et al*., 2014). This technology offers an inexpensive alternative in developing countries, producing little residual water and high product stability.

Laboratory and field evaluations of blastospore applications of an *L. attenuatum* isolate revealed *M. persicae* mortality of approximately 80% (Kim *et al*., 2008). The field evaluations on glasshouse pepper showed aphid mortality from 72% to 97%. Another strain was selected for its high virulence against *A. gossypii*, producing 100% mortality (Kim and Kim, 2008).

To clarify the potential role of endophytic fungi in IPM on cotton, an endophytic isolate of *L. lecanii* was tested against *A. gossypii* with nine insecticides, both *in vitro* over 14 days and *in planta* (Gurulingappa *et al*., 2011). Most insecticides inhibited the germination of conidia and the growth of hyphae under *in vitro* conditions. However, in contrast with laboratory tests, the *in planta* tests showed that *L. lecanii* established on all plant treated by the insecticide tested, supporting the hypothesis that endophytes might compliment the chemical management of pests in cotton.

Entomophthoromycota

GLASSHOUSES. Inoculative augmentation has been attempted experimentally to establish *Neozygites fresenii* (Neozygotales) and *Pandora neoaphidis* (Entomophthorales) for aphid control in glasshouses in Europe. Under optimal conditions, Dedryver (1979) achieved some success releasing living aphids infected with *N. fresenii* on bean plants infested with *A. fabae*. Similarly, Latgé *et al*. (1983) and Silvie *et al*. (1990) applied *in vitro* mycelia of *P. neoaphidis* as an aqueous spray; although the fungus infected some aphids (*A. solani* and *M. euphorbiae*), population suppression was not achieved. Glasshouse trials of

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P. neoaphidis formulated as dried mycelium or in alginate beads have shown some potential for the control of *M. euphorbiae* (Shah *et al*., 1998). A novel air-extrusion method was optimized successfully to embed *Conidiobolus thromboides* hyphae at high density in alginate pellets that, on rehydration, ejected hyphae infective to aphids (Chen *et al*., 2014).

OPEN FIELDS. Fungal epizootics are often observed in cereals, where aphid mortality sometimes exceeds 60% (Steenberg and Eilenberg, 1995). There is an example of classical biological control from the 1970s in Australia, with an isolate of *Zoophthora radicans* to control *T. trifolii maculata*. The fungus subsequently spread by itself and controlled the aphid effectively (Milner *et al*., 1982).

Inoculative augmentation in cereals and legumes in Europe has been attempted experimentally several times to encourage early impact of *P. neoaphidis* and *N. fresenii* where they occur indigenously (Latteur and Godefroid, 1983; Wilding *et al*., 1990; Poprawski and Wraight, 1998). It appears that the artificial introduction of *E. neoaphidis* acts too slowly for cereal aphid control.

Conservation approaches, including habitat manipulation, are currently becoming more important for improving the impact of naturally occurring Entomophthorales species in field crops without the requirement for augmentation (Ekesi *et al*., 2005). However, before applying such strategies, it is necessary to understand better the complete process of initiation and development of epizootics (Nielsen and Steenberg, 2004).

The potential for classical biological control of *N. fresenii* against cotton aphids has been studied since 1995 (Steinkraus *et al*., 2002). However, mass production is a very limiting factor. Another important characteristic of *N. fresenii* is its ability to survive long periods as mature hyphal bodies or early-stage conidiophores in dried, frozen aphids (Steinkraus *et al*., 1993). Considering these two features, it is less expensive and more efficient to harvest a pathogen from field epizootics and store it for future use (Steinkraus, 2000). This approach requires that workers are able to identify aphids at the correct stage for harvesting. Steinkraus and Boys (2005) speculated that cotton growers might harvest large numbers of aphid-infested leaves from epizootic fields and then dry, freeze and store the leaves for use during the next season to inoculate cotton fields.

LABORATORY AND EXPERIMENTAL DATA

Mass production. A major constraint on the use of Entomophthorales and Neozygotales as biocontrol agents is the difficulty of mass production. Within the genus *Pandora*, *Pandora nouryi* is the only species proven to produce resting spores, a source of inoculum for the next season. It appears that, *in vivo*, resting spore formation is regulated primarily by the concentration of host-infecting conidia discharged from *M. persicae* cadavers, and is facilitated by low temperatures and long daylight (Zhou and Feng, 2010).

Even when mass production of *Pandora* spp. and *Z. radicans* (Entomophthorales) is possible, yields remain poor. Therefore, new production technologies have been developed using broomcorn millet grain cultures for *Pandora delphacis* (Feng and Liang, 2003) and *P. neoaphidis* (Hua and Feng, 2003). Using a polymer gel for *P. nouryi*, high sporulation and discharge capabilities were obtained even at reduced humidity, allowing long-term storage at low temperature (Zhou and Feng, 2009). The novel air-extrusion method optimized by Chen *et al*. (2014) for embedding *C. thromboides* hyphae (Basidiobales) in alginate pellets appears to be promising for use in biological control.

Aphid–fungi relationships. Numerous recent studies focus on the epidemiology of fungal agents and their relationships with their aphid hosts as well as aphid behaviour. When assessing the role of an entomopathogenic fungus as a conservation biological control agent, it is important to understand the habitat, propagation and transmission of the fungus during the aphid life cycle (Baverstock *et al*., 2009). Baverstock *et al*. (2008) demonstrated that the presence of two species of co-occurring *Aphidius* parasitoids (*A. rhopalosiphi*, a non-enemy, and *Aphidius microlophii*, an enemy of the target pest aphid) and a caterpillar (*Aglais io*, a competitor for food) benefited *P. neoaphidis* and significantly enhanced its transmission to the susceptible host aphid *Microlophium carnosum* (common nettle aphid), reinforcing the importance of guild members in a biocontrol strategy.

In a study on the natural epizootics of *M. persicae* and other aphid species on vegetables in southern China, Feng and Li (2003) tested multiple regimes of temperature and relative humidity to determine the optimal epizootiology of *Zoophthora anhuiensis* in *M. persicae* populations; *Z. anhuiensis*

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is better adapted to cool climates or seasons. The data confirmed that *Z. anhuiensis* would cause severe epizootics from October to December, corresponding to the optimal RH and temperature conditions, but was rarely found in other seasons. The possible use of *Z. anhuiensis* for biological control should incorporate these considerations.

Chen and Feng (2004) present data from a simulated flight experiment of *P. neoaphidis*-infected *S. avenae* alatae. They demonstrated successful transmission of alate-borne *P. neoaphidis* to their progeny, supporting the hypothesis of primary dispersal of aphid epizootics by alates across a wide geographic area, including from crops to forests or other ecosystems. A similar study on *M. persicae* and *P. neoaphidis* also supported a significant role for infected alates in the dispersal of *P. neoaphidis* (Chen and Feng, 2006).

Nielsen and Steenberg (2004) focused on the fungal epizootics on *R. padi*, which split its life cycle between a primary (bird cherry) and a secondary host (cereals). The authors never observed infected *R. padi* on bird cherry in spring. In contrast, several entomopathogenic fungi were documented in autumn (*Entomophthora planchoniana*, *P. neoaphidis*, *Zoophthora phalloides*, *Conidiobolus obscurus* and *N. fresenii*). It was concluded that *R. padi* feeding on bird cherry did not play an important role in the spread of entomopathogenic fungi and that epizootics in cereal aphids did not originate from infected individuals migrating from bird cherry.

A study on *P. neoaphidis* overwintering in fields demonstrated that this fungus preferred to infect hosts if they were available prior to overwintering (Zhou, 2012). Fungal survival in winter is thus of prime importance for maintaining an important inoculum in the field, enabling early spread when aphids appear on crops. In conclusion, keeping plants in field margins to support fungal survival in non-pest hosts between crop cycles may improve early-season multiplication and dispersal to crop aphids.

Future of mycopesticides and genomic advances

Factors that contribute to the performance of a successful mycoinsecticide have been studied intensively, including the optimization of mass production, host specificity, *in vivo* life cycle, nutrient availability and environmental conditions (relative humidity, ambient temperature and solar UV radiation) (Fargues, 2003). Nevertheless, mycopesticides still constitute a small percentage of the total pest control market, mainly because the market share of a product is proportional to its killing speed, and mycopesticides only kill slowly (St Leger and Wang, 2009).

The sequencing of the whole genomes of *B. bassiana* (Xiao *et al*., 2012), *Metarizhum* spp. (Gao *et al*., 2011) and *Cordyceps militaris* (Zheng *et al*., 2011) has provided phylogenetic information about their respective evolution and their relationships with other (entomopathogenic) fungi. Genetic sequencing has also enabled the mapping of many species-specific virulence genes in *B. bassiana*, and may provide new insights for improving these traits. Molecular techniques for the genetic engineering of entomopathogenic fungi have provided, and will continue to provide, new opportunities for the mycobiocontrol of insect pests (St Leger *et al*., 2011). Engineered strains have been produced with desirable traits such as increased tolerance to abiotic stress and faster kill (St Leger *et al*., 2011; Keyhani, 2012). In other studies, strains were constructed that (over)expressed various proteases and chitinases (St Leger *et al*., 1996; Fan *et al*., 2007) or were transformed with insecticidal toxins or insect-derived molecules (Wang and St Leger, 2007; Fan *et al*., 2012). However, fungal transformations required the use of antibiotic- or herbicide-resistance markers, which may be a substantial drawback for field use. Furthermore, most *M. anisopliae* and *B. bassiana* strains have intrinsic resistance to many antibiotic-selective markers, rendering these agents unsuitable in transformation systems. In that context, Ying *et al*. (2013) developed a markerless transformation system for *B. bassiana* based on the uridine auxotrophy.

Although genetic engineering offers new possibilities, there is a strong need for assessing the risks to the environment, non-target insect fauna and human health as part of an evaluation of ethical issues.

General Conclusions

In recent years, techniques for biological control against aphids have been greatly expanded, especially regarding augmentative biocontrol, in which the commercial availability of natural enemies is increasingly important. However, augmentative biocontrol as yet concerns mainly protected crops (van Lenteren, 2012b). To date, the greatest success has been achieved with hymenopteran parasitoids, the predatory midge *A. aphidimyza* and the syrphid

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E. balteatus, which are currently used in more than ten countries (Cock *et al*., 2010; van Lenteren, 2012b). Concerning classical biological control, the number of introductions of new natural enemies in countries where they did not previously exist has declined substantially in recent years. This is due largely to the risk of invasion associated with introducing a new species and the potential negative effects on the environment. In addition, a new constraint has arisen with the Convention on Biological Diversity (CBD), which rules on the legal rights of countries over their genetic resources. The CBD requires the sharing of benefits associated with the use of a local resource in another country. In the case of biological resources, such benefits are particularly difficult to evaluate in monetary terms (Cock *et al*., 2010). Interest in classical biological control has also diminished because of a new emphasis on conservation biocontrol and the potential use of generalist native natural enemies (Chapter 21, this volume). In this context, augmentative biological control can be viewed as a complementary tool for controlling unpredicted pest outbreaks in crops that are currently managed with a conservation biocontrol approach. However, many challenges remain for outdoor crops, related mainly to natural enemy dispersal. Here, the use of apparent competition and field management with grassy strips, combined with occasional corrective releases of natural enemies, may serve as an elegant and less expensive solution in the medium term (Langer and Hance, 2004; Levie *et al*., 2005, Frere *et al*., 2007). Moreover, the use of semiochemicals to attract natural enemies to the field (Leroy *et al*., 2010), and the conditioning of parasitoids to enhance their propensity to remain where they have been released (Dumont *et al*., 2011), have promise for the future.

Entomopathogenic fungi also have great underexploited potential within IPM strategies, although several difficulties remain (Shah and Pell, 2003). Several factors need improvement to increase their utilization: (i) the selection of new strains with high virulence and speed of kill; (ii) ensuring their efficacy and persistence under variable abiotic conditions in open fields; (iii) improving mass production; (iv) improving their integration with other means of control; (v) reducing their potential side effects on the environment and human health; and (vi) providing extension services to increase their acceptance by farmers and the public (Lacey *et al*., 2001). Formulation technology may improve persistence, such as for the control of grasshoppers using *M. anisopliae* var. *acridum* (Burges, 1998), where ultra-low-volume sprays of oil formulations of conidia ensure the infection of the target insect even at extremely low ambient humidity. Another important limitation is the prohibitive costs of registration, particularly when the target pest is on a low-value crop. This issue requires legislative advances, based on scientific input at the national and international level. The ecological impact of ascomycete species with broad host ranges must be understood better to facilitate registration (van Lenteren *et al*., 2003; Wang *et al*., 2004). For entomophthoralean fungi, the challenges for mass production remain a weak point.

This review carries several important messages. First, the practical use of biological control by augmentation will always require the precise determination of the timing of the intervention and of the ratio between the natural enemy and the aphid pest, because of the rapid exponential growth rate of aphid populations. Intervention must occur early in the aphid population growth curve. This window of opportunity is often narrow, but could be extended by combining biological control with other strategies such as the breeding of crop varieties with partial resistance to the pest (Chapter 22, this volume) and the ecological manipulation of agricultural ecosystems to conserve and enhance populations of natural enemies. Second, in this context, contrary to common practice since the beginning of agricultural intensification, it is necessary to restore diversity in agricultural landscapes, so that when natural enemies are released en masse, they can find necessary resources near crops, limiting their dispersal and so allowing their populations to increase locally. Much work remains to be done in relation to field crops, which are a challenge for the future of biological control considering the area they occupy on the Earth's surface and the quantity of pesticide still used worldwide. Third, the multiplicity of interactions across trophic levels and their consequences on the implementation of biocontrol still requires substantial attention. Intraguild predation may improve (Messelink and Janssen, 2014; Northfield *et al*., 2014) or reduce the efficiency of biocontrol (Almohamad and Hance, 2014; Frago and Godfray, 2014), and strategies to enhance parasitoid populations also benefit hyperparasitoids. The potential risk of pathogens spreading by predators or parasitoids should also be taken into account (Noël *et al*.,

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2016). Because several natural enemies with different traits may be released in the same glasshouse or in open fields where a predatory fauna is already present, their function at the community level must be analysed. Finally, climate change may also change plant quality and the synchrony between pests and enemies, and may favour an increase in the number of pest generations. Temperature changes may affect the diapause process, precocity and the balance in plant–insect–natural enemies systems (Hance *et al*., 2007; Jeffs and Lewis, 2013; Aguilar-Fenollosa and Jacas, 2014). All of these points should be considered in the near future.

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21 Cultural Control[1]

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Introduction

In this chapter, a variety of techniques is described under the heading of cultural control. The unifying theme is the reduction of aphid damage through management of the physical or biological environment of the crop, either at establishment or during its growth. However, several mechanisms are involved. These range from preventing aphid access by physically protecting crops, to enhancing aphid mortality by providing neighbouring habitats that provide out-of-season refuges for aphid predators. Some methods are widely known, pre-dating intensive agrochemical use (Gurr *et al*., 2000). Others are the product of more recent research activity (Gurr *et al*., 2012). Some are used in conjunction with insecticides, and others are considered as more benign alternatives (Harrewijn and Minks, 1989). The mechanisms may be well understood, or they may involve multitrophic-level interactions between species that are very difficult to predict (Tscharntke and Hawkins, 2002; Brewer and Elliott, 2004).

The following section provides an overview of methods of cultural control and the mechanisms through which they affect aphid control. Subsequent sections review approaches that have attracted recent interest among researchers, drawing on studies from a range of crop types and climates. The discussion focuses on the ecological mechanisms by which the control techniques operate, rather than on the full range of socio-economic factors that must be evaluated before the methods can be commercialized.

Overview

Figure 21.1 lists the techniques of cultural control of aphids, based on the way in which the technique is interpreted in this chapter. In addition to the environmental factors included in the figure, genetic features of the crop have an important influence on susceptibility to aphid damage. Manipulating genetic variation, including the choice of crop species for a particular climate, and variation between cultivars in their aphid resistance might be considered as cultural methods of aphid control. However, host-plant resistance is discussed by van Emden in Chapter 22, this volume. Techniques that involve the enhancement of natural enemies through release programmes are discussed by Hance *et al*. in Chapter 20, this volume.

In Fig. 21.1, a diversity of approaches is apparent, which arises in two ways. First, a reduction in aphid damage can be achieved via effects on one or more of the processes determining aphid population size, or on the damage imposed by each aphid. Second, these aspects of aphid biology can be affected directly by cultural practice, or the effects can be achieved through the manipulation of abiotic conditions, host-plant quality, or natural enemy populations.

[1] Material from the first edition of this chapter has been included, and the contribution of Katherine A. Robinson is gratefully acknowledged.

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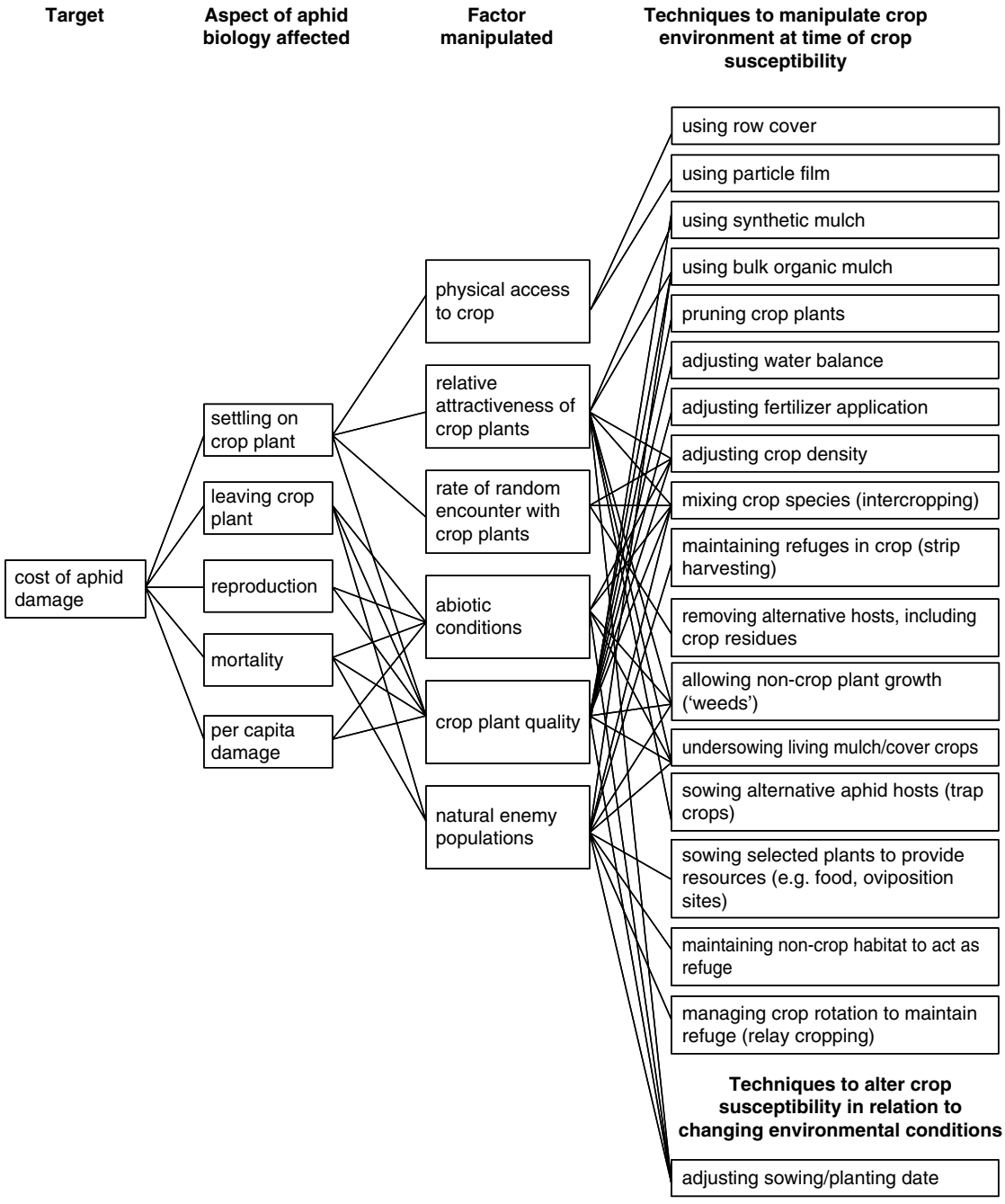

Fig. 21.1. Cultural methods for managing aphid populations and the mechanisms by which they affect levels of aphid damage. These methods may be applied within the cropped area or in the surrounding landscape. The influences represented by linking lines can be positive or negative and may be deliberate or inadvertent effects of employing the technique.

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More important are the various ways in which any particular technique operates. If it has multiple effects, each may increase or decrease aphid damage, and the net effect will depend on the state of other components of the system. For example, almost all techniques have the potential to affect aphids indirectly by altering host-plant quality. Furthermore, the techniques will affect crop yield in ways other than via aphid control, and these must also be considered.

Although there are interacting factors to be considered, manipulations of the physical environment are relatively amenable to experimental research. The use of synthetic mulches can affect many determinants of plant growth, including soil temperature, water balance and competitive weed growth (e.g. Brault *et al*., 2002). These factors can affect both the susceptibility of the crop to damage by a given aphid population and the degree to which the crop supports aphid population growth. However, research has shown that, in many situations, the overriding effect is that on the ability of the aphids to find the host plants (Kennedy and Booth, 1963). The reflectivity of the mulch alters the aphid's visual perception of the crop and, consequently, the rate at which alatae find host plants (Kring and Schuster, 1992; Brown *et al*., 1996; Farias-Larios and Orozco-Santos, 1997a,b).

Several cultural methods of control involve manipulating the biotic environment by increasing plant diversity. These are discussed below under 'Intercropping, Living Mulches and Cover Crops', 'Trap Crops', 'Provision of Resources for Natural Enemies' and 'Provision of Refuges for Natural Enemies'. The complexity of the interacting mechanisms involved in approaches using increased plant diversity means that theoretical community ecology has often been used to inform experimental research.

An inverse relationship between herbivore populations and plant diversity is found in many ecological communities (Letourneau *et al*., 2011). As discussed in the relevant sections below, the various mechanisms by which increasing plant diversity can reduce herbivore populations may operate directly through the plants themselves or via their effect on predators. In an agroecological context, Root (1973) summarized these perspectives as two hypotheses. First, the 'enemies' hypothesis places emphasis on natural enemies of the herbivore and 'top-down' control (Root, 1973). According to this hypothesis, the natural enemies receive some benefit from non-crop plants that increases their impact on herbivore populations in diversified systems. In contrast, the 'resource concentration' hypothesis emphasizes 'bottom-up' influences on community dynamics. It states that herbivores are more likely to aggregate in monocultures because the concentration of resources in pure stands facilitates the finding and/or recognition of the host (Kennedy and Booth, 1963). Numerous studies have addressed this subject and have provided evidence for both hypotheses (van Emden, 1990; Andow, 1991; Gurr *et al*., 1998; Wratten *et al*., 1998; Landis *et al*., 2000). Together with work addressing the ecology of key species in particular crop systems, this reinforces the need for a multiplicity of factors to be considered in the design and use of biocultural techniques in pest management (Dent, 2000).

In discussing the efficacy of methods of aphid control, it should be recognized that there is not a simple relationship between aphid populations and 'satisfactory control'. The degree to which populations must be suppressed to keep damage at acceptable levels depends on the nature of the damage (Chapter 14, this volume). For example, low population densities may cause significant yield losses through the transmission of severe plant virus diseases, yet the removal of nutrients through feeding, even by high aphid densities, may cause only modest yield loss.

Mulches

Mulches (ground coverings) are a widely recognized cultural technique for improving the yield of horticultural crops by conserving water (Farias-Larios *et al*., 1994), inhibiting weed growth (Brault *et al*., 2002), improving the biological and chemical composition of the soil (Lal *et al*., 1980) and increasing soil temperature (Farias-Larios and Orozco-Santos, 1997a,b). Altering the microclimate and host-plant quality can also affect aphid damage indirectly through changes in aphid reproductive rate and survival, but recent attention has focused on deterring alate aphids through reflectance of short-wavelength radiation by the mulch surface. This reduces the conspicuousness of crop plants against the background of bare soil, leading to disruption of host-plant location by settling alatae, for which visual stimulation is known to be an important factor (Prokopy and Owens, 1983). Undersown plants may have a similar effect on crop perception (Dempster, 1969).

Many studies have investigated the optical properties of different mulches alongside their effect on aphid colonization and the incidence of aphid-borne

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viruses (Kring and Schuster, 1992; Brown *et al*., 1996; Farias-Larios and Orozco-Santos, 1997a,b; Greer and Dole, 2003; Jenni *et al*., 2003; Saucke and Döring, 2004; Summers *et al*., 2004). These studies have compared plastics of various colours, metallic surfaces, spray-on latexes and organic materials such as straw. For example, transparent and aluminium-painted plastic mulches have been found to reduce populations of aphids better than black or blue plastic mulches (Kring and Schuster, 1992; Brown *et al*., 1996; Farias-Larios and Orozco-Santos, 1997a,b). Nevertheless, a recent study in Croatia on watermelon (*Citrullus lanatus*) showed that black mulches led to more *Brachycaudus helichrysi* (leaf-curling plum aphid) and *Phorodon humuli* (damson–hop aphid) than straw mulch, whereas use of the latter led to fewer individuals of *Aphis fabae* (black bean aphid) and *Myzus persicae* (peach–potato aphid) (Zanic *et al*., 2013). Kring and Schuster (1992) found that aluminium-painted plastic mulch reflected approximately four times more UV light (<390 nm) than black or white mulches. This increased reflectance led to lower densities of aphids (also of thrips) on pepper and tomato plants grown in Florida, USA. More evidence for the importance of reflectance comes from the observation that the aphid-repellent effects of white mulches diminish as they become duller or yellow with time (Summers *et al*., 1995). Another strategy that involves the manipulation of aphid host finding is the use of UV-absorbing films as mulches (Legarrea *et al*., 2010). This material significantly reduces the population of *Brevicoryne brassicae* (cabbage aphid) in Brussels sprouts (*Brassica oleracea* var. *gemmifera*), because this aphid species is highly sensitive to UV intensity, avoiding environments with low UV radiation. Polyethylene mulches appear to have their greatest impact on aphid colonization early in the season (Liotta and di Trapani, 1994; Brown *et al*., 1996). A study in Alabama, USA, showed that early season aphid densities in summer squash (*Cucurbita pepo*) plants were low, and *Zucchini yellow mosaic virus* and *Cucumber mosaic virus* were absent in treatments with an aluminium-painted plastic mulch. However, as the season progressed, aphid numbers began to increase, leading to an increase in the incidence of virus diseases (Brown *et al*., 1996). This delay in the onset of mosaic virus disease was attributed to a decrease in intensity of the short-wavelength light reflected from the mulch as the plants grew over the mulch.

Water-miscible silver spray mulches also show promise for the management of aphids. Not only do they confer reflectivity to the soil surface on which they are sprayed, thereby repelling aphids, but also they have advantages over polyethylene in that they are biodegradable and can be incorporated into the soil at the end of the season, requiring no removal or landfill (Summers *et al*., 1995). Biodegradable plastics have been developed, but may degrade prematurely (Greer and Dole, 2003).

By altering the microclimate and habitat at ground level, mulches also have the potential to affect populations of epigeal predators. The use of organic materials such as straw and compost is particularly likely to have this effect, and may also affect prey/host quality indirectly by providing nutrients. In some crops, the observed impacts on aphid populations have been attributed to these mechanisms rather than to the optical properties of the materials. For example, in an experiment comparing the arthropod fauna of plots with and without compost in an apple orchard, compost was associated with lower numbers of the nymphs of *Eriosoma lanigerum* (woolly apple aphid) on some sampling dates (Brown and Tworkoski, 2004). Aphid populations on sampled tree roots, however, were not significantly different. In a study where aphids were added to cereal plots (so that the results were not due to the effect of mulch on immigration rates), Schmidt *et al*. (2004) found that straw mulch led to lower aphid populations later in the season, and mulching was associated with higher spider populations. However, against expectation, the effect of mulch on aphids was stronger when ground predators were excluded.

Recent work conducted in Florida, focusing on the pests of snapdragon plants, compared mulches of cowpea, sunn hemp, sorghum-sudangrass, pine bark nuggets and an unmulched control (Gill and McSorley, 2012). Arthropod sampling of various taxa using pitfall and board traps showed the soft-bodied herbivores including aphids were more numerous in the control and cowpea plots. This was attributed to the higher abundance of weeds in those treatments, a conclusion supported by the finding that numbers of predators did not differ consistently between treatments.

Row Covers

Lightweight row covers of spun-bonded polyester or polyethylene, designed to rest ('float') on the surface of crop plants, provide protection by excluding insects. Floating row covers can reduce aphid

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density and virus incidence in potatoes (Harrewijn *et al*., 1991), cantaloupe (*Cucumis melo*) (Espinoza and McLeod, 1994), squash/muskmelon (*C. pepo*) (Webb and Linda, 1992; Walters, 2003), bell pepper (*Capsicum annuum*) (Avilla *et al*., 1997) and lettuce (Rekika *et al*., 2008). They act by repelling alate aphids and preventing alighting aphids from inserting their stylets (Webb and Linda, 1992). Tunnels have been used to similar effect (Jenni *et al*., 2003).

Covers made from needle-punched wool have also been examined for crop protection. Although such covers carry the advantage of being biodegradable, they offer significantly poorer protection against aphids on cabbages than do synthetic fibres (Evans *et al*., 1997).

Plastic mulches have been used in conjunction with floating row covers (e.g. Webb and Linda, 1992). However, high-intensity light reflected from the mulch may accelerate degradation of the covers, without providing any aphid management benefits beyond those of the covers alone (Webb and Linda, 1992).

Particle Films

Spraying crops with inert reflective materials (e.g. whitewash) can reduce aphid populations. By altering the visual cues presented to alatae, as occurs with reflective mulches, the sprays reduce settling rates (Glenn *et al*., 1999). Early trials found that spraying peppers and potatoes with various whitewash formulations reduced the rates of aphid-transmitted virus infection on some sampling dates (Marco, 1986). In the potato study, aerial aphid populations were monitored, and although catches of one aphid species, *Aphis gossypii* (cotton or melon aphid), were higher in treated plots, the principal species (*Sinomegoura citricola*) was less abundant (Marco, 1986). However, spraying reduced yields of peppers and potatoes, possibly because the shading effect of whitewash outweighed the benefits of reduced viral infection.

Recent improvements in technology have allowed the development of more sophisticated particle films (Fig. 21.2) based on kaolin ($Al_4Si_4O_{10}(OH)_8$) (Glenn and Puterka, 2005). These are multifunctional, reducing disease and solar injury as well as insect damage. As described above, the high reflectivity acts as a visual repellent. In addition, those insects that do colonize the sprayed crop are affected adversely by kaolin particles covering the plant surface or adhering to their exoskeleton. Particles on their tarsi impair insect mobility and grip; foraging behaviour can be disrupted by excessive time spent grooming, and particles interfere with feeding and oviposition. These effects combine to increase mortality and reduce the rate of reproduction (Glenn and Puterka, 2005).

Fig. 21.2. Kaolin mixed with water and applied to vine plant foliage by a tractor sprayer.

Laboratory studies have shown that *Tinocallis caryaefoliae* (black pecan aphid) prefers unsprayed to sprayed pecan (*Carya illinoinensis*) foliage, and longevity and nymph production are lower on treated seedlings (Cottrell *et al*., 2002). However, laboratory studies on *M. persicae* concluded that particle films had no significant impact on the survival and reproduction of this species, although in the first 20 min after spraying, a clear avoidance of the treated plants by the aphids was seen (Barker *et al*., 2007). Mortality of *Aphis spiraecola* (green citrus aphid) was increased by particle films in a test on apple leaves (Glenn *et al*., 1999). This effect was partly attributed to aphids falling from the sprayed leaves.

In apple and pear orchards, field trials with kaolin have controlled a range of arthropod pests successfully (Glenn *et al*., 1999; Glenn and Puterka, 2005), although their efficacy against aphids has been relatively low. Knight *et al*. (2001) sampled apple trees on six dates over 2 years and found that aphid (*Aphis* spp.) populations on trees that had received kaolin applications were not lower than on unsprayed trees. This could be explained by the concentration of aphids at the growing tips, where, despite repeated spraying, the leaves were sufficiently particle free for the treatment to have no significant effect. In the short-term laboratory studies of Glenn *et al*. (1999) and Cottrell *et al*. (2002), this

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effect would not have been apparent. On two dates in the field, the aphid infestations were actually higher on sprayed trees. Populations of spiders and other natural enemies were often reduced by spraying (Markó *et al*., 2010), suggesting that aphids might have benefitted from a negative effect of the particle film on their predators (Knight *et al*., 2001). In a study conducted in The Netherlands, kaolin-sprayed apple orchards had lower numbers of *Aphis pomi* (green apple aphid), no significant effect on *Dysaphis plantaginea* (rosy apple aphid), but an increase in *E. lanigerum* populations, producing severe damage to the trees (Markó *et al*., 2008). This unexpected increase was attributed to the absence on sprayed trees of natural enemies, such as earwigs (*Forficula auricularia*), mites (*Allothrombium fuliginosum*), spiders (*Philodromus* spp., *Dictyna* spp., *Theridion* spp., Erigoninae and *Clubiona* spp.), scarabs (*Exochomus quadripustulatus*), the 14-spot ladybird (*Propylea quatuordecimpunctata*) and heteropterans (*Himacerus apterus* and *Orius minutus*). Aditionally, there was an increase in *A. gossypii* populations after a kaolin spray on a cotton (*Gossypium hirsutum*) crop in the USA, but in this case, this was attributed to the lower temperature on ventral surfaces of kaolin-sprayed leaves, enhancing the fitness of this species (Showler and Armstrong, 2007). In this study, natural enemies were not affected by the kaolin spray.

Sowing and Planting Date

In seasonal climates, there is natural variation in the rate of growth, reproduction and dispersal of aphids, and of their natural enemies. Similarly, in rotational cropping systems where there is a cycle of crops in the landscape, the availability of source populations for a particular field will vary. By altering the time that a crop is established, the grower can control the time of crop susceptibility in relation to these fluctuations. Sowing date also affects the size of plants at the time of aphid colonization, with potential effects on the between-plant movement of aphids and the perception of the crop by incoming alatae. The degree to which aphid damage can be managed in this way is clearly limited by the direct effect of the weather on plant growth, but it has proved a successful strategy in some situations.

For example, work with oilseed rape (*Brassica napus*) in Pakistan examined the effect of six sowing dates, ranging from 1 October to 20 November (Shafique *et al*., 1999). Aphid (species unstated) density ranged from 94/plant in the early-sown treatment to 392 in the latest-sown treatment. Yields declined markedly with later sowing dates, ranging from 496 to 21 g of seed/2.7 m^2 plot. A similar effect was evident in Indian work (Saha and Baral, 1999). Late-sown rape was attacked more heavily by *Lipaphis pseudobrassicae* (mustard aphid) and was lower yielding than were treatments sown up to a month earlier (in early November). Another study of this system used regression techniques to determine that each 10 days of delay in sowing resulted in an increase of 36 aphids/5 cm of stem length and a yield loss of 93 kg/ha (Bhadauria *et al*., 1992). A broadly similar trend was evident in Bangladesh for the effect of *L. pseudobrassicae* on Indian mustard (*Brassica juncea*) and rape (Rahman *et al*., 1989).

In tobacco production in Georgia, USA, planting date again influenced infestation by *Myzus persicae nicotianae* (tobacco aphid) (McPherson *et al*., 1993). Plants sown in late or mid-April rather than in late March had higher aphid population peaks in 2 of the 3 years of study. In contrast, delayed sowing was associated with low aphid densities in barley grown in northern England (McGrath and Bale, 1990). The same pattern associated with late sowing and low aphid damage has been seen with wheat aphids in Transylvania (Malschi *et al*., 2013) and Pakistan (Wains *et al*., 2010). However, late sowing of a cereal may not be economically viable because of the yield penalty resulting from the shorter growing season (Selman, 1980). In a comparison of wheat production systems in the UK, Holland (1997) concluded that the gross margin for later, spring-sown crops was £170/ha lower than for autumn-sown crops, despite substantially lower densities of *Sitobion avenae* (English grain aphid) and *Sitodiplosis mosellana* (orange wheat blossom midge).

High densities of *Aphis craccivora* (cowpea aphid) on cowpea (*Vigna unguiculata*) in Uganda tended to be associated with late planting (6 weeks after the onset of rains) (Karungi *et al*., 2000). However, in the case of *A. gossypii* on cotton in Texas, USA, planting date had no effect on abundance (Parajulee *et al*., 1999).

The incidence of aphid-borne virus infections can vary independently of aphid populations, and may also show seasonal fluctuations. Sowing date may lead to differences in the incidence of plant diseases such as *Barley yellow dwarf virus* (BYDV)

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(Snidaro and Delogu, 1990). In temperate cereals, a high level of aphid activity during autumn may cause early-sown crops to suffer particularly heavy attack. From these crops, there is then more virus transmission to young plants in the latest planted fields in the subsequent spring (Hunger *et al*., 1992). For this reason, delayed sowing of winter wheat has been practised in Australia and has led to a decline in BYDV infection (Johnstone *et al*., 1990). A study of *Diuraphis noxia* (Russian wheat aphid) in western USA, where it had been a pest since 1986 (Stoetzel, 1987), concluded that a delay in planting of just 12 days from an early September sowing date was sufficient to manage the viral diseases vectored by *D. noxia* and to increase grain yield (Hammon *et al*., 1996). In a multivariate analysis of field characteristics and agronomic practice, Foster *et al*. (2004) found sowing date to be a key risk factor for BYDV in UK cereals. The incidence of aphid-borne *Potato virus Y* (PVY) in potatoes increases when the stage of greatest crop susceptibility coincides with the main period of aphid flight. Where soil conditions prevent earlier sowing, crops can be established before aphid activity by pre-sprouting. In late varieties however, potatoes that have not been pre-sprouted will emerge after peak aphid flight, and pre-sprouting may then increase virus infection rates (Saucke and Döring, 2004).

Plant Density

The density of crop plants at the time of peak aphid susceptibility affects the appearance of the crop to alatae, the dispersal of aphids within the crop and the prevailing microclimatic conditions. The effects of interplant competition on host-plant quality may also influence aphids. These mechanisms may have conflicting effects on aphid damage.

High densities of *A. craccivora* on cowpea in Uganda tended to be associated with low planting density (Karungi *et al*., 2000). The same pattern has been observed with *A. gossypii* in cotton crops in Texas, USA (Parajulee *et al*., 1999). Where cotton was planted in rows with two empty rows in between, the mean number of aphids/leaf was 4.71, significantly higher than where cotton was planted in every row (1.82 aphids/leaf), with intermediate densities where cotton was planted in alternate rows. This effect is consistent with the greater visibility of crop plants against the background of bare soil in unplanted rows, leading to easier location by settling alatae, as discussed above. A similar effect was seen in Australian studies of narrow-leaved lupins (*Lupinus angustifolius*); wide row spacings resulted in higher incidence of *Bean yellow mosaic virus* (BYMV) (Jones, 1993). It was considered that delayed canopy closure resulted in prolonged exposure of bare earth between rows and led to a higher population of vector aphids. More recent studies of this system suggest scope for avoiding high aphid immigration in crops at low densities by retaining the stubble of the previous crop (Bwye *et al*., 1999). In contrast, wider tree spacing in young plantations of Sakhalin fir (*Abies sachalinensis*) resulted in lower infestation levels of the aphid *Cinara todocola* in Japan (Furuta and Aloo, 1994). This is to be expected, since in this system, tree-to-tree dispersal of aphids within plantations is largely by apterous females, not alatae.

Crop Plant Pruning

Aphids often feed preferentially on certain parts of a plant; also, some parts may be more susceptible to damage. In some situations, pruning the crop plants may provide an appropriate means of reducing the effect of aphids. Pruning can also interact with other cultural practices such as nitrogen fertilizer use to influence aphids, as in a study of *M. persicae* on peach (*Prunus persica*) (Grechi *et al*., 2010). In developing countries, relatively low labour costs can allow techniques that would be uneconomical in developed countries. Work in central Africa investigated the effectiveness of hand removal of the terminal shoots of cotton plants at the end of the growing season (Deguine *et al*., 2000). This was important, because *A. gossypii* otherwise feed on the terminal shoot and secrete honeydew that falls on to the open bolls and causes 'sticky cotton'. The removal of terminal shoots using a pruning knife in large-scale field experiments on seven sites in Cameroon had no effect at sites with low aphid densities, but did reduce aphid densities and the proportion of leaves infested at the most heavily infested site. This method was considered inexpensive and well suited to local conditions. In Brazil, the time of pruning related to boll maturity was investigated in order to reduce aphid damage in cotton. Pruning at 50% of mature bolls reduced aphid numbers significantly when compared to pruning at the opening of the first boll (Dos Santos *et al*., 2010). Under other conditions, however, host-plant pruning can exacerbate aphid

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infestation, because it encourages the growth of lush new shoots favoured by herbivores. The aphid *Hyadaphis tataricae* feeds on the succulent new growth of honeysuckle (*Lonicera* spp.). Fieldwork in Nebraska, USA, indicated that plants that were pruned and watered had greater aphid densities than plants that were either only watered or only pruned or untreated (Coffelt and Jones, 1989). Similarly, studies of *M. persicae* on peach (Grechi *et al*., 2008) found that pruning enhanced shoot growth and the level of aphid infestation of trees. This effect was considered to be due chiefly to the increase of the proportion of growing shoots, on which aphid development was enhanced compared to that on other plant parts. This, in turn, led to higher levels of aphid-induced shoot-tip damage, leaf curling and leaf fall (but not eventual fruit quality or weight).

Irrigation and Fertilizer Management

Irrigation and fertilization are important management practices in agricultural landscapes. These practices can have profound indirect effects on aphids, but usually not targeting aphid populations, and for this reason we do not explore this approach, but provide some key references here for further reading: van Emden (1972); Godfrey *et al*. (2000); Bi *et al*. (2003); Huberty and Denno (2004); Amini *et al*. (2012); Banfield-Zanin *et al*. (2012); and Hopmans and Elms (2013).

Intercropping, Living Mulches and Cover Crops

Intercropping is the growing of multiple crops in a field, spatially integrated in such a way as to alter the environment of the plants of each crop relative to a monoculture. When aphid-susceptible crops are mixed with non-hosts, a key aspect of this environment is the combination of cues available to aphids arriving at, and moving within, the field. Undersowing a non-crop species or allowing weed cover to develop has a comparable effect to intercropping on plant diversity. These practices may also have benefits such as fixing nitrogen, suppressing undesirable weeds, retaining soil moisture, or reducing erosion.

It has been suggested that non-host plants may interfere with the host-finding ability of specialist herbivores such as aphids (Root, 1973). This hypothesis is in accordance with the frequent observation that reduced aphid densities in high-diversity crops are the result of the slower colonization of host plants (Costello and Altieri, 1994; Lehmhus *et al*., 1996; Vidal, 1997) rather than differences in the rates of reproduction or survival (Costello and Altieri, 1995; Lehmhus *et al*., 1996). However, Helenius (1997) highlighted the importance of spatial scale and regional management in the colonization patterns through a metapopulation approach. When acting this way, the effect of increased vegetation diversity on aphid colonization would depend on the host-finding mechanism (Chapter 9, this volume) employed by a particular species of aphid. If an aphid species locates its host using chemosensory information, volatiles produced by non-crop plants may mask the chemical cues required by aphids for host location (Tahvanainen and Root, 1972). However, chemosensory information may only be sufficient to arrest a dispersing aphid in the general vicinity of a host plant, rather than provide explicit directional information on its location (Finch and Collier, 2000). At this point, visual information may be of primary importance for host location. If an aphid species relies on visual information for host location, increased crop diversity may provide a confusing landscape mosaic, making it difficult for winged aphids to identify host plants.

In an intercropped system, aphid attack on the 'primary' crop may also be affected by the density of the 'secondary' crop (Fig. 21.3). For example, when maize was sown at differing densities within beans, the positive relationship between density and the population of *A. fabae* was partly attributed to variation in the amount of bare soil and the impact of this on aphid landing responses (Ogenga-Latigo *et al*., 1992). A more important factor reducing the incidence of aphids on the intercropped beans, however, was disruption of the aphid's location of the host plants. Trap data indicated that few aphids penetrated the maize canopy to reach and settle on the beans. Host location by alatae involves landing on potential host plants and probing (Chapter 9, this volume). This is followed by settling, or rejection, and take-off. *Aphis fabae* may have tended to land on the taller maize plants in the intercropped bean system and dispersed from the area after its probing had detected the non-host status of maize. A final contributing factor may have been adverse microclimatic conditions, particularly low light levels, inhibiting colonization of alatae on the beans (Ogenga-Latigo *et al*., 1992).

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Fig. 21.3. An intercrop of maize and beans (*Phaseolus vulgaris*) in north-west Peru.

Australian work on cultural methods to reduce losses caused by *Zucchini yellow mosaic virus* (ZYMV) in vegetable cucurbits was concerned with melon aphid (*A. gossypii*) and *M. persicae* (Coutts *et al*., 2011). Among the promising methods was the use of tall-growing barriers of millet (*Pennisetum glaucum*) between infected crops and 'clean' crops. While the width of these barriers (25 m) may make them impracticable for use in highly intensive systems where land area is limited, as is common in Western Europe, such strategies may be practicable in more extensive agricultural areas such as Australia.

Many phytophagous insects avoid landing on brown surfaces such as soil (Kostal and Finch, 1994), but if non-crop plants are present rather than bare soil, winged aphids arrested by olfactory stimuli may still have difficulty locating their host. This confusion will be particularly important if an insect requires contact stimuli from more than one 'appropriate' landing (i.e. host plant) before colonization (Finch and Collier, 2000). Consistent with this hypothesis is the observation that aphids prefer to colonize low-density crops (discussed above; Heathcote, 1970) as well as monocultures. In addition, the presence of cover crops between rows of broccoli reduces light reflectance at certain spectral wavebands (Costello and Altieri, 1994). As aphid colonization rates (and numbers of winged aphids trapped in yellow water pan traps) are correlated positively with reflected light intensity in the blue-green, yellow and orange wavebands (Costello and Altieri, 1994), the increased reflectance offered by clean-cropped or widely spaced crop plants appears to be more attractive to incoming alate aphids (Costello and Altieri, 1994). If the mechanism of visual interference prevails, any species of non-crop plant, or even increased densities of crop plants (of the same or mixed species), potentially could be used to reduce aphid colonization rates.

Horn (1981) examined the effects of a weedy background on the colonization of collards (*Brassica oleracea* var. *viridis*) by *M. persicae* and its predators. In both study years (1978 and 1979), *M. persicae* preferentially invaded (and developed higher densities on) weed-free collards. However, this difference in aphid density was considerably more pronounced in 1979, when weed-free collards averaged nearly twice the height of weedy collards than in 1978, when there was no apparent difference in collard size between treatments. The preference for larger plants (perhaps due to easier location or improved nutrition) may therefore have been partially responsible for the increased aphid abundance on weed-free collards in 1979. Showler and Greenberg (2003) found higher peak populations of aphids in weed-free than in weedy cotton plots. This was associated with lower populations of some (but not all) predatory orders. However, the implications of weeds for crop damage were not clear, because some herbivores were affected positively by weeds and the effect of weeds varied through the season.

Increasing crop diversity may have an indirect effect on aphid abundance by altering crop-plant quality. The quality of the crop plant may be improved (e.g. by intercropping with a legume) or impaired (if the non-crop plant competes with the crop plant for resources) by increased diversity, leading to variation in aphid abundance. In autumn 1990, Costello and Altieri (1994) found an increased rate of broccoli infestation by *B. brassicae* in clean, cultivated plots (55%) compared with plots where

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strawberry clover (*Trifolium fragiferum*) was used as a living mulch (7.5%). However, this increase in infestation was apparent only in treatments with low soil nitrogen (i.e. where compost rather than synthetic fertilizer was applied); nitrogen fixed by the strawberry clover was more likely to affect plant quality than synthetic fertilizer applications, in which nitrogen was easily available for plant uptake. In summer 1991, this increase in infestation rates was evident in both fertilizer treatments, although it was still more severe in low nitrogen treatments. Although post-colonization aphid population growth was unaffected by nitrogen levels, *B. brassicae* did appear to be more attracted to nitrogen-stressed flower buds (Costello and Altieri, 1994). Likewise, Lehmhus *et al.* (1996) found that although undersowing white cabbage with clover significantly reduced colonization by *B. brassicae* and *M. persicae*, the natural increase in aphid numbers over time was unaffected, or even enhanced, by crop diversification. Plant quality may therefore affect host location/choice more than population growth of aphids.

Although plant quality potentially is important, it is unlikely to be a sole cause of differences in aphid colonization between mono- and polycultures, since Horn (1981) and Costello and Altieri (1994) both still found differences, though less pronounced, in aphid infestation in experiments where plant quality did not appear to be a major factor. Moreover, when broccoli plants were grown in containers to reduce competition for soil nutrients and water, undersowing with rye grass reduced densities of *B. brassicae* significantly, despite there being no difference in leaf water, nitrogen content, or specific dry weight between treatments (Vidal, 1997).

Finally, recent work has shown scope to exploit for aphid management the general phenomenon that herbivore performance is impaired when switching from one host-plant species to a second species, even though both are within the generally recognized host-plant range of the herbivore. *Sitobion avenae* clones from wheat performed relatively poorly when moved to barley plants (Gao and Liu, 2013). This suggests that sowing barley adjacent to wheat, or intercropping wheat with barley, could suppress this major cereal pest aphid.

It is logical that many of the mechanisms discussed above in the context of their effect on aphids should also have an analogous impact on predatory arthropods. For example, enemies that search for prey using visual, tactile, or host-plant chemical cues are likely to be less effective at locating, and hence reducing, aphid populations in diverse systems (Sheehan, 1986). A complex set of tritrophic interactions operates whereby a predator may be affected not only directly by variation in diversity but also indirectly by the effects of diversity on its prey. Understanding these relationships is also necessary if the effects of these cultural methods of control are to be predicted.

Trap Crops

If non-crop plants that are attractive to aphids are planted near to crop plants, they can act as a sink or barrier, known as a 'trap crop'. Trap crops may be used either to prevent pests from reaching the target crop or to localize them in an area that allows easier chemical or other control such as plant destruction (Hokkanen, 1991). Although trap crops may be a different species from the target crop, this is not a prerequisite. If the pest has a limited host range, the use of an area of the main crop (e.g. borders) as a trap may be preferable. For aphids, earlier sowing of the barrier will give it a height differential particularly effective at filtering out some of the immigrating aphids and concentrating the deposition of others in the edge of the main crop (Lewis, 1965).

Even if the trap crop does not act as a permanent sink for pests, it may slow colonization of the target crop or, more importantly, act as a sink for aphid-borne diseases (Fereres, 2000). Trap crops have been shown to reduce the spread of non-persistent viruses PVY and BYMV, either by acting as barriers to viruliferous aphid movement or because aphids lost infectivity by probing the non-crop plant (Hooks and Fereres, 2006). Recently, the use of barley strips within potato fields in Japan reduced aphid numbers by promoting the early movement of natural enemies into the potato fields from the barley strips that earlier had acted as refugia for the biological control agents (Nakahira *et al.*, 2012).

Trap crops can also act as a sink for aphidophages. Thus, unless they also operate as a source, overall they may have a negative effect on biological control. For example, when a population of the parasitoid *Aphidius ervi* was maintained on a population of *Acyrthosiphon pisum* (pea aphid) outside the target cereal crop, the parasitoids did not readily transfer later to the cereal aphid pest *S. avenae* (Cameron *et al.*, 1984). After four to five generations on *S. avenae*, *A. ervi* began to parasitize this species more readily, and this adaptation to the new host was associated

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with the loss of several esterase bands revealed during electrophoretic examination of parasitoid proteins (Cameron *et al*., 1984). The time taken for this species to adapt to new hosts may make ineffective the use of alternative hosts to accumulate reservoirs of parasitoids.

Provision of Resources for Natural Enemies

Most predators or parasitoids require nutritional resources other than those provided by aphids or the target crop, and these can often be provided by sowing flowering plants among or alongside the crop (Figs 21.4, 21.5 and 21.6; Hickman and Wratten, 1996; Baggen and Gurr, 1998; Stephens *et al*., 1998; Wratten *et al*., 1998; Landis *et al*., 2000; Collins *et al*., 2002; Gillespie *et al*., 2011; Gurr *et al*., 2016). A simple acronym that usefully summarizes the processes involved is SNAP (shelter, nectar, alternative food and pollen – Barnes *et al*., 2010). Sugars from floral and extrafloral nectaries can have beneficial effects on parasitoids (Heimpel and Jervis, 2005). Nectar can enhance an aphid parasitoid's exploratory behaviour (Araj *et al*., 2011; Varennes *et al*., 2016), and pollen can provide an important protein source for female predators (e.g. hover flies) approaching sexual maturity (Hickman *et al*., 1995; Irvin *et al*., 2000). If flowers are to be used to enhance natural enemy populations, the floral architecture must be compatible with the feeding morphology and behaviour of the target biological control agent (Gilbert, 1985; Patt *et al*., 1997a,b). This approach has recently been used in the USA. Enhancing the population of syrphid flies was carried out to test their ability to reduce the population of *E. lanigerum* by using sweet alyssum (*Lobularia maritima*) plants in apple orchards as a source of nectar (Gontijo *et al*., 2013). However, the early reduction in aphid populations was not related to consumption by syrphid larvae; rather, it was attributed to the enhancement of populations of other natural enemies, mainly spiders, coccinellids and earwigs (Gontijo *et al*., 2013). Nonetheless, in a 2-year study (2006–2007) performed in Poland, a significant reduction of 40% in *A. fabae* numbers on broad bean was attributed to predation by syrphid larvae; this reduction was higher when phacelia plants (*P. tanacetifolia*) were established as an intercrop (Wnuk and Wojciechowicz-Zytko, 2007). Similar results were obtained when nectar provision was enhanced through the establishment of the marigolds, *Calendula officinalis* and *Tagetes erecta* against *B. brassicae* (Jankowska, 2007). In that study, the main cause of pest reduction was attributed to the enhancement of the numbers of the parasitoid *Diaeretiella rapae*, and second, of syrphid flies. Although it is not aphid related, a very relevant

Fig. 21.4. Flowering buckwheat (*Fagopyrum esculentum*) strips beneath apples to increase biological control of a range of caterpillars species by parasitoid wasps, New Zealand.

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Fig. 21.5. Flowering phacelia (*Phacelia tanacetifolia*) in maize to increase biological control of *Rhopalosiphum padi* (bird cherry–oat aphid) by providing nectar for parasitoid wasps, *Aphidius* spp., New Zealand.

Fig. 21.6. Buckwheat (*Fagopyrum esculentum*) strips sown in a vineyard to improve biological control of toriricid leaf rollers by the braconid parasitoid, *Dolichogenidea tasmanica*, New Zealand.

4-year study conducted in Vietnam, Thailand and China enhanced nectar provision for natural enemies by planting flowering strips in rice crops, to reduce the damage produced by rice planthoppers. Based on the effects on these rice natural enemies of pests, a further reduction of 70% in the frequency of sprays to control this pest was also achieved. Additionally, an increase of 5% in rice yield occurred (Gurr *et al*., 2016). This recent large-scale study highlights the potential contribution of flower strips to biological control, agricultural sustainability and food supply.

Natural enemies may also need alternative hosts or prey to maintain high population densities

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before the establishment of pest populations (van Emden, 1990; Corbett and Rosenheim, 1996; Landis *et al*., 2000; Langer and Hance, 2004; Harwood *et al*., 2007). Where an aphid is not a pest in a particular system, the aphid and its host plant can be introduced as a 'banker plant system' to a glasshouse where a different crop is to be grown later. Thus, *Schizaphis graminum* (greenbug) on wheat and its associated poly- or oligophagous parasitoids (*Aphidius colemani* and *Lysiphlebus testaceipes*) provide a banker system for glasshouse beans (Chapter 20, this volume). This 'alternative host and parasitoid in first' method provides a reservoir of natural enemies in case the target pest (*M. persicae*) is introduced accidentally (Starý, 1993). In a more open environment, *Aphis carduella* on sunflowers has been used as an alternative host for *L. testaceipes* when the pest *S. graminum* was absent from the sorghum crop (Powell, 1986). The aggregation of natural enemies around resource-providing plants has frequently been recorded (Root, 1973; Hickman and Wratten, 1996; Hooks *et al*., 1998; Berndt *et al*., 2002). This can lead to higher, early-season densities of predators and parasitoids in mixed crops (Horn, 1981; Costello and Altieri, 1995; Hickman and Wratten, 1996; Lehmhus *et al*., 1996, 1999; Goller *et al*., 1997; Vidal, 1997), but these natural enemies may disperse readily to monocultures later in the season (Horn, 1981; White *et al*., 1995). More recently, it has been shown that predation by the spider *Pachygnatha degeeri* on aphid populations, during their establishment phase in winter wheat, is crucial for aphid control (Harwood *et al*., 2005). Similar effects of early predation on aphid populations have been found in organic tomato production in Italy (Balzan and Moonen, 2014) and in Australia on cotton and horticultural crops attacked by *A. gossypii* (Costamagna *et al*., 2015). These results highlight the importance of refuges for natural enemies, such as semi-natural habitats (see next section), which can greatly improve the effectiveness of aphid control, at both farm and landscape scales (Rusch *et al*., 2016). It should be noted, however, that an increase in predator abundance does not always translate to reduced aphid density (Lehmhus *et al*., 1996; Goller *et al*., 1997), particularly if predator numbers are high only in response to high aphid population densities rather than to floral or other resources in mixed crops. For example, although border planting with phacelia enhanced biological control of brassica pests by hover flies, the flies did not disperse far from the pollen source (White *et al*., 1995). Increased diversity can enhance (Letourneau, 1987), reduce (Helenius, 1993; Costello and Altieri, 1995), or have no effect (Letourneau, 1990) on the rates of parasitism, making it difficult to predict a general effect of increasing diversity on aphid natural enemies.

As an alternative to managing non-crop plants, supplementary foods can be provided as foliar applications. Formulations containing sugars, proteins and yeasts have been developed to attract or retain natural enemies in fields while pest populations are still low (Wade *et al*., 2004). This technique can lead to short-term, localized increases of aphidophagous ladybird, lacewing and hover-fly populations in lucerne (*Medicago sativa*) (Evans and Swallow, 1993; Evans and Richards 1997). It has not, however, been developed fully as a method for aphid management. Recently, a technique using synthetically produced herbivore-induced plant volatiles (HIPVs) such as methyl salicilate (MeSA) in a slow-release sachet, has been used successfully to attract parasitoids to crops for pest management (Orre-Gordon *et al*., 2010). This technique is also combined with a floral resource for the parasitoids attracted, such as buckwheat *(F. esculentum)* ('attract and reward'; Simpson *et al*., 2011), to improve parasitoid fitness and enhance the parasitism of aphids (Orre-Gordon *et al*., 2013). Nevertheless, the use of MeSA could also alter the structure of higher trophic levels, such as hyperparasitoids, in the food web (Orre-Gordon *et al*., 2013).

Provision of Refuges for Natural Enemies

Monocultural crops or their associated field margins rarely provide a consistently favourable habitat for natural enemies (Figs 21.7, 21.8). At one extreme, natural enemy populations in annual crops are likely to suffer high mortality or enforced dispersal at the time of harvesting, although this can often be managed. However, many perennial crops will also vary seasonally. Independently of changes in the crop itself, the requirements of natural enemies may change over time. The agricultural landscape can be managed to provide alternative habitats that act as refuges for natural enemies at times when crops or the within-field microclimate are unfavourable.

The maintenance of grass strips around or within fields can increase populations of predatory beetles,

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spiders and parasitoids in adjacent crops, and some studies have shown reduced aphid populations in association with such 'beetle banks' (van Emden, 1990; Thomas *et al*., 1992; Kidd and Jervis, 1996; Gurr *et al*., 1998; Landis *et al*., 2000; Collins *et al*., 2002; Langer and Hance, 2004; MacLeod *et al*., 2004; Levie *et al*., 2005; Amaral *et al*., 2013; Balzan and Moonen, 2014; Morandin *et al*., 2014).

Additional techniques may be used to encourage the dispersal of natural enemies. For example, it may be profitable in the following spring to set out sources of aphid sex pheromone to attract emerging parasitoids that have overwintered as mummies in grass strips. The parasitoids are attracted to the pheromone, but at this time it has no effect on the aphids (Powell, 2000). Additionally, predator populations may increase between years, reaching levels that would otherwise have been unlikely in a wholly disturbed cropping system (Thomas *et al*., 1992). Where different stages of a crop are present simultaneously, their appropriate spatial arrangement can allow the dispersal of natural enemies from harvested areas to susceptible areas. Strip harvesting employs this technique and can enhance predator populations in, for example, lucerne (Hossain *et al*., 2002). Strategically located crops that have a complementary growth cycle can also serve as refuges, a system known as 'relay cropping'. In an experimental study with cotton grown adjacent to lucerne, aphid numbers were lowered in the cotton by cutting the lucerne, and the numbers of spider and lacewing predators showed a corresponding increase (Lin *et al*., 2003).

Fig. 21.7. An extreme example of a field boundary with no margin vegetation. The line of traps is for sampling hover fly and parasitoid populations.

As with natural enemy populations enhanced by the provision of food resources or alternative hosts, the effect of increased populations in refuges may be limited, because of either low enemy dispersal or a weak correlation between aphid mortality and enemy population. Nevertheless, landscape-scale patterns of habitat have been shown to be important for several aphid predators and parasitoids (Elliott

Fig. 21.8. Monocultural cotton in New South Wales, Australia. (Photograph courtesy of P. Gregg.)

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et al., 2002; Thies *et al*., 2003, 2005). In a recent study in Serbia, heterogeneous landscapes showed higher aphid abundance and higher parasitism rates than did homogeneous ones (Plećaš *et al*., 2014). This was attributed to the connectedness between non-crop habitats and the intensity of the farming practices over the region studied (Plećaš *et al*., 2014). The same conclusion was reached by Jonsson *et al*. (2012) after analysing data on aphid and parasitoid populations in Canterbury, New Zealand. They concluded that the regime of agricultural disturbances and intensive use of agrochemicals was the major driver to explain the low efficacy of natural enemies at a regional scale in *B. oleracea*. Nevertheless, a reduction in agricultural intensity is not enough to reduce aphid populations. The connectivity between these non-crop vegetation shelters and/or food sources is a critical factor for the success of aphid control at broader spatial scales (Koh *et al*., 2013). Additionally, a recent quantitative synthesis using 15 studies from Europe and North America suggested that aphid control was 46% lower in simplified landscapes (homogeneous) when compared with complex ones (Rusch *et al*., 2016). In complex landscapes, the colonization of predators in the field, and therefore the reduction in aphid numbers, occurs earlier during the crop season than in simple ones, as has been seen in central Chilean wheat fields (Raymond *et al*., 2015). As discussed previously here, early predator pressure on aphid populations is crucial to reducing subsequent pest outbreaks. It follows that habitat manipulation, such as flowering strips in cropping systems, or the conservation of semi-natural and/or natural areas to provide shelter, pollen, nectar and alternative food for natural enemy communities are key strategies to achieve control of aphid populations in agricultural landscapes.

Conclusions

The potential for achieving control of aphid damage by manipulating the physical and biological environment of the crop is enormous. However, the potential for causing unintended detrimental effects on crop yields is similarly large. Research has investigated the mechanisms by which new and traditional cultural methods may influence aphid populations. There is still much to be learned about the complex relationships between the many components of agroecosystems, and as this knowledge grows, so should our ability to predict which techniques are appropriate in particular pest management scenarios.

Many cultural methods of control have intrinsic benefits over alternative means of reducing aphid damage. In particular, they do not impose the externalized costs often associated with insecticide use; that is, environmental damage and health risks (Rajendran, 2002). As Tilman *et al*. (2002) have said: 'Further increases in agricultural output are essential for global political and social stability and equity. Doubling food production again, and sustaining production at this level, are major challenges. Doing so in ways that do not compromise environmental integrity and public health is a greater challenge still.' Cultural pest management has an important role in meeting this challenge. However, there is another equally important context for these approaches. This is that multiple ecosystem services beyond pest management are likely to be derived from even the simplest of changes to farm practices. These other services can include pollination, higher soil quality, better shelter for livestock, nesting and roosting habitats for birds, biofuel production and, of course, aesthetics. Many of the dynamics associated with such apparently simple changes to the farm landscape are reviewed by Wratten *et al*. (2012).

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22 Host-plant Resistance

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Introduction

In this chapter, the word 'variety' will be used as an umbrella word for the many types of variation involved; varieties, cultivars, accessions, breeders' lines may all be included. The practical use of host-plant resistance (HPR) for aphid control in different crops is explored in the pest management section of this volume (Chapters 24–33).

It might be assumed that the role of symbionts in nitrogen metabolism (Chapter 6, this volume) should enable aphids to compensate for nutritional differences between crop varieties, and that the phloem-feeding habit would enable aphids to avoid many deterrent surface characters and allelochemicals in plants. However, the literature probably has more examples of HPR to aphids than to any other group of crop pests, including examples of nearly all the mechanisms of HPR known for insect pests in general. Moreover, HPR to aphids can be highly effective and dramatic; for example, the resistance of 'Avoncrisp' lettuce to *Pemphigus bursarius* (lettuce root aphid) (Fig. 22.1).

Resistance rankings between varieties can change with age, and resistance to one aphid species may not give resistance to another. HPR to *Diuraphis noxia* (Russian wheat aphid) in wheat and barley seems especially specific and has no effect on the several other species of cereal aphid (Robinson, 1992; Messina and Bloxham, 2004).

In recent years, molecular biology techniques have become routine, and much progress has been made in screening aphid populations for genetic variability. However, whether or not such genetic variability matches phenotypic variability (Thomas *et al*., 2012), only differences in reaction to different varieties are relevant to HPR (Pompon *et al*., 2011). Also, possibly because of the success against other pests of crops genetically engineered to express the *Bacillus thuringiensis* (Bt) toxin, the emphasis in HPR studies on aphids has shifted to identifying genes (e.g. Shufran and Payton, 2009). This puts emphasis on single genes coding for proteins expressing a high level of toxins, a narrow and perhaps not the most desirable HPR mechanism (Chapter 23, this volume).

Before the advent of direct gene transfer, wild relatives within the natural crossing barriers were often the source of resistance genes (e.g. Hesler, 2013). Table 22.1 lists some of the wild relatives of crops often involved in resistance breeding for aphids, usually entailing the transfer of characteristics (e.g. hairiness, toughness, high toxin levels) lost in the process of domestication (van Emden, 1997).

Finally, HPR need not necessarily involve genetic change. It can sometimes be produced by some extrinsic influence on a susceptible variety ('pseudoresistance' or 'induced resistance'). Plant resistance to *Schizaphis graminum* (greenbug) in wheat after fertilization with silicon (Gomes *et al*., 2005) is one example. HPR also is manifested when the aphid pest does not synchronize with a 'susceptibility window' in the plant's phenology. Plant resistance to aphids generally tends to increase with age ('age-related resistance'); Sarwar and Sattar (2013) reported that early-sown oilseed rape was effective in reducing incidence of and damage by *Myzus persicae* (peach–potato aphid).

Associated organisms (see 'endophytes' below) may also induce HPR.

Types of Host-plant Resistance to Aphids

The classification of Painter (1951), modified by Kogan and Ortman (1978), still has great value.

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Fig. 22.1. Junction of experimental lettuce plant testing for host-plant resistance to *Pemphigus bursarius*. The impact of variety as an aphid control measure is seen clearly in the contrast between the susceptible variety 'Mildura' in the foreground and the resistant 'Avoncrisp' behind. (Photograph courtesy of J.A. Dunn.)

Antixenosis (close to Painter's 'non-preference')

This is resistance to colonization by aphids and shows in the high proportion of immigrating alatae that take off from a plant after superficial probes and within a few hours of landing. At the immigration stage, aphids seem to exhibit a high degree of non-preference, even on susceptible plants. Müller (1958) showed that the eventual fourfold greater population of *Aphis fabae* (black bean aphid) on the susceptible broad bean variety Schlandstedt than on the resistant Rastatt was based on respective retake-off rates of 95% and an only slightly higher 99%. Antixenosis is usually assessed by liberating alatae over different varieties, in both choice and no-choice situations (Adams and van Emden, 1972), although van Emden *et al*. (l99l) devised a test (involving systemic insecticide with a correction for any detection thereof by the aphids) that identified which aphids had ingested from the plants.

Tjallingii's (1988) electrical penetration graph (EPG) technique (Chapter 9, this volume) enables the continuous monitoring of aphid penetration and probing activity (Fig. 22.2; Mentink *et al*., 1984).

Antibiosis

This negatively affects the multiplication of aphids that have colonized the plant, usually showing as

Table 22.1. Some examples of wild relatives as sources of genes in traditional breeding for host-plant resistance to aphids.

'Wild' relative	Crop	Resistance character (if known)	Sample reference(s)
Helictotrichon macrostachyum and *Avena barbata*	Oats		Weibull (1987)
Solanum habrochaites and *Lycopersicon pennellii*	Tomato		Simmons *et al*. (2005)
Solanum peruvianum	Tomato	Glandular hairs and high tomatine	Kok-Yokomi (1978)
Solanum tuberosum	Potato		Novy *et al*. (2002)
Brassica fruticolosa and *Brassica spinescens*	Cabbage	Gluconapin; lectin	Cole (1994a,b)
Triticum monococcum	Wheat		Sotherton and van Emden (1982); Deol *et al*. (1995); Di Pietro *et al*. (1998) Migui and Lamb (2004)
Triticum monococcum subsp. *aegilopoides* *Triticum urartu*	Wheat		Di Pietro *et al*. (1998)
Solanum berthaultii	Potato	Glandular trichomes	Gibson (1976)

Note: The same source of resistance may influence several aphid species attacking the same crop; hence, names of aphids affected are not included in the table. However, aphid names are usually given in the reference titles.

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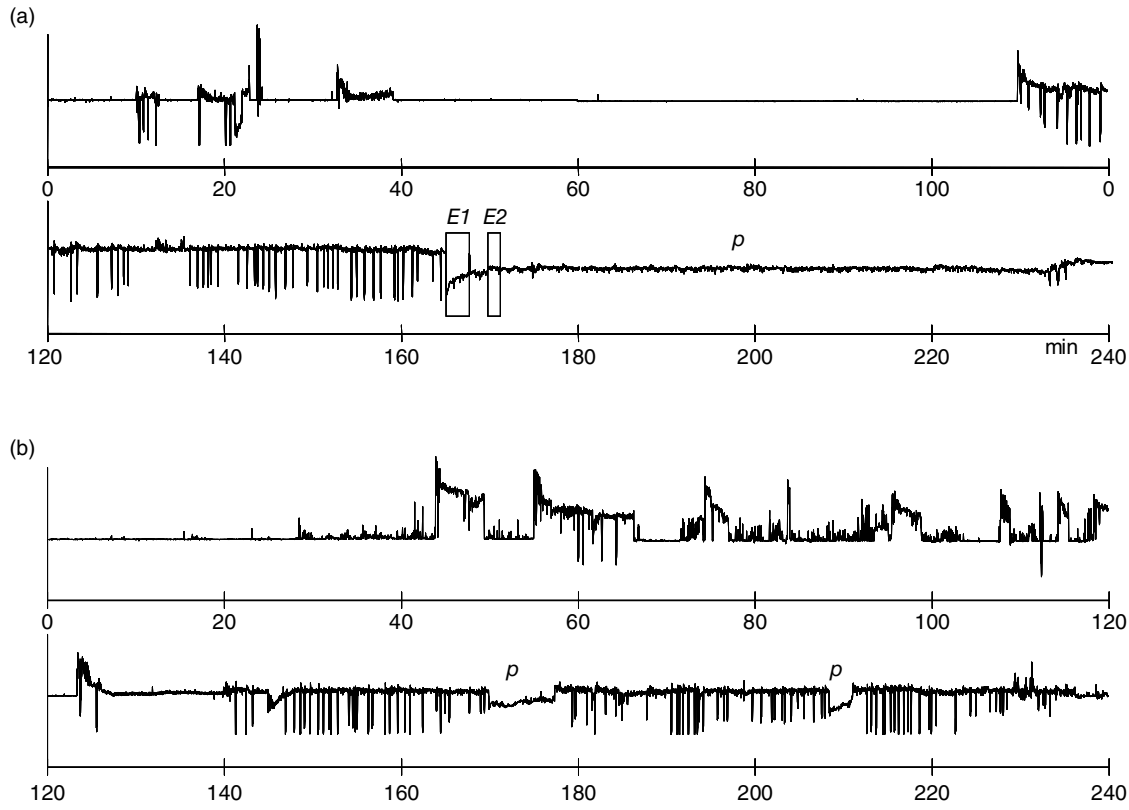

Fig. 22.2. Electrical penetration graph (EPG) recordings for *Nasonovia ribisnigri* (currant–lettuce aphid) on susceptible (a) and nearly isogenic resistant (b) lettuce varieties. On susceptible lettuce, beginning at about 170 min, one long continuous phloem phase (*p*) is shown. This starts with sieve element (watery) salivation (waveform *E1*) and continues for the rest of the 4 h recording (only the first 2 h are shown) with sieve element ingestion (waveform *E2*). In contrast, the graph from the resistant lettuce shows only two short phloem-feeding periods (*p*), mainly of *E1* waveform with some very brief switches to *E2*. The average start of the first phloem phase does not differ between the graphs from the two varieties; a phloem factor prevents sieve element ingestion. (Courtesy of W.F. Tjallingii.)

reduced survival, growth and fecundity and extended development time. These are measured easily on individuals confined on leaves in small clip cages, although care needs to be taken to ensure that any apparent antibiosis is no more than a first-generation expression of transfer to a novel plant. Survival, development time and fecundity can be combined into a single statistic, the intrinsic rate of increase (r_m), and another useful single statistic is the integral of the daily weight increase of individual aphids over a few days (mean relative growth rate, or MRGR) (Chapter 5, this volume). r_m can readily be converted into 'population doubling time'.

Tolerance

Tolerance of a variety shows as a better yield under the same aphid burden, both in numbers and duration. This is difficult to quantify, since any antibiosis defeats the 'equal burden' requirement, and intolerance to infestation will result in plant damage, which may cause a crash in the aphid population and defeat the 'equal duration' requirement. Havlickova (1997) has proposed a covariance model in which the main component is the slope of the relationship between the weights of infested and control seedlings. However, tolerance may perhaps be quantified better by the slopes of regressions of yield or plant biomass on initial aphid infestation.

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What is the preferred type of resistance?

Antixenosis is rarely effective in a no-choice situation, and puts pressure on the population for selection of genotypes not affected by the antibiosis (see 'biotypes' later), a danger not applicable to tolerance. Burd and Puterka (2009) challenged the prioritization of tolerance over antibiosis on the grounds that crop selection was not a factor in the appearance of adapted greenbug genotypes. Moreover, a potential hazard of relying on tolerance is that farmers growing such varieties would not need to control aphids and so would breed populations to infest their neighbours' crops. Thus, there is general agreement (van Emden, 1997) that the preferred resistance is antibiosis coupled with some antixenosis, as has been found in some soybean lines (Hesler, 2013). Buschman and Ramaswamy (2012) have modelled HPR stability arising from two genes, one expressing an oviposition deterrent and the other a toxin. When the antibiosis was dominant, insect populations were managed for 150 years, but for much longer when it was recessive, presumably because the toxin was modelled as a stronger selection pressure than the deterrent. The combination of antibiosis and tolerance has also been recommended (Murugan *et al*., 2010) as delaying biotype selection in *D. noxia*.

This chapter reviews HPR to aphids by the various anatomical, physiological and biochemical mechanisms that have been correlated with HPR phenomena, and Fig. 22.3 shows these with an indication of the order in which the aphid would encounter them. However, correlations are not the same as 'cause and effect'. Kazemi and van Emden (1992) found that some proposed chemical correlations with HPR in wheats to *Rhopalosiphum padi* (bird cherry–oat aphid) broke down when a wider range of wheats was tested. Similarly, Weibull (1994) found that corre1ations of chemistry with resistance to *R. padi* in parental barley lines broke down in the F1 generation. It seems it is not difficult to correlate resistance rankings with whatever chemical group represents one's own particular interest.

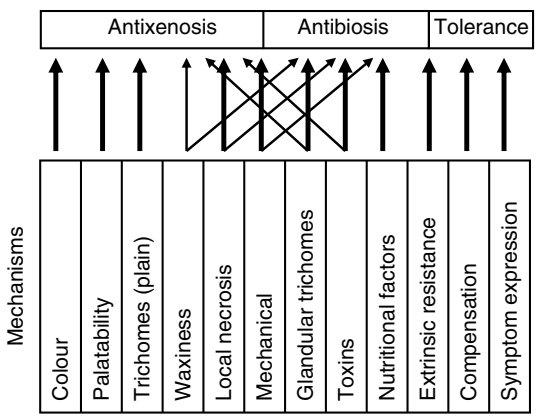

Fig. 22.3. Mechanisms of host-plant resistance to aphids, from left to right approximately in the sequence in which they will affect colonizing aphids. Thickness of arrows indicates the likely outcome of the interaction between mechanism and aphid in terms of plant antixenosis, antibiosis, or tolerance.

Mechanisms of Host-plant Resistance to Aphids

Mechanisms of antixenosis

Colour

Colour can influence the preference of immigrating aphids. Alatae of *Brevicoryne brassicae* (cabbage aphid) do not settle well on red cabbage varieties, even though apterae caged on such varieties have a better growth rate than those on green varieties (Radcliffe and Chapman, 1965, 1966). Similarly, in a study of 50 mustard and oilseed rape varieties in India (Rana *et al*., 2001), purple-leaved cultivars had fewer colonizing *Lipaphis erysimi* (mustard aphid) than dark green ones, which in turn were less infested than those that were light green. Differences in the brightness of the yellow flowers had no effect on aphid colonization.

Palatability

That so many common or Latin names of aphids reflect particular host plants (e.g. lupin aphid, *B. brassicae*, etc.) shows that aphids often accept or reject a plant on the basis of its secondary chemistry, even before reaching the phloem. Thus, toxins (which would otherwise reflect antibiosis) become deterrents. Polyphagous aphids such as *M. persicae* will tolerate levels of secondary compounds such as glucosinolates in brassicas, but elevating levels still tolerable to the specialist *B. brassicae* will lead to antibiosis (van Emden, 1978; Cole, 1997b). In screening wild and cultivated brassicas for resistance to these two aphids, Cole (1997a) found that most of the variation in HPR was explained by four glucosinolates (2-OH-3-butenyl, 2-propenylglucosinolate, 3-methoxyindolyl

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and 4-pentylglucosinolate). High total phenol (especially ortho-dihydroxy phenol) content in oilseed brassicas deters infestation by *L. erysimi* (Sarwan Kumar Sangha, 2013), and the phenolic hydroxamic acids (Hx), often associated with antibiosis to aphids in cereals, are also a deterrent to *Metopolophium dirhodum* (rose–grain aphid), *Sitobion avenae* (English grain aphid) and *Sch. graminum*. *Rhopalosiphum maidis* (corn leaf aphid), however, is not deterred because it avoids Hx in high-Hx plants by reducing puncturing of the cells by the stylets on their way to the phloem (Givovich and Niemeyer, 1995). In lucerne, other Hx compounds (the 3-amyl-4-hydroxycoumarins such as coumestrol) are deterrent to *Acyrthosiphon pisum* (pea aphid), as are saponins (Nicholas *et al*., 2005). In tobacco, the antixenosis of some varieties to *M. persicae* is ascribed to sugar ester levels and alpha and beta monols on the leaf surface (Johnson *et al*., 2002).

One mechanism of antixenosis in tomato to *Macrosiphum euphorbiae* (potato aphid) involves ethylene signalling. This has been shown to induce opposite effects in susceptible and resistant tomato varieties. It promotes aphid infestation on susceptible genotypes, but contributes to antixenosis in resistant ones (Wu *et al*., 2015).

Recently, a trial of GM wheat with a gene (resynthesized from peppermint to eliminate inhibitory compounds) expressing the alarm pheromone of aphids was carried out (Bruce *et al*., 2015). Although cereal aphids were deterred in laboratory tests, no substantial reductions in the population of cereal aphids were observed in the field, but the idea of using behaviour-modifying compounds in this way is novel and has potential.

Waxiness

Waxiness of the leaf surface (Fig. 22.4) has sometimes been linked positively with antixenosis to aphids; for example, the epicuticle of some lucerne varieties resistant to *Therioaphis trifolii maculata* (spotted alfalfa aphid) had wax ester levels 50% higher than those in susceptible lucerne (Bergman *et al*., 1991). Similarly, Ren *et al*. (2014) found that the wax content on the leaf surface of the highly *Aphis gossypii*-resistant cucumber variety 'Axin' was 30 times higher than for the susceptible variety 'Pepino'. Wojcicka (2015) used the EPG technique (see earlier) to show that components in the wax of waxy genotypes of wheat completely stopped salivation and active ingestion by *R. padi*, yet it is often the less waxy (glossy) varieties that are resistant because of higher levels of deterrent chemicals in the reduced wax layer. Glossy wheats, antixenotic to *S. avenae*, contain dihydroketones as the deterrent compounds (Lowe *et al*., 1985). With *A. pisum* studied on seven pea varieties, the glossy ones again were resistant (White and Eigenbrode, 2000), and glossy brassica varieties were also antixenotic to *B. brassicae* (Thompson, 1963; Ellis *et al*., 1996), with reductions in aphid populations as high as 95% (Stoner, 1992).

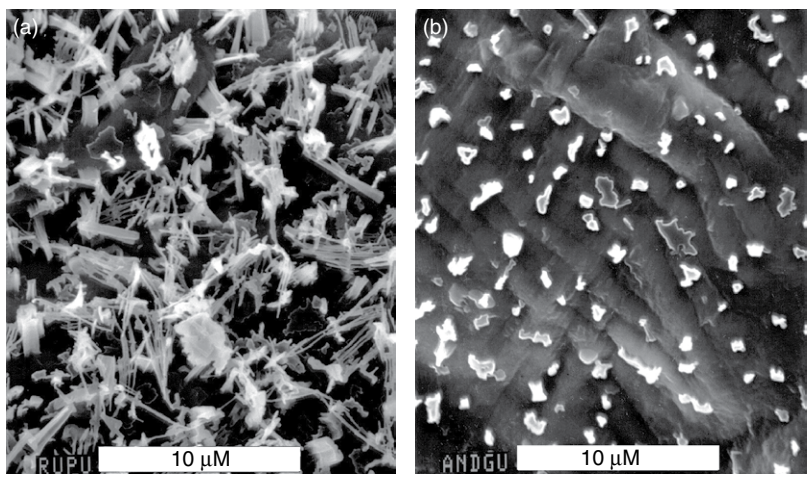

Fig. 22.4. Electronmicrographs of wax quantity and its distribution on normal (a) and glossy (b) cabbage leaf surfaces. (Courtesy of S.G. Eigenbrode.)

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Leaf surface wax components have also been implicated in the resistance of European red raspberries to *Amphorophora idaei* (large European raspberry aphid) conferred by gene A_{l0} (Robertson *et al*., 1991; Shepherd *et al*., 1999a,b).

Ni *et al*. (1998) tested whether the ranking of resistance to *D. noxia* of wheat (most susceptible), oat (intermediate) and barley (most resistant) had a basis in surface wax by removing this with ethyl ether, but the resistance rankings remained as before.

Mechanical

Hardness of the plant surface is a common resistance mechanism to chewing insects, but not for aphids, where a more common cause of mechanical antixenotic resistance is difficulty in reaching the phloem. Pectin in the cellular middle lamella has a role in hindering access to the phloem (Dreyer and Campbell, 1984). Resistance to *S. graminum* in some sorghum varieties is due to increased methylation of the middle lamellar pectin (Dreyer and Campbell, 1984). A variety of melon resistant to *A. gossypii* deposits callose in attacked leaf veins.

A major qualitative chemical feature of two wild brassicas resistant to *B. brassicae* was the presence of gluconapin rather than the more usual glucobrassicin, but the former had no effect on the aphid in artificial diet. Cole (1994a) proposed that the resistance mechanism was stylet blocking.

Local necrosis

Local necrosis, that is, the death of cells with the production of deterrent polyphenols wherever the aphid tries to insert its stylets, is a valuable resistance mechanism since it also gives protection against other piercing organisms such as fungal hyphae and nematodes (van Emden, 1987). The polyphenols are produced when aphid damage brings substrate and enzyme into contact. This is a 'hypersensitive response', perhaps an unusual concept of 'resistance'. It is the mechanism of resistance of apples to *Eriosoma lanigerum* (woolly apple aphid) (Wartenberg, 1953) and *Dysaphis plantaginea* (rosy apple aphid) (Alston and Briggs, 1970). Another example is the hypersensitive cell death response of some resistant barleys to attack by *D. noxia* (Belefantmiller *et al*., 1994), though some aphid species may have reducing compounds in their saliva that counter the hypersensitive response of the plant (Miles, 1999).

Trichomes (non-glandular)

Non-glandular trichomes are mechanical barriers to many small insects, including aphids. For example, high trichome density on wheat leaves deters *Sipha flava* (yellow sugarcane aphid), but any effect on *S. graminum* is questionable (Webster *et al*., 1994). Pompon *et al*. (2010) attributed the resistance of two wild potato species to *M. euphorbiae* and *Myzus persicae* to the trichomes on the leaf surface; high trichome density also deters *M. persicae* on crosses of tomato with wild potato (Simmons *et al*., 2005). Pubescent broccoli is as resistant to *B. brassicae* as glossy varieties (see earlier) (Stoner, 1992). However, with *A. gossypii* on cotton, it is the glabrous varieties that have fewer aphids (Weathersbee *et al*., 1994, 1995).

Mechanisms of antibiosis

Glandular trichomes

These are of two types: long slender ones that secrete drops of fluid from the tip, and short ones bearing a spherical glandular head (Fig. 22.5). Septa in the head separate substrate and enzyme, which are brought together to form polyphenols when the head is ruptured by contact with an aphid. These polyphenols are not only distasteful to the aphid (see earlier), but also harden on, and disable, the mouthparts and tarsi. Great interest has focused on breeding the presence of such trichomes on wild potato (especially *Solanum berthaultii*) and tomato crossed with *Lycopersicon pennellii* (Simmons *et al*., 2005) into varieties for resistance to aphids (Gibson, 1976), but none has ever been commercialized. Any *M. euphorbiae* on the stems, however, multiply faster than on varieties without glandular trichomes (Ashouri *et al*., 2001). The wild tomatoes *Solanum habrochaites* and *S. peruvianum* have a dense pubescence with both glandular and non-glandular trichomes (Kok-Yokomi, 1978), and Dreyer and Campbell (1987) observed that the resistance attributable to the glandular trichomes decreased as the density of non-glandular trichomes increased.

Toxins

These are often the same chemicals that can also cause antixenosis, and they may only be induced following disruption of plant cell walls by aphid probing. The plant then produces signalling compounds such as jasmonic, salycilic, abscisic and

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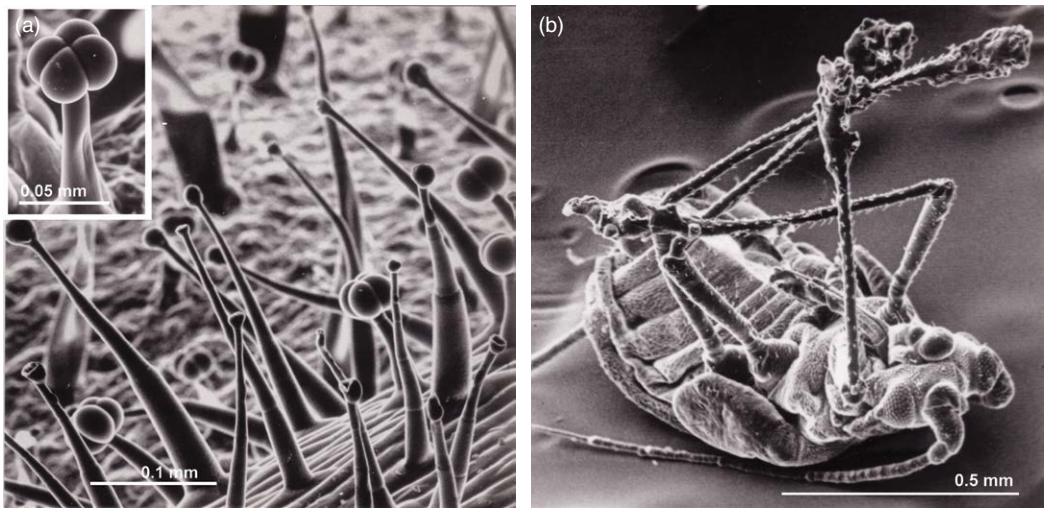

Fig. 22.5. Glandular trichomes. (a) Scanning electron micrograph of the leaf surface of *Solanum berthaultii* showing both trichomes with the four-celled head (magnified on insert) and those surmounted by a glandular vesicle. (b) Scanning electron micrograph of an aphid that was on *Solanum polyadenium*, showing the material from the glandular trichomes hardened on the feet. (Courtesy of R.W. Gibson.)

gibberellic acids, which lead to the mobilization of direct chemical defence responses (Smith and Boyko, 2007; Pompon *et al*., 2010; Chapter 8, this volume). The resistance to *M. euphorbiae* of tomatoes carrying the *Mi-1.2* gene results from jasmonic acid triggering a proteinase inhibitor (Cooper *et al*., 2004).

Hydroxamic acids (Hx) are deterrent to many aphids (see earlier), but also decrease feeding in artificial diet of, for example, *S. avenae*. Also in diet, 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA) decreases the survival of *M. dirhodum* (Cambier *et al*., 2001), as do low concentrations of its decomposition product 6-methoxybenzoxazolin-2-one (MBOA) for *S. avenae* (Hansen, 2006). In whole-plant studies, a wheat cultivar with high Hx was found to be antibiotic to *S. avenae* (Fuentes-Contreras and Niemeyer, 1998), and the growth rate of the aphid on three wheat and two oat cultivars was correlated negatively with Hx levels (Fuentes-Contreras *et al*., 1996). Also, 26 Hungarian cultivars showed a negative correlation between Hx levels and populations of *R. padi* (Gianoli *et al*., 1996).

Legumes are also well known to contain toxins. Ansari *et al*. (1989) discovered some varieties of cowpea (*Vigna unguiculata*) in which the leaves produced a powerful graft-transmissible but unidentified toxin that killed *Aphis craccivora* (cowpea aphid) very quickly, but did not seem to be detected by the aphid. Another example is lupin; the alkaloids in narrow-leaved lupins (*Lupinus angustifolius*) depress the fecundity of *Macrosiphum albifrons* (lupin aphid) (Berlandier, 1996). *Myzus persicae* is less affected by these alkaloids (gramine, sparteine, lupanine, lupinine, 13-hydroxylupanine and angustifoline) than *A. craccivora*, both in plants and in artificial diet (Ridsdill-Smith *et al*., 2004).

On cotton, *A. gossypii* showed shorter longevity and lower fecundity on varieties bred to have high levels of the polyphenol gossypol than on two with lower levels (Du Li *et al*., 2004).

Unique among the role played by alkaloids in plant defence against insects, including aphids, is the production of nitrogen-rich compounds by asexual *Epichloe/Neotyphodium* spp. facultative fungal endophytes of temperate grasses (Fig. 22.6). The bioactive compounds produced by these endophytes are ergot alkaloids (particularly ergovaline), indole diterpenes (lolitrems), pyrrolopyrazines (peramine) and pyrrolizidines (lolines). Ergot and lolitrem, but not peramine and lolines, are toxic to livestock (Young *et al*., 2013).

Lolines alone protect infected tall fescue and perennial rye grass (*Lolium pratense*) from *R. padi* (Siegel *et al*., 1990; Eichenseer *et al*., 1991; Wilkinson *et al*., 2000; Schardl *et al*., 2007). Additionally,

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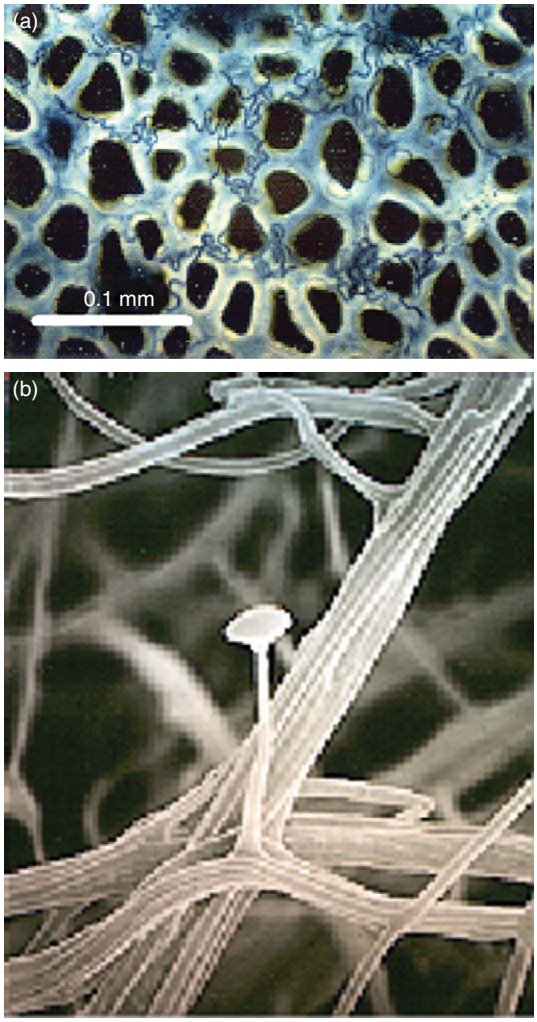

Fig. 22.6. The endophytic fungus *Neotyphodium*. (a) Section through a tall fescue (*Lolium arundinaceum*) seed showing mycelium between the aleurone cells. (b) Electronmicrograph of hyphae, conidiophore and conidium (4 μm long) in culture. Host is wild barley (*Hordeum* sp.). (Courtesy of S.L. Clement.)

lolines alone in meadow fescue (Wilkinson *et al*., 2000) and peramine only in other infected grasses (Siegel *et al*., 1990) have been associated with resistance to *S. graminum*. Compared to endophyte-free plants, infected perennial rye grass (Clement *et al*., 1992), tall fescue (Clement *et al*., 1996) and some wild perennial barley (*Hordeum* spp.) (Clement *et al*., 1997) are strongly resistant to *D. noxia*. Endophyte infection of another wild temperate grass, *Phleum alpinum*, confers resistance to *R. padi* (Clement *et al*., 2011). The expression of insect resistance (antixenosis, antibiosis) is affected by the host grass species/genotype, endophyte strain (including associated alkaloid profile) and insect species/biotype involved in a given interaction (Clement *et al*., 1994; Popay, 2009; Crawford *et al*., 2010) and soil nutrition (Lehtonen *et al*., 2005).

Perennial rye-grass cultivars harbouring a specific endophyte strain (AR37) are used for protection against the root aphid, *Aploneura lentisci*, and other pasture pests on farms in New Zealand (Hume *et al*., 2007; Popay and Hume, 2013) and Australia (Moate *et al*., 2012).

Although endophytic fungi are also frequently found in dicotyledenous plants (Saikkonen *et al*., 1998), any role they may have in HPR to aphids (or indeed any other insect) has yet to be established.

Bt toxins used in genetically modified (GM) crops resistant to Lepidoptera are not regarded as aphicides, but a GM potato cultivar with Bt against *Leptinotarsa decemlineata* (Colorado potato beetle) also depresses the growth and fecundity of *M. euphorbiae* (Ashouri *et al*., 2001).

Other toxins studied specifically for their potential in GM crops against aphids include lectins, but these usually give only partial resistance to aphids. When 30 were tested in artificial diet against *A. pisum* (Rahbe *et al*., 1995), most caused only low toxicity. However, those from jack pine (*Pinus banksiana*), love-lies-bleeding (*Amaranthus caudatus*), lentil (*Lens culinaris*) and snowdrop (*Galanthus nivalis*) induced worthwhile mortality. Concanavilin A (the jack-pine lectin) was then tested on five other aphid species, but with very variable results. A chitin-binding lectin in two wild brassicas shows some insecticidal activity against *B. brassicae* (Cole, 1994b). There have also been studies with proteinase inhibitors. Oryzacystatin 1, effective against leaf-chewing insects in transgenic oilseed rape, inhibited growth of *A. gossypii*, *A. pisum* and *M. persicae* (Rahbe *et al*., 2003) and (in transgenic aubergine) of *M. persicae* and *Macrosiphum euphorbiae* (Ribeiro *et al*., 2006). Tobacco genetically engineered to accumulate two ketosteroids (cholestan-3-one and cholest-4-en-3-one) in the phloem caused high mortality of *M. persicae* (Bouvaine *et al*., 2014).

Nutritional factors

Given the limiting levels of nitrogen dietary requirements for aphids in the phloem (Chapter 6, this

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volume), one might expect nutrition to be a valuable source of HPR. Auclair *et al.* (1957) studied several pea varieties and found a negative correlation between their resistance to *A. pisum* and the soluble and total amino nitrogen content of the leaves. Kazemi and van Emden (1992) analysed a wide provenance range of wheats (European, Iranian and the 'ancient' diploid wheat Einkorn (*Triticum monococcum*)) and found that the leaf concentration of three amino acids (alanine, histidine and threonine) was an excellent predictor for the performance of *R. padi*, accounting for over 95% of the variation in the fecundity of the aphid. By contrast, Weibull (1994) analysed EDTA (ethylenediaminetetraacetic acid) leaf exudates as a better reflection of phloem content than whole-leaf analyses, but found a negative correlation between several amino acids and the performance of *R. padi* on common barley (*Hordeum spontaneum*). However, since the segregating offspring of crosses showed no such relationship, no cause and effect was attached to the correlation.

Although nutritional factors are a mechanism of HPR to aphids, such resistance is particularly likely to fail under different environmental conditions such as different soils and fertilizer regimes.

Extrinsic factors

Factors extrinsic to the plant may be responsible for greater mortality on the apparently 'resistant' than on the 'susceptible' variety. In the absence of such factors, true HPR may be much less, or even absent. Thus, Gowling and van Emden (1994) showed that the number of *M. dirhodum* falling from wheat plants was doubled when parasitoids were added, and doubled again if the wheat variety was partially aphid resistant. The partially resistant variety 'Rapier' was only 25% resistant compared with the susceptible 'Armada', yet the increased falling of aphids in the presence of searching parasitoids caused it to appear 86% resistant.

Another example of extrinsic resistance is that of the 'leafless' pea varieties bred for low leaf area to be resistant to powdery mildew (*Erysiphe polygoni*), and instead of leaves, it has a profusion of photosynthesizing tendrils (Fig. 22.7; Kareiva and Sahakian, l990). The apparent resistance to *A. pisum* in the field was considerably greater than the true intrinsic resistance of only some 8%, because the ladybirds *Coccinella septempunctata* and *Hippodamia convergens* could grip the tendrils, whereas a high proportion fell off the shiny leaves of normal peas. The proportion falling was reduced from 47 to 26% for *C. septempunctata* and from 32 to 9% for *H. convergens*.

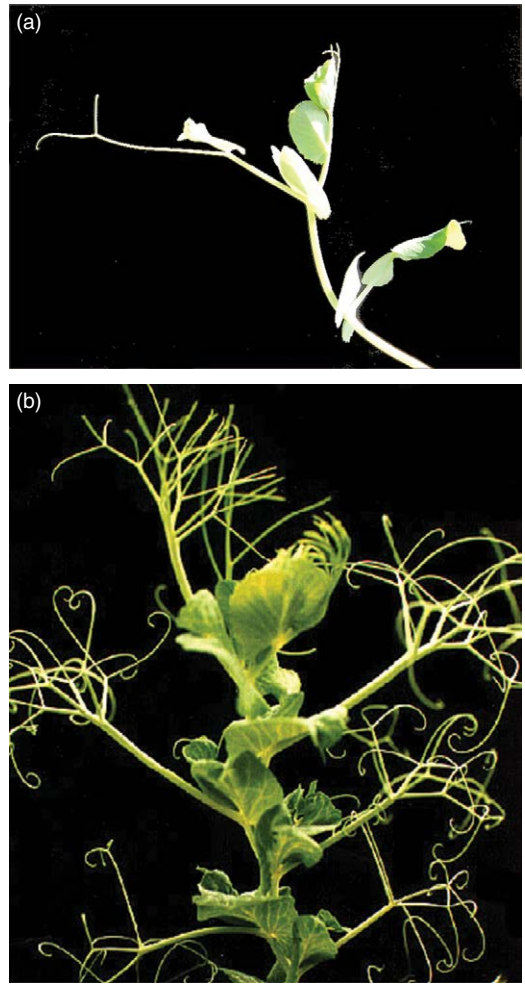

Fig. 22.7. (a) Normal and (b) 'leafless' cultivars of peas. ((b) courtesy of C. Coyne.)

Mechanisms of tolerance

Rather little is known about the mechanisms of tolerance of plants to aphids. Tolerance is often coupled with antibiosis, and the latter may explain the increased yield sufficiently for tolerance not to be identified. The examples of tolerance reported in the literature therefore tend to be dramatic, with crop growth and yield little affected despite high

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aphid infestation. For example, Hesler (2005) found that three triticale (× *Triticosecale* spp.) accessions showed no difference in shoot length whether infested or not infested with *R. padi*.

Compensation

Some lines of wheat show much enhanced growth with increased tillering when attacked by *S. graminum* or *D. noxia* (Castro *et al*., 2001). Such compensatory growth as a response to aphid attack may, however, lead to a delay in harvest.

Symptom expression

The plant reaction to aphid saliva can vary with the particular genotypes of both aphid and plant involved. Thus, some genotypes of wheat are specifically tolerant to the E biotype of *S. graminum* with a lack of symptoms (Morgham *et al*., 1994). A mechanism for such tolerance to *S. graminum* was proposed by Maxwell and Painter (1962), who compared two wheats, 'Dickson' (tolerant) and 'Pawnee' (intolerant). These two varieties differ as to the timing of the cessation of further expansion of the flag leaf, on the photosynthesis of which much of the grain yield depends. Since the aphids tend to feed in an aggregation on the underside of the leaf, growth there is inhibited, while the upper leaf surface continues growing. The leaf therefore curls strongly, reducing the effective leaf area exposed to solar radiation. In 'Dickson', the growth of the flag leaf stops earlier than with 'Pawnee', and feeding by the aphids on the underside of the leaf therefore does not induce curling.

Further Considerations

Yield drag or other fitness costs

The majority of HPR mechanisms involve the production by the plant of more chemical compound or additional plant tissue, yet fitness costs of pest resistance have rarely been reported. Thus, Assad *et al*. (2004) found no negative correlations between the height, grains per spike or total biomass of 14 wheat genotypes and their antixenosis to *D. noxia*, and two Rag genes for resistance to *Aphis glycines* (soybean aphid), even when pyramided (i.e. combined on the same variety), incurred no yield penalty (Hesler *et al*., 2013). Data of Gershenzon (l994) suggest that different secondary compounds can account for between 0.01 and 30% of the glucose in leaf tissue, but such static concentrations are negligible in comparison with the glucose production by photosynthesis over a period of time. Foyer *et al*. (2007) calculated that 30–40 min of photosynthesis (4–6% of the total photosynthetic output over a 12-h day) would suffice to synthesize the DIMBOA in wheat and maize. Moreover, photosynthesis is more often sink than source limited, and so any fitness costs would reveal themselves only under conditions of extreme stress.

Negative effects on natural enemies

Crop varieties developed for resistance to aphids can have deleterious effects on natural enemies, especially where the resistance is based on toxins (see above). DIMBOA, a hydroxamic acid studied extensively in relation to HPR to cereal aphids (see earlier), is toxic to the ladybird *Eriopis connexa*. Paradoxically, maize varieties with high DIMBOA cause less mortality of this predator than varieties with intermediate levels, since it can detect the compound in the aphids and avoid ingesting a toxic dose (Martos *et al*., 1992). In contrast, the ladybird *Propylaea japonica* showed increased weight and faster development on a high gossypol aphid-resistant cotton variety (Du Li *et al*., 2004).

The parasitoid *Aphidius rhopalosiphi*, reared on the smaller individuals of *M. dirhodum* on the partially aphid-resistant wheat 'Rapier', showed progressively smaller size and reduced egg load on emergence in consecutive generations. After ten generations on 'Rapier', size and egg load had decreased by 15 and over 50%, respectively. However, parasitoids returned to an aphid-susceptible variety ('Huntsman') regained their fitness in one generation (Salim Jan and H.F. van Emden, unpublished, but summary data given by van Emden, 1995). Reductions in size and fecundity of *Aphidius nigripes* emerging from *M. euphorbiae* reared on Bt potato have also been attributed to the poorer quality of the host aphids (Ashouri *et al*., 2001; Ashouri, 2004). *Aphis glycines* showed such reduced longevity on aphid-resistant soybeans that fewer *Binodoxys communis* could develop to the mummification stage (Ballman *et al*., 2012).

Problem trading

There is always the possibility that the plant modification made in developing HPR to aphids will make the plant more susceptible to another

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damaging organism. An early example is found in the hairy South African cottons, resistant to leafhoppers but especially susceptible to *A. gossypii* (Dunnam and Clark, 1938). When lucerne varieties resistant to lucerne wilt (*Verticillium albo-atrum*) were released in California, USA, they proved especially susceptible to *T. trifolii* (van den Bosch and Messenger, 1973).

Glossy brassica varieties resistant to *B. brassicae* suffer from increased *Phyllotreta cruciferae* (flea beetle) damage compared with waxy ones (Stoner, 1992; Eigenbrode *et al*., 2000), and glossy peas resistant to *A. pisum* are more heavily attacked by *Sitona lineatus* (pea and bean weevil) (White and Eigenbrode, 2000).

Surprisingly, problem trading has also been reported in tall fescue plants resistant to *R. padi* because of alkaloids produced by the fungal endophyte *Neotyphodium coenophialum*. The noctuid armyworm *Spodoptera frugiperda* showed enhanced performance on the endophyte-infected plants (Bultman and Bell, 2003).

In breeding F2 hybrid willows as biomass fuels, resistance to a *Chaitophorus* sp. aphid and the eriophyid mite *Aculus tetanothrix* were found to be inversely related (Czesak *et al*., 2004).

Biotypes

Species of aphid often show genotypic variation expressed through different behavioural traits, including sensitivity or tolerance to varieties bred for HPR. Tolerant variants are often referred to as 'resistance-breaking biotypes', but Blackman and Eastop (Chapter 1, this volume) express doubts about the use of the word because such genotypes may be just a single clone subject to recombination by sexual reproduction. However, the word 'biotype' is so well embedded in the literature of HPR that it would probably be misleading to the reader to use an alternative terminology here.

Some cowpea varieties producing a toxin strongly aphicidal to *A. craccivora* collected at the International Institute for Tropical Agriculture (IITA) in Nigeria proved susceptible to the first aphids collected from another location (Ansari, 1984), and the 'biotype problem' with pests indeed seems particularly common with aphids; 8% of 423 references between 1972 and 2015 concerning HPR and aphids are about this aspect, although many identify resistance-breaking biotypes in the glasshouse rather than reporting a problem in the field.

Biotypes in relation to HPR have proved particularly important with *S. graminum* on cereals, with the biotypes distinguished according to their responses to a clearly defined set of plant varieties. The resistance-breaking biotypes have proved a major headache in the field. For example, biotype E breaks the resistance incorporated in some sorghum varieties (Eisenbach and Mittler, 1987). No single resistance gene in either sorghum or wheat is effective against all biotypes of *S. graminum*. Anstead *et al*. (2003) located several biotypes of *S. graminum* on wild grasses, including one new biotype, and proposed that new biotypes were formed on wild grasses rather than on cereal crops.

The use of HPR against *A. glycines* in soybean has similarly identified at least three biotypes, although it is still possible to find soybean accessions resistant to all (Bansal *et al*., 2013).

Attempts in the USA to manage *D. noxia* on cereals ran into biotype problems only 5 years after the appearance of the pest in Texas in 1986. Five biotypes have been distinguished (Shufran and Payton, 2009). The emergence of biotype 2 in Colorado made all resistance genes, other than one in rye, ineffective (Murugan *et al*., 2010). However, even the resistance-breaking biotypes vary in the chlorosis and stunting they cause (Shufran *et al*., 2007). Some of the resistance genes no longer effective in the USA are still effective in South Africa (Tolmay *et al*., 2013). Merrill *et al*. (2014) released two biotypes of *D. noxia* differing in their tolerance to resistant wheat in a known proportion at three sites along a gradient from northern Colorado to Florida, and found that the resistance-breaking biotype rapidly displaced the other, with an apparent more than tenfold advantage.

Since the late 19th century, grapes in most parts of the world have been grafted on to rootstocks of old communion wine varieties resistant to *Daktulosphaira vitifoliae* (grape phylloxera) and brought from Europe to North America by the early settlers. This resistance lasted for a long time, but was finally broken by a biotype appearing in Germany in 1994 (Anon., 1994). Thus, in spite of the potential for 'biotypic breakdown' of resistance, HPR to aphids may be quite durable. Di Pietro and Caillaud (1998) reared *S. avenae* on resistant wheat (including highly resistant 'Einkorn') for 2 years and could find no selection for breaking HPR.

As can be seen from the above, the occurrence of biotypes is variable both between and within species (in relation to geographical distribution).

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Puterka *et al*. (1992) recorded seven biotypes of *D. noxia* worldwide, but as yet only a few have been found in the USA. A detailed study of *Elatobium abietinum* (spruce aphid) compared 40 populations each from the UK and New Zealand (Nicol *et al*., 1998). There were 28 genotypes (but of course not necessarily 28 biotypes) in the UK collections, but only one in New Zealand.

There is little information as to the mechanisms whereby aphid biotypes break HPR. It is, however, known that resistance to *S. graminum* in sorghums, based on increased methylation of the middle lamellar pectin, is defeated in resistance-breaking biotypes of the aphid by their saliva possessing enhanced pectin methylesterase activity (Dreyer and Campbell, 1984). Biotypes of *Nasonovia ribisnigri* (currant–lettuce aphid) not affected by the Nr gene in resistant lettuce suppress the wound response of the sieve elements (ten Broeke, 2013). There is also the intriguing hypothesis that it is the symbionts that enable biotypes of *T. t. maculata* to break the resistance of some lucerne varieties (Ruggle and Gutierrez, 1995) and of some *M. euphorbiae* wiyh resistant tomato varieties (Francis *et al*., 2010).

Coping with the biotype problem involves the continual development of varieties with new resistance genes available if control begins to fail, as has been the history with *S. graminum* (Puterka and Peters, 1990). The breakdown of plant resistance is usually far more serious with fungal diseases, and plant pathologists have developed strategies for deploying resistance genes so as to delay such breakdown. These strategies are equally applicable to HPR against aphids. One such strategy is combining more than one resistance gene in a variety ('pyramiding'). Porter *et al*. (2000) used a model for *S. graminum* to test whether pyramiding or sequential release of genes would maintain HPR for longer. The model predicted that pyramiding was the longer-lasting strategy, but Porter *et al*. claimed that experimental evidence actually pointed to the opposite conclusion. Bush *et al*. (1991) studied the value of variety mixtures against greenbug biotypes C and E. They used three varieties of wheat, one susceptible to the aphid (S) and one resistant to each of the biotypes C and E (CR and ER). The mixtures 3R:1S in separate experiments for each biotype, or 1CR:1ER:1S with both biotypes, managed the biotypes successfully, and the two-variety mix worked as well as the three-variety one.

Spread of viruses (see also Chapter 15, this volume)

Some workers have argued that, because aphids on resistant varieties are more restless, the spread of virus in such varieties is likely to be accelerated, particularly with non-persistent virus diseases. Atiri *et al*. (1984) reported such greater spread of *Cowpea mosaic virus* in small cage experiments with *A. craccivora* on cowpeas. Other work in Africa (Roberts *et al*., 1993) appears to confirm this in field experiments on chemical control of the same aphid with pyrethroids (which increase restlessness of aphids – van Emden and Service, 2004). In these experiments, the secondary spread of virus was greater on an aphid-resistant than on a susceptible cowpea variety. It is also possible that the phenomenon may occur with aphids in watermelon (Webb and Linda, 1993 – but see Kishaba *et al*., 1992, below) and with *M. persicae* in sugar beet, on which this aphid shows high mortality, especially as the plants get older. Survival is improved on plants infected with either *Beet yellows virus* or *Beet mild yellowing virus* (Kift *et al*., 1996). Yet such reports are in the minority, perhaps partly because much of the spread of non-persistent viruses is by alatae of species for which the crop is not a host, and therefore totally resistant regardless of its resistance status to other aphid species. Even in respect of pest species, the overwhelming evidence is that HPR to aphids leads to less virus spread (van Emden, 1987). Thus, Kishaba *et al*. (1992,) compared *Watermelon mosaic virus 2* transmission by *A. gossypii* in one aphid-susceptible and three resistant watermelon lines that were all equally good virus sources, and yet transmission by the aphid on the three -resistant lines was reduced by 31, 71 and 74%. The number of aphids needed to give 59% infection was only 20/plant on the susceptible line, but varied from 60 to 400 on the three aphid-resistant lines. Chen *et al*. (1997) also found that, for the watermelon/*A. gossypii* combination, levels of non-persistent virus were correlated negatively with resistance to the aphid.

Interactions with other control measures

The aphid literature provides many examples of HPR having a positive effect on the impact of natural enemies. HPR also affects the susceptibility of aphids to insecticides. Such interactions are not discussed here, but are reviewed in Chapter 23, this volume.

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Conclusions

Host-plant resistance has far greater potential for reducing populations of aphids than has as yet been exploited. This is partly because plant breeders have sought to use HPR as a single-component control measure, and have therefore screened for high resistance to aphids. Such levels of resistance are most likely to be based on toxic allelochemicals, often the expression of a single gene. This has certainly been the approach with the industrial production of insect-resistant transgenic crops, although as yet no transgenic event effective against aphids has been commercialized.

It will be evident from this account of HPR that such monogenetic resistance/high expression of allelochemicals is likely to accentuate the potential disadvantages of HPR as a control method, including damaging side effects on natural enemies and biotypic breakdown. The increased tolerance to insecticides that such HPR may cause is discussed in Chapter 23, this volume.

It is more broadly based, partial HPR to aphids that needs to be given greater research emphasis, especially given the worldwide move towards the integration of several control methods represented by IPM.

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23 Integrated Pest Management and Introduction to IPM Case Studies

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Introduction

Modern IPM (Integrated Pest Management) began with aphids, having evolved from the 'Integrated Control' (IC) concept of Stern *et al*. (1959). IC integrated the chemical and biological control of *Therioaphis trifolii maculata* (spotted alfalfa aphid) on lucerne (alfalfa), *Medicago sativa*. Following the arrival of the aphid from Europe to California, USA, in 1954, resistance to organophosphate insecticides (OPs) rapidly appeared. Since the OPs killed the indigenous natural enemies, *T. t. maculata* was destroying the lucerne crop in California by the late 1950s. To solve the OP-resistant *T. t. maculata* problem, the Californian workers integrated a reduced dose of an OP insecticide with the biological control that the low dose allowed to survive. Stern *et al*.'s (1959) 'integration' referred to integration of control methodologies, therefore integrated control of an aphid pest was a meaningful concept. Its first successor, 'Pest Management' (PM), dates from a conference at Raleigh, North Carolina, in 1970 (Beirne, 1970), and embraces both single and multiple control measures against a pest. Still later, IPM emerged (Apple and Smith, 1976), defined as follows: 'The concept of Pest Management has now been broadened to include all classes of pests (pathogens, insects, nematodes and weeds) and in this context is commonly referred to as IPM.' Thus, the 'I' of IPM originally included an integration of crop protection disciplines (i.e. entomology, plant pathology, nematology, weed science, etc.), and Apple and Smith (1976) would have regarded the IPM of aphids as a contradiction in terms. Yet, since 1976, definitions have loosened; today, IPM seems indistinguishable from PM.

The drivers behind PM/IPM were pest *mis*management in the 1940s and 1950s, and the methods available for reversing this are reviewed elsewhere in this volume (Table 23.1). Apart from those representing the reciprocals of pest mismanagement, using semiochemicals to modify the behaviour of aphids and their natural enemies (Chapter 8, this volume) is a more recent contribution of considerable potential for inclusion in the IPM armoury.

What is missing from Table 23.1 is the 'I' for the integration of at least two methods, which is surely implicit in the concept of IPM, and from which logically follow two 'Golden rules for IPM' (van Emden, 2002):

- If a single method gives adequate control on its own, then there is the danger of a tolerant pest strain increasing in gene frequency and no opportunity to use a second method in addition. The method therefore needs to be made less efficient (reduced dose of pesticide, partial host-plant resistance rather than immunity) for there to be value in introducing another control method to supplement it.
- Methods are increasingly worth combining to the extent that the control then achieved exceeds the additive effects of the two methods in isolation.

Integration of Chemical and Biological Control

The prevalent expression of the impact of insecticides on biological control in the literature is that most insecticides are toxic to natural enemies of aphids. This is often misinterpreted as meaning that

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Table 23.1. Pest mismanagement and the techniques for reversing it, with relevant chapters in this volume in brackets.

Elements of pest mismanagement	The pest management reciprocal
Overdosing with pesticides and prophylactic treatments, resulting in the appearance of tolerant pest populations	Decisions on chemical control are guided by forecasting and economic thresholds, and selective materials are chosen where they are available (Chapters 16, 17, 18)
Loss of biological control through use of broad-spectrum pesticides and loss of habitat diversity in agroecosystems	Biological control is conserved by selective pesticides and promoted by habitat modification, including planned biodiversity in farm management. Agents may be recolonized where they have disappeared, or new agents, especially from overseas, introduced (Chapters 20, Chapters 21)
Introduction of genetically uniform high-yielding but pest-susceptible crop cultivars	The use of aphid-resistant crop varieties (Chapter 22)
Abandonment of labour-intensive cultural controls	Introduction or reintroduction of cultural controls, especially to improve conditions for natural enemies of aphids (Chapter 21)

they inevitably damage the biological control of aphids. However, assuming there are no harmful sublethal effects of the pesticide on the surviving natural enemies (as shown for imidacloprid with the hemerobiid *Micromus tasmaniae* (Walker) by Walker *et al*., 2007), biological control is only damaged if the ratio of aphids to natural enemies increases after the pesticide application. If it decreases (i.e. even if the application is only marginally selective), there is the potential for improved biological control, though some, or even many, of the natural enemies are killed (van Emden and Service, 2004).

Use of a selective active ingredient

The classic example is the carbamate pirimicarb, to which only the acetylcholinesterase in the nervous system of aphids and Diptera is sensitive (Silver *et al*., 1995). In addition, pirimicarb increases coccinellid voracity by reducing the mobility of surviving aphids, making their capture easier (Cabral *et al*., 2011).

Natural enemies of aphids are not necessarily more susceptible to insecticides than their aphid prey. Croft and Brown's (1975) literature review identified that, for 36 aphid–coccinellid combinations, the coccinellid was more tolerant to insecticide than the aphid in 31 cases, the extreme being a 43-fold difference. Acheampong and Stark (2004) found that pymetrozine was not only non-toxic to the parasitoid *Diaeretiella rapae* at 0.212 g a.i./ha, but also that the r_m of treated parasitoids increased by 11%.

Plant extracts such as neem (Khan *et al*., 2013) and herb extracts (Ketabi *et al*., 2014) are often much more selective than conventional insecticides, where any selectivity tends to be partial.

Cypermethrin has repeatedly been reported as partially selective (e.g. Al-Antary *et al*., 2010; Irshaid and Hasan, 2011), and today candidate insecticides are usually screened for their effects on the natural enemies of aphids (e.g. Bangels *et al*., 2011; Morita *et al*., 2014). Selectivity found in favour of one natural enemy may not apply to others; Bacci *et al*. (2009) tested six aphicides on the ladybird *Cycloneda sanguinea*, a predatory anthicid beetle, and the parasitoid *D. rapae*, and found considerable specificity for any selectivity.

Fungicides and herbicides also need checking for impact on aphid natural enemies. Jansen *et al*. (2008) tested 16 fungicides and 16 herbicides for toxicity to *Aphidius rhopalosiphi*, *Adalia bipunctata*, *Episyrphus balteatus* and two ground-living aphid predators, the staphylinid *Aleochara bilineata* and the carabid *Bembidion lampros*. Not all the compounds were safe for the beneficials. In Belgium, 'selectivity lists', reporting on the safety to natural enemies of a wide range of plant protection products, are available for potato and vegetable crops (Jansen, 2014).

Dose reduction

This was the approach to achieve selectivity of a broad-spectrum OP insecticide mentioned at the start of this chapter (Stern *et al*., 1959). Similarly, Khan *et al*. (2012) reduced the dose of thiacloprid on potatoes by 20% and recorded better survival of ladybirds, with no loss of tuber yield compared to the full dose treatment.

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Such studies confirm Plapp's (1981) hypothesis that the per cent kill of carnivores will reduce faster than that of herbivores as the pesticide dose reduces. This hypothesis implies a steeper slope of the regression of probit mortality on toxin concentration for carnivores than herbivores (Fig. 23.1, comparison of green solid and red dashed line). Biologically, this means that a carnivore population shows less variation in tolerance to insecticides than a herbivore population. Plapp's (1981) reasoning was that herbivores required a diverse armoury of enzymes for detoxifying foreign toxins (i.e. plant defensive compounds) to an extent carnivores did not.

In relation to the widely held view that dose reduction encourages the appearance of insecticide-tolerant genotypes, it should be remembered that predators would only have available as prey the aphids that have survived the insecticide.

Selectivity in space

Even broad-spectrum aphicides will show some selectivity if they are applied as soil treatments or as systemic compounds rapidly withdrawn into the plant. Another approach is that of spot treatments; for example, Choi *et al.* (2009) could control aphids on peppers in glasshouses with releases of *Aphidius colemani* together with spot treatments of insecticide on limited areas of high aphid density.

Selectivity in time

Early sprays may reduce aphid populations before natural enemies appear. Thus, Hull and Sterner (1983) found that one early application of pesticide gave control of *Dysaphis plantaginea* (rosy apple aphid) on apples without disrupting later predation by natural enemies, though the lowered aphid numbers might also have resulted in fewer natural enemies colonizing the crop. Fagan *et al.* (2010) recommended that soil drenches of imidacloprid to lettuce should be restricted to early spring and late summer, to allow natural enemies to control aphids between these periods.

Morse (1989) suggested allowing *Aphis craccivora* (cowpea aphid) to attract coccinellids, but once the beetles had laid their eggs, reducing aphid numbers with an ephemeral insecticide while the coccinellid embryos/larvae were still protected by the egg shell. It has similarly been suggested that parasitoid larvae within mummies often survive insecticide applications, provided that the residues on the mummy cuticle have reduced when the adult parasitoids emerge.

Integration of Chemical Control and Host-plant Resistance (HPR)

Aphids are usually (but not invariably) smaller on resistant plants. Since the toxicity of an insecticide is a function of body weight, one would expect

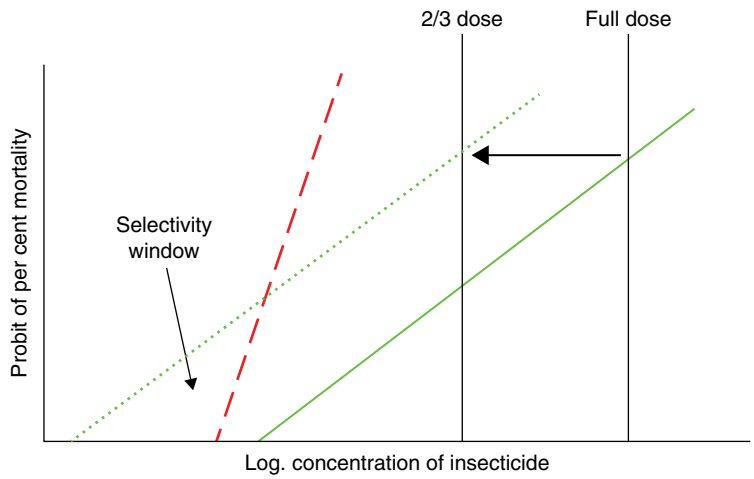

Fig. 23.1. The theoretical integration of partial host-plant resistance, biological control and insecticides. Green solid line = mortality response of aphids treated with normal dose on susceptible variety; green dotted line = mortality response of aphids treated with a dose reduction (horizontal arrow) of one-third on a resistant variety. The mortality response of a natural enemy (red dashes) is assumed to be unaffected by the plant resistance.

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aphids on resistant plants to show enhanced susceptibility to toxins. The first report of this phenomenon concerned *Myzus persicae* (peach–potato aphid), *Aphis gossypii* (cotton or melon aphid) and *Aulacorthum solani* (glasshouse and potato aphid) on chrysanthemum (*Chrysanthemum morifolium*) (Selander *et al*., 1972). The LD_{50} (the dose adjusted for aphid weight required to kill 50% of the aphids) of malathion, dimethoate and lindane on the resistant variety 'Princess Anne' was between 50 and 66% lower than on the susceptible variety 'Tuneful'. Nicol *et al*. (1993) compared the tolerance to deltamethrin of *Sitobion avenae* (English grain aphid) on two wheat varieties, of which 'Altar' possessed resistance to aphids based on high DIMBOA levels (Chapter 22, this volume). On 'Altar', deltamethrin was three times more toxic than on the susceptible wheat ('Dollarbird').

Reduced aphid size alone usually cannot account for their susceptibility to insecticides on resistant plants. After correction for differences in aphid weight between the varieties in the DIMBOA example above, the LD_{50} on 'Altar' was still reduced by over 90%. With *M. persicae* on Brussels sprouts, Mohamad and van Emden (1989) calculated that the 45% increase in mortality from malathion on the only slightly aphid-resistant variety 'Early Half Tall', was still as large as 42% after correcting for the small difference in aphid weight on the two varieties. Similarly with *Metopolophium dirhodum* (rose–grain aphid) on the susceptible wheat variety 'Maris Kinsman' and the partially aphid-resistant 'Emmer' wheat (*Triticum turgidum* subsp. *dicoccon*), Attah and van Emden (1993) found that the mortality increase of over 50% on the resistant variety was only reduced by about 5% after correction for weight. Some stress of HPR on the aphids, perhaps poorer nutrition and lower fat levels in the body, appear more important than body weight differences. Clayson *et al*. (2014) found that a 35% reduction in the concentration of malathion was possible on the partially resistant wheat 'Rapier' compared with that on the susceptible 'Huntsman' to achieve 50% mortality of *M. dirhodum*. Again, correction for aphid weight still left an unexplained 20% reduction. It would appear that a reduction of 30% in aphicide concentration on a variety that is only slightly aphid resistant should give control equal to that on a susceptible variety.

However, aphids on resistant plants may sometimes show the converse phenomenon, i.e. greater tolerance to insecticides. Ahmad and Shakoori (2001) found higher mortality from demeton-S-methyl of *Brevicoryne brassicae* (cabbage aphid) on the aphid-susceptible Ethiopian mustard (*Brassica carinata*) than on four aphid-resistant accessions of Indian mustard (*Brassica juncea*). With caterpillars (Lepidoptera), it has been shown that such results arise from the induction by secondary plant compounds of insecticide-detoxifying enzymes in the insect (Kennedy, 1984; Yu and Hsu, 1985).

Integration of Biological Control and HPR

Of 53 examples of the interaction of HPR with biological control in the literature, 31 show positive synergism, 8 show simple additivity and 14 show a negative interaction. Negative interactions are typical of strong HPR (e.g. Kersch-Becker and Thaler, 2015). In this chapter, however, the emphasis will be on the contribution positive synergy may make to the IPM of aphids.

There are a few data sets (Fig. 23.2) where, across a time interval, measurements have been made of the effect on an aphid population of plant resistance without biological control, biological control without plant resistance (i.e. on the aphid-susceptible variety) and the combination of plant resistance and biological control. From these data, a population can be expressed as a proportion of that on the susceptible variety without biological control. The expected reduction by the combination of plant resistance and biological control, assuming no synergy between them, is the product of the proportions after their effect in isolation (van Emden, 2003). This can then be compared with the actual experimental outcome. In five of the eight data sets, there is very strong positive synergism – the population reduction is between twice and 20 times that expected, were there no synergism between the two restraints. In one of the data sets (Fig. 23.2G), the positive synergism was rather small, but even so resulted in an enormous (99.3%) reduction in aphid numbers over the season (McCarville and O'Neal, 2012).

The phenomena for positive synergism can be divided into numerical and functional responses of the natural enemies:

Numerical responses

- Slower reproduction of aphids on resistant varieties increases the potential of natural enemies

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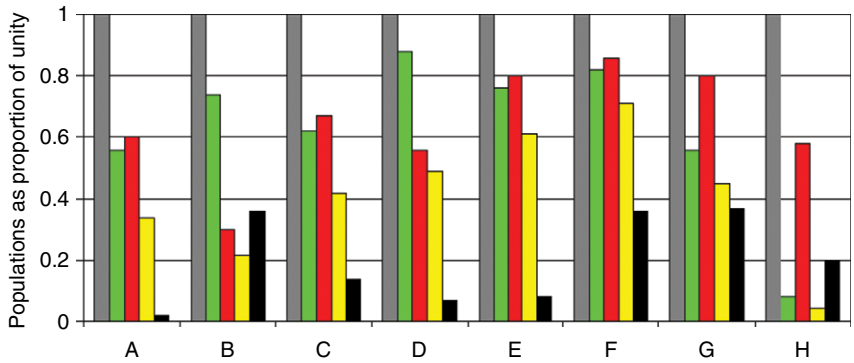

Fig. 23.2. Integration of partial host-plant resistance to aphids with biological control. Aphid populations are expressed as a proportion of that on susceptible varieties without biological control (grey). Histograms in each block from left to right: green = after reduction by plant resistance alone; red = after reduction from biological control on susceptible variety; yellow = predicted population on resistant variety with biological control (= green × red proportions); black = experimental result on resistant variety with biological control. A = *Schizaphis graminum* parasitized by *Lysiphlebus testaceipes* on barley (Starks *et al*., 1972); B = *Sitobion avenae* parasitized by *Aphelinus abdominalis* on wheat (Lykouressis, 1982); C and D = *Metopolophium dirhodum* parasitized by *Aphidius rhopalosiphi* on wheat (Gowling, 1989); E = *Brevicoryne brassicae* and natural predation in brassicas (Gowling, 1989); F = *Brevicoryne brassicae* and natural predation in brassicas (Dodd, 1973); G = *Aphis glycines* in soybean (McCarville and O'Neal, 2012); H = *Brevicoryne brassicae* and parasitization by *Diaeretiella rapae* on Brussels sprouts (van Emden, 1978).

to contain the aphid population (van Emden and Wearing, 1965).

- Aphids on resistant varieties usually show increased development times (e.g. Sotherton and Lee, 1988). This increases their chance of being predated before they reproduce.
- Parasitoids may show constancy to variety (van Emden *et al*., 2015) and so will continue searching on resistant varieties even though aphid numbers are reduced.
- Both coccinellids and parasitoids sometimes show shorter development time and increased fecundity on aphid-resistant varieties (Table 23.2). Such differences in reproductive rates may even be found between crop varieties with no HPR to aphids (e.g. *Aphidius matricariae* and *Aphis fabae* (black bean aphid) on sugar beet – Adabi *et al*., 2010).

Functional responses

- Natural enemies can often detect the locations of aphid colonies on the plant by plant-emitted chemical cues (Storeck *et al*., 2000), so searching time may not be increased by lower pest densities.
- Predators will eat smaller aphids (as typical on resistant varieties) in greater numbers before becoming satiated (Fig. 23.3). Hassell *et al*. (1977) showed that a positive density-dependent voracity of the ladybird *Coccinella septempunctata* extended to higher densities of prey if the latter (different instars of *B. brassicae*) were smaller (Fig. 23.3).
- Smaller aphids on resistant varieties are less able to escape natural enemies by rapid locomotion or effective kicking. Dixon (1985) showed that *Microlophium carnosum* (common nettle aphid) were able to survive encounters with larvae of *Adalia decempunctata*.
- The activity of natural enemies searching in aphid colonies disturbs aphids and causes them to fall from the plant (a so-called 'non-consumptive' effect); this is considerably more pronounced on resistant varieties (Gowling and van Emden, 1994; Fig. 23.4). Note in Fig. 23.4 that total per cent parasitization of *M. dirhodum* on the resistant wheat 'Rapier' was higher than on 'Armada', partly because more fallen aphids were parasitized and mummified on the soil. The greater restlessness of aphids on resistant varieties, and therefore their exposure to fungal spores, was suggested by Hatting *et al*. (2004) as explaining the improved control of *Diuraphis noxia* (Russian wheat aphid) on aphid-resistant wheat by the fungus *Beauveria bassiana*.

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Table 23.2. Some examples of the positive effects of HPR on natural enemies of aphids.

HPR	Aphid(s)	Natural enemy(ies)	Form of effect on natural enemy	Reference
Transgenic potato expressing protease inhibitor	*Macrosiphum euphorbiae*	*Aphidius nigripes*	Increased size and fecundity	Ashouri *et al*. (2001)
High gossypol cotton	*Aphis gossypii*	*Propylaea japonica*	Reduced development time; greater adult weight	Du *et al*. (2004)
Partially resistant cabbage varieties	*Brevicoryne brassicae* and *Myzus persicae*	*Aphidius colemani*	Usually a reduced development time	Kalule and Wright (2005)
Partially resistant broad bean (glasshouse experiments)	*Aphis fabae*	*Coccinella septempunctata*	Increased weight; delayed development but increased fecundity	Shannag and Obeidat (2008)
Partially resistant wheat	Cereal aphids	Coccinellids	Increased populations	Khan *et al*. (2011)
Resistant 'Ommid' wheat	*Diuraphis noxia*	*Hippodamia variegata*	Reduced development time; increased longevity and voracity	Zangeneh *et al*. (2014)

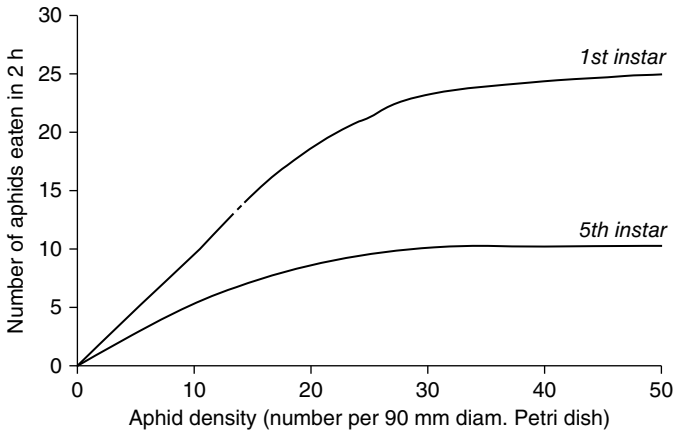

Fig. 23.3. Predation by *Coccinella septempunctata* on first- and fifth-instar *Brevicoryne brassicae* at different aphid densities. (From two different graphs at two different scales several pages apart in Hassell *et al*., 1977.)

- Plant structure may interact with biological control. Resistant varieties may have less deformation in the form of leaf rolling. Natural enemies then find their aphid prey more easily (Reed *et al*., 1992). Lower amounts of leaf wax give coccinellids a better grip (Eigenbrode *et al*., 1998). Plant structures may protect natural enemies from parasitization (e.g. the eggs of predatory bugs inside leaf domatia (small pockets with hairs often induced by other organisms)) (Agrawal *et al*., 2000).
- Natural enemies may spend less time cleaning off wax particles on aphid-resistant varieties with low surface wax (Eigenbrode *et al*., 1998). Parasitoids will also divert searching time to cleaning activity if there is copious aphid honeydew, as more characteristic of aphid-susceptible than of aphid-resistant varieties (Wickremasinghe, 1989).

Three-Way Integration of Chemical Control, HPR and Biological Control

Taking together two phenomena already mentioned – that insecticide dose can often be reduced on aphid-resistant varieties and that dosage reductions are

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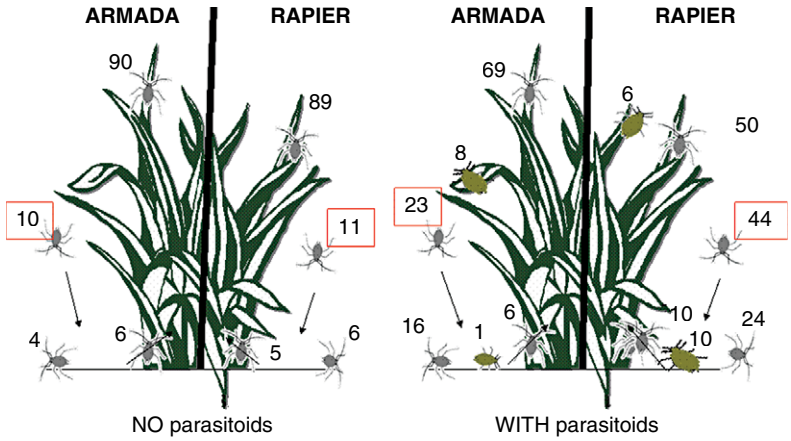

Fig. 23.4. Percentage fate of *Metopolophium dirhodum* on 'Armada' (susceptible) and 'Rapier' (partially aphid resistant) wheat after 6 days with and without activity of the parasitoid *Aphidius rhopalosiphi*. The image shows live aphids (grey) on the plant, falling (percentage in red and boxed), those climbing back on the plant and those failing to do so. In dark green are aphids mummifying on the plant and on the ground (data of Gowling, 1989).

likely to increase selectivity in favour of natural enemies – a three-way interaction seems to be indicated. This is illustrated in Fig. 23.1 by the red dashed line remaining stationary while the green solid line moves left to become the green dotted line. As yet, the only experimental test to confirm this interaction in relation to aphids stems from laboratory work on cereal aphids, parasitoids and coccinellids (Tilahun and van Emden, 1997; Fig. 23.5), and here both *A. rhopalosiphi* and third-instar larvae of *C. septempunctata* actually showed greater tolerance to malathion when reared on *M. dirhodum* on the partially aphid-resistant wheat 'Rapier' than on the aphid-susceptible 'Maris Huntsman'.

Integration of Cultural Control and Biological Control

Although there is considerable interest in using cultural measures directly to promote the biological control of aphids (Chapters 20 and 21, this volume), the integration of cultural measures primarily for controlling aphids and biological control seems relatively unexplored. However, such interactions almost certainly exist and therefore should not be ignored in designing IPM programmes. An attempt to investigate such interactions was made by Ul-Haq (1997) in glasshouse experiments on the effects of fertilizer applications, water stress and wheat/pea (*Pisum sativum*) 'intercrops' on aphids and the size and fecundity of parasitoids. He found that 'cultural treatments' that decreased the size of aphids also decreased the size and fecundity of the parasitoids.

One cultural control measure aimed against aphids is mixed cropping, and a potato/burseem clover (*Trifolium alexandrinum*) cropping system in Pakistan to reduce populations of *M. persicae* on the potato increased the numbers of ladybirds, hover flies, lacewings and parasitoid mummies (Saljoqi *et al*., 2009).

In the absence of much experimental evidence, Table 23.3 lists the principal approaches to the cultural control of aphids and aphid-transmitted viruses, with speculation on how biological control may be affected.

The IPM Case Studies (Chapters 24–33)

The crop scenarios

This introduction to the IPM of aphids is followed by ten case studies, where scientists working on the control of aphids in particular crop scenarios were asked to report on the state of IPM in their specialized area of interest. The case studies have been chosen to represent a wide diversity, with the result that the various case studies could not be presented to a formula. At one end, cotton is a single crop with one important aphid species; at the other, the case study on temperate fruit trees and stone fruit

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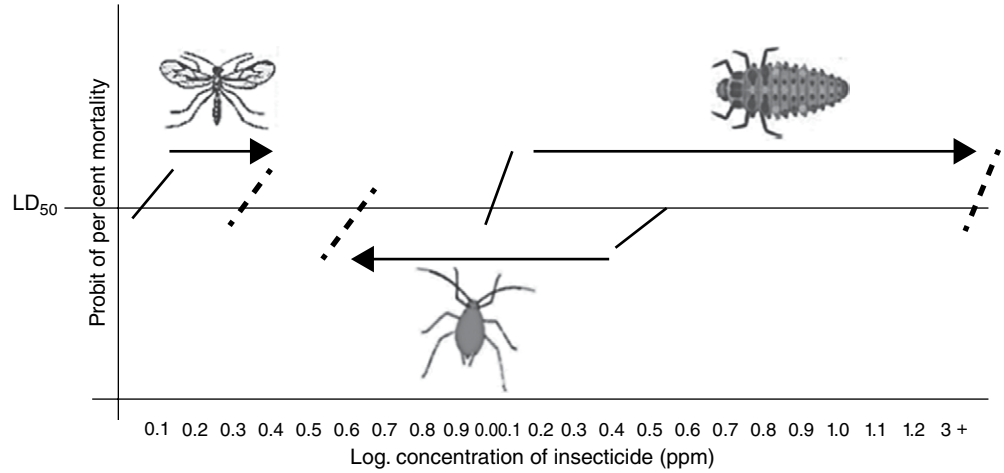

Fig. 23.5. Effect of a partial aphid-resistant wheat ('Rapier') on susceptibility to malathion of *Metopolophium dirhodum*, the parasitoid *Aphidius rhopalosiphi* and third-instar larvae of the coccinellid *Coccinella septempunctata*. Solid lines = LD_{50} and slope of probit regression on the aphid-susceptible wheat 'Maris Huntsman'; dotted line = LD_{50} and slope of probit regression on 'Rapier'; arrows = direction and degree of change in susceptibility to malathion. (From Tilahun and van Emden, 1977.)

Table 23.3. Cultural control of aphids and potential effects on natural enemies.

Control measure	Potential effects on natural enemies	Supporting evidence (if any)
Limited N fertilization	As for partial plant resistance; greater impact, but parasitoids smaller and less fecund	Ul-Haq (1997)
Avoidance of intermittent drought stress	As for partial plant resistance; greater impact, but parasitoids smaller and less fecund	Ul-Haq (1997)
Reducing late leaf area by techniques such as termination of irrigation and early harvest	Greater impact at the stage of reducing the aphid population at the end of the crop season	
High plant density	Effects of plant ground cover? Larger numbers of anthocorids, syrphids and epigeal predators	Smith (1969, 1976); Powell *et al*. (1981)
Earlier sowing	As for plant resistance (increases with plant age); greater impact, but parasitoids smaller and less fecund, and poorer temporal synchronization with natural enemies	
Delayed sowing (especially for reduction of virus problems)	Better synchronization between natural enemies and aphids	van Emden (1966)
Hand removal of terminal shoots	Probably some partial resistance, therefore greater impact, but parasitoids smaller and less fecund	
Intercropping	Effects of plant ground cover? Larger numbers of anthocorids, syrphids and epigeal predators	Saljoqi *et al*. (2009)
Trap crops	May form sink for natural enemies and delay their movement to the commercial crop	Chapter 21, this volume
Removal of weed sources of virus	Unlikely to have a major effect?	
Crop isolation	Specific predators and parasitoids may be lacking or scarce in the new areas	
Reflective mulches	May affect colonizing natural enemies less than aphids, and thus increase natural enemy:aphid ratio	
Crop covers	Likely to exclude natural enemies as well as aphids, but any reaching the crop will remain confined over it	

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considers over ten crops with over 25 pest aphid species.

In order to make it easier to compare and contrast IPM in the case studies, each finishes with an 'executive summary', recapitulating the main points in a consistent order.

Each case study is written by a scientist working in a particular region of the world, mostly in developed agriculture. Thus, the case studies are both crop specific and, to a large extent, location specific, though often reference has been made to contrasts with other regions. This specificity to location is seen clearly in the active ingredients of the insecticides mentioned; products mentioned may well be banned or have been withdrawn in other regions of the world.

Conclusions from the Case Studies

For certain crops (e.g. potatoes, cucurbits and some berry crops where virus is the main problem), economic thresholds are probably not relevant, though they are available in cucurbits based on monitoring water traps. Otherwise, economic thresholds have been developed, although with variable uptake; increasingly, the abundance of the natural enemies is being included in the calculation. Insecticides clearly remain the mainstay of aphid control. However, in nearly all the scenarios, considerable emphasis is placed on selecting active ingredients so as to avoid damage to natural enemies as far as possible. This is very much 'stage one IPM', the 'Integrated Control' of Stern *et al*. (1959) (see earlier). Particularly in salad crops, brassicas, potato and cotton, the development of aphid resistance to insecticides is a constant challenge to this approach.

Examples of inundative biological control are very limited. Parasitoids are commercially available for release on salad crops and cucurbits in glasshouses, and are also released on some berry crops; control of *Eriosoma lanigerum* (woolly apple aphid) by *Aphelinus mali* on apples has been practised for very many years.

What we can regard as 'stage two IPM', where host-plant resistance and/or cultural control are key additions, is found in the sorghum, potato and berry scenarios. Greenbug control in sorghum, phylloxera control in grapes and aphid control in raspberries has for many years relied principally on plant resistance. Rouging of virus sources such as groundkeepers is important with potatoes and strip intercropping and early harvesting/termination of irrigation can contribute to control of aphids in cotton. Crop covers are used to reduce aphid immigration in salad crops, brassicas and cucurbits.

Supporting one control approach that is inadequate on its own with another can be said to represent 'stage 3 IPM', and clearly shows its potential against greenbug in sorghum and aphids in wheat. In the sorghum scenario from the USA, resistant varieties and biological control by indigenous natural enemies were not only together able to control greenbug in most years without the need for insecticides but also made the resistance less vulnerable to the selection of resistance-breaking greenbug biotypes. In wheat, agri-environmental schemes (including the provision of nectar sources) may reduce, or even eliminate, the need to use insecticides against aphids.

The case histories give no example of manipulating the behaviour of aphids and their natural enemies with semiochemicals, a 'stiletto' addition to the traditional IPM components of chemical, biological, varietal and cultural control. Such methods have huge potential and are currently being actively researched; perhaps their addition to future practice will constitute a 'stage 4 IPM'.

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24 IPM Case Studies: Grain

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Introduction

Today, aphids are major insect pests in many cereal-growing regions of the world. Damage results from direct feeding and honeydew production, as well as virus transmission. Although first descriptions of outbreaks date back to 1970, cereal aphids are still a focus of agricultural research and extension services to estimate damage potential, to develop forecasting and control models, to select partially selective IPM-compatible pesticides, to improve pesticide application methods and to elucidate and re-establish natural control by predators and/or parasitoids, in particular in programmes aimed at improving ecosystem services. In central Europe, mainly *Sitobion avenae*, *Rhopalosiphum padi* and *Metopolophium dirhodum* are the most important aphid pests of cereal crops, particularly winter wheat, and are therefore the focus of this chapter, although other worldwide important species will also be mentioned.

Basic Characteristics of the Main Aphid Species in Cereals (Species, Population Dynamics, Damage)

Cereal aphids of major importance in central Europe

Basic characteristics

Sitobion avenae (English grain aphid, Fig. 24.1a) is widespread and very common in Europe, the Mediterranean area, as well as in the Middle East, Central Asia, India, Africa and North, Central and South America. This species infests mainly the upper leaves, but moves to the ears as soon as they emerge. *Sitobion avenae* overwinters as an egg on winter cereals and wild grasses. Viviparous overwintering on young winter cereals and other Poaceae in field boundaries is common if winter conditions are mild. Four lineages differing in their strategy of reproduction have been identified (Dedryver *et al*., 1998): (i) clones without sexual morphs reproducing permanently anholocyclicly; (ii) androcyclic clones producing males but only viviparous females; (iii) cyclic parthenogenetic lineages capable of producing both sexes; and (iv) intermediate clones partly producing sexual morphs after a certain timespan.

Rhopalosiphum padi (bird cherry–oat aphid, Fig. 24.1b) is a cosmopolitan pest of wheat, oats and barley, especially in temperate regions. It is very common and widespread worldwide, and probably of Palaearctic origin. *Rhopalosiphum padi* overwinters as an egg on bird cherry, but occasionally also on other *Prunus* spp. On cereals, it tends to colonize those parts of its host where the temperature is lower and humidity higher. Viviparous overwintering on autumn-sown winter cereals and other Poaceae is common in mild winters. The same four types of lineages as in *S. avenae* (see above) have been described (Simon *et al*., 1996; Delmotte *et al*., 2003).

Metopolophium dirhodum (rose–grain aphid, Fig. 24.1c) is a widely distributed pest of many cereal crops, except in the tropics. In Europe, *M. dirhodum* is mostly holocyclic, with winter eggs on wild and cultivated roses. Overwintering viviparously is possible under mild winter conditions. Recent analysis of genetic diversity suggests the existence of multiple host races within *M. dirhodum* (Lopes-da-Silva and Vieira, 2007). Abundance in cereals is highly

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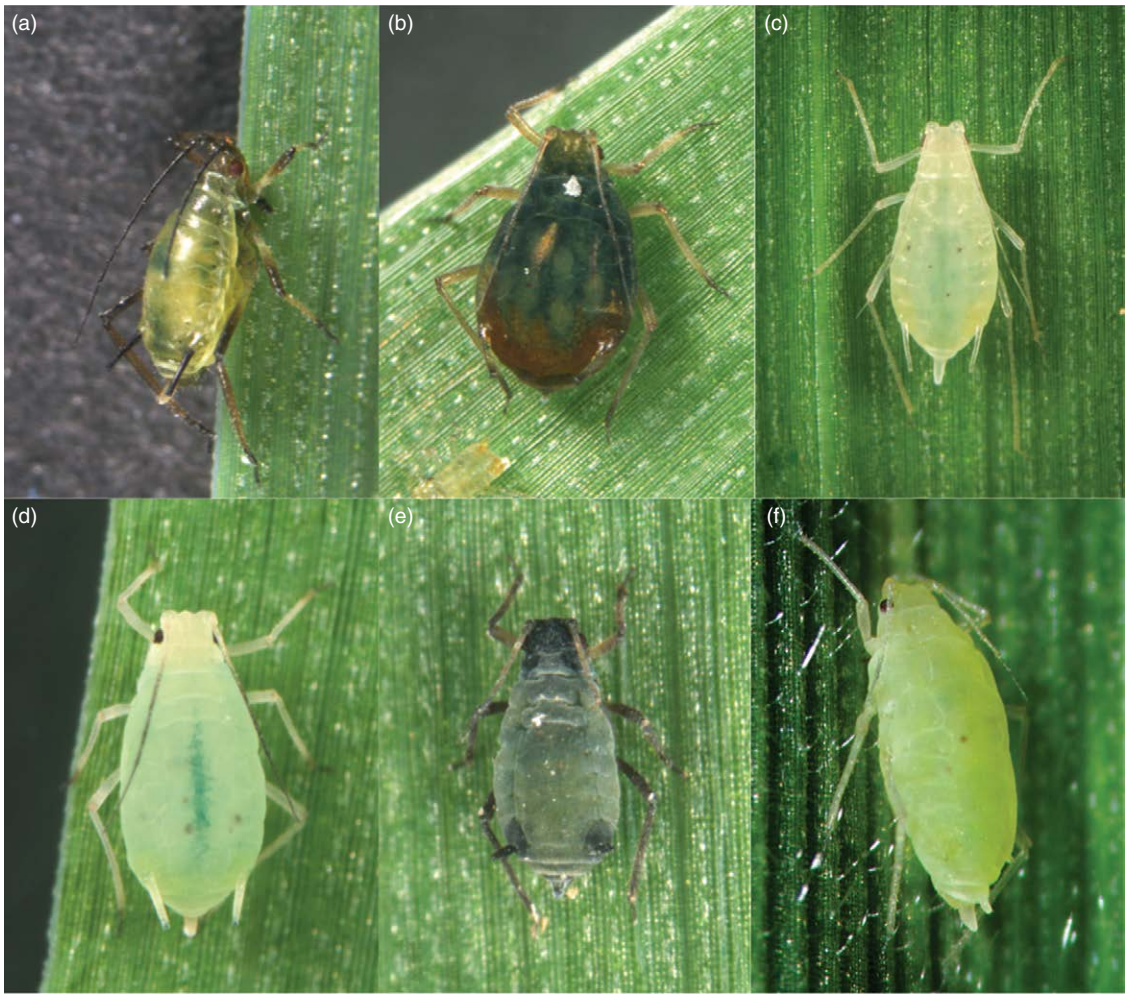

Fig. 24.1. Main species of cereal aphids: (a) *Sitobion avenae*; (b) *Rhopalosiphum padi*; (c) *Metopolophium dirhodum*; (d) *Schizaphis graminum*; (e) *Rhopalosipum maidis*; (f) *Diuraphis noxia*. (Photographs by T. Thieme.)

variable between years, sometimes alternating with *S. avenae*. In maize, *M. dirhodum* is often the most common and numerous species.

Population dynamics

Holocyclic clones of these species appear on cereals late in April, and can coexist with anholocylic clones in time and space. Analysis of patterns of holoyclic/anholocyclic clones across regional gradients in Europe (Dedryver *et al*., 2001) revealed a higher percentage of anholoyclic clones in the south, compared to northern areas; however, no clear east–west gradient, nor any clear relationship with preceding winter severity, was found. High populations are rarely reached before the end of May, corresponding to the start of heading in winter wheat. The three species can occur simultaneously and settle on the same plant, but usually not forming mixed colonies. Population build-up is correlated closely with the maturation of host plants, and reproduction is greatly reduced after the soft dough stage (BBCH growth stage 85 – Hack *et al*., 1992). The critical period for aphid infestations in spring and early summer is generally not longer than 6 weeks (Wratten *et al*., 1979; Freier and Wetzel, 1984; Rossing, 1991). Population density usually remains low until flowering;

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thereafter, there is often an exponential increase, which can vary widely between sites and years. After a short period of high density, the population rapidly crashes due to plant maturation, crowding and natural enemies. After this decline, cereal aphids reappear in autumn on newly sown winter barley and winter wheat. Early sowing and early emergence of the plants can lead to high infestation levels in autumn. Certain models of population dynamics have been based on modelling the movement and dispersal (uplift, dispersal flight and transportation, deposition and local movement; Parry, 2013; Ciss *et al*., 2014), winter survival or spring/summer population build-up (Gosselke *et al*., 2001; Hansen, 2006 Klueken *et al*. (2009) compared different models but see also Chapter 13, this volume).

Damage

DIRECT. Feeding on phloem sap reduces the transport of phloem compounds to the grains; moreover, the metabolism of the colonized host area can be affected by secreted proteolytic enzymes. Excretion of honeydew, which blocks the stomata and leads to the growth of sooty moulds, reduces the photosynthetic efficacy of the plants and is an additional reason for yield losses (Rossing, 1991). In addition, aphid infestations also spoil the baking quality of the grains (Oakley *et al*., 1993). Strong infestations can cause severe yield losses. The amount of damage depends on expected yield level, the aphid species, aphid number and site of attack. Leaf and stem attack, as dominating with *R. padi* or *M. dirhodum*, causes yield losses per aphid amounting to only about half as much as ear attack by *S. avenae* (Niehoff and Stäblein, 1998). Infestations during flowering are about twice as detrimental as during green ripeness or later (Wratten *et al*., 1979; Entwistle and Dixon, 1987; Möwes *et al*., 1997). Damage models use aphid peak density and/or the aphid index (i.e. number of aphids and days of infestation per tiller) to predict the impact on grain yields.

INDIRECT. Cereal aphids vector destructive plant viruses in cereals. The most serious are the group of *Barley yellow dwarf viruses* (BYDV - family Luteoviridae, Fig. 24.2), comprising BYDV-PAV, -MAV, -PAS, -kerII and -kerIII species of the genus *Luteovirus*, *Cereal yellow dwarf virus*-RPV (CYDV-RPV, formerly

Fig. 24.2. Typical symptoms of *Barley yellow dwarf virus*. (Photographs by T. Thieme.)

BYDV-RPV), -RPS and -RMV in the genus *Polerovirus*, as well as other BYDV viruses that have not yet been assigned to any genus (Wu *et al*., 2011). Moreover, it is impossible to separate BYDV and WDV (transmitted by leafhoppers) infections in the field because of similar symptoms (Schubert *et al*., 2013). BYDV infections result in plants unable to survive cold stress, with fewer ears, fewer grains per tiller and lower thousand grain weights; yield losses can be up to 62% (Riedell *et al*., 2003). Strong and frequent outbreaks of BYDV in Europe occur particularly in regions with mild Atlantic weather and anholocycly of the vectors. First infections of winter cereals occur during the autumn migration, and early disease incidence is related to the proportion of winged aphids, mostly *R. padi* and *S. avenae*, carrying the virus (Fabre *et al*., 2005). BYDV epidemiology depends largely on the weather conditions following aphid immigration. No functional relationship between aphid infestation and virus-related damage has yet been established, preventing the development of reliable aphid thresholds for BYDV infection.

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Cereal aphids of minor importance in central Europe

Rhopalosiphum maidis (corn leaf aphid, Fig. 24.1e) infests maize and various other cereals in warmer regions of the world, and is probably of Asian origin. The species is completely anholocyclic. Regular trapping (e.g. suction traps, yellow water traps) on spatial gradients has verified seasonal south–north migration in Europe. *Rhopalosiphum maidis* colonizes the stems and the upper surface of leaves of maize and sorghum, and occasionally barley and rye. The most severe damage on maize occurs when the aphid becomes extremely abundant within the protective sheath of the tassel; this affects pollination adversely and leads to the formation of incomplete ears. In addition, *R. maidis* is a vector of several persistent (e.g. *Barley yellow dwarf*, *Maize leaf fleck* and *Millet red leaf*) and non-persistent viruses (e.g. *Abaca mosaic*, *Maize dwarf mosaic* and *Sugarcane mosaic*).

Schizaphis graminum (greenbug, Fig. 24.1d) is a cosmopolitan pest attacking many cereal crops, including sorghum, and probably originated in the south of European Russia. Nowadays, it is widespread and very common in southern Europe, the Middle East, Asia, Africa and all the Americas. Greenbugs overwinter as eggs on grasses, and viviparously wherever winter conditions permit. Their feeding activity causes loss of assimilates, but also strong phytotoxic reactions; generally, plants are damaged heavily if infested before tillering. In addition to direct damage, the aphid can transmit *Barley yellow dwarf virus* (Gray and Gildow, 2003) and other viruses.

Diuraphis noxia (Russian wheat aphid, Fig. 24.1f), is of central Asian origin, but is now widespread in southern Europe (reaching Austria and southern Germany), central Asia, the Middle East, North Africa, South Africa, North America and Argentina. It is a significant pest of barley and winter wheat (Blackman and Eastop, 1984; Thieme *et al*., 2001; Anderson *et al*., 2003). *Diuraphis noxia* usually feeds at the base of the youngest leaves, and feeding induces physiological and morphological changes, leading to phytotoxic effects (Kazemi *et al*., 2001). Since 2003, a number of new biotypes have been discovered that cause damage to wheat cultivars with *D. noxia* resistance (Haley *et al*., 2004; Burd *et al*., 2006).

Monitoring and Control

Monitoring, forecasting and decision-making systems

Forecasting and decision-making should help avoid insurance spraying. Thresholds are different in autumn, winter/spring and summer. Autumn thresholds aim mainly to reduce the risk of BYDV infestation of young cereal plants by *R. padi* and *S. avenae*, winter/spring forecasting aims to calculate the probability of holo- and anholocyclic hibernation with the risk of BYDV spread in early spring, and summer monitoring should trigger the control of aphid population mass increase to avoid direct damage.

Autumn

Models forecasting BYDV risk in autumn cereals have been developed, in France for example (Fabre *et al*., 2003; Dedryver *et al*., 2010), consisting of decision support systems coupling population models of BYDV vectors with BYDV yield loss models. However, decision tools that are much simpler in practice are used; for instance, farmers are advised to assess locally the percentage of aphid-infested plants, and spraying is recommended at infestation levels of 10–15%.

Hibernation

Temperature-driven models based on the cold-hardiness of different aphid morphs provide prediction of hibernation types. Models such as SIMLAUS (Kleinhenz, 1994) can give a relatively precise prediction of the winter survival of *S. avenae* and/or *R. padi*. Spring migration models are expected to improve considerably the link between hibernation models and summer population simulation in future.

Summer/mass development

Simulation models such as GETLAUS (Gosselke *et al*., 2001) exist for imaging the mass propagation of aphids in the summer period (May–July), but their reliability for control decisions is not always convincing, particularly if early decisions are desired. Hence, decision making in practice still relies on 'simple' threshold models based on determination of local aphid infestation levels ('scouting') at fixed crop stages. In most models, monitoring should start

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at ear emergence, and between BBCH 59 and 61 is the suitable period for decision making, in Germany for example (Basedow *et al*., 1994), but earlier decision making can be required in milder climates such as the UK (Oakley and Walters, 1994). Several field experiments, in Germany for example, came to more or less identical action thresholds; namely, three to five aphids either per ear and flag leaf, similar to between 60 and 70% ears infested. This is quite similar to the UK threshold of 50% infested tillers before BBCH 61, or 66% after BBCH 61. Action thresholds assume that aphid densities are likely to reach the economic threshold level in the following 1–3 weeks. More flexible thresholds include the prevalence of natural enemies (e.g. Rappaport and Freier, 2001); however, the high workload these thresholds involve makes such approaches less acceptable to farmers.

Chemical control and pesticide resistance

Chemical control is still the main control option, even in IPM strategies. In the EU, several efficient insecticides are registered for the control of cereal aphids, either as BYDV vectors or to control their direct damage. Most commonly used are different pyrethroids, the carbamate pirimicarb and organophosphates for spraying and neonicotinoids as a seed treatment. Of major concern are the possible side effects of spray drift or dust when sowing insecticide-treated seed on non-target organisms in adjacent areas, since large areas of cereals can be treated simultaneously. However, the more stringent demands of EU pesticide regulation have selected progressively for safer compounds and application techniques, but have also led to a paucity in modes of action. The principles of the good agricultural practice codex offer suitable guidelines for IPM-compatible treatments. Moreover, improved technical standards of spray application and seed treatment equipment can reduce considerably the risk of side effects to non-target organisms and contamination of no-crop areas.

Since cereal aphid infestations occur over large areas, there is a risk of the selection of resistant aphid genotypes. The first cases of resistance have been reported for *R. padi* in Europe and Asia (Chen *et al*., 2007), and recently for *S. avenae* in the UK (Foster *et al*., 2014), Belgium and Germany (T. Thieme, unpublished). The progressive selection of *S. avenae* with pyrethroid resistance needs to be countered with improved insecticide management according to IRAC guidelines (see http://www.irac-online.org/).

Biological control

Natural enemies

Cereal aphids are attacked by a large number of natural enemies, which consist mostly of entomopathogenic fungi, non-specific predators (e.g. carabids, staphylinids, spiders, chrysopids), more or less specific predators like syrphids and coccinellids and different species of parasitoids.

The efficacy of entomopathogenic fungi (Entomophthorales) very much depends on weather conditions and host density. In moist and warm periods and in dense aphid populations, they can cause epizootics, and most often contribute to the late crash of aphid populations (Dedryver, 1982; Ardisson *et al*., 1997).

The efficacy of predators and parasitoids can be high, but varies between years and locations resulting from species-specific habitat preferences and the degree of synchronization in time and space with aphids and intraguild effects. Exclusion studies have revealed that the guild of aerial natural enemies (e.g. syrphids, coccinellids, parasitoids) contributes more to aphid control than do the epigeal predators (carabids, spiders) (see Plantegenest *et al*., 2001; Schmidt *et al*., 2003; Holland *et al*., 2008, 2012). Epigeal predators, however, can be quite valuable, because they often forage early in the season in the developing crop stand and encounter hibernating or immigrating aphids or those falling from the plants as a result of abiotic events (wind, rain). They can reduce initial infestation, but in the longer term only retard population build-up (Ekbom *et al*., 1992; Winder *et al*., 1994, 2005; Holland and Thomas, 1997; Lang, 2003; Östman *et al*., 2003; Madsen *et al*., 2004).

The more specialized and mobile aerial antagonists arrive in the crop later, but can show efficient numerical and functional responses. There is considerable inconsistency in how the role of parasitoids is viewed in the literature, and the relative importance of parasitoids as compared to vegetation-dwelling predators differs greatly in different parts of Europe. High parasitization rates during an early stage of the aphid infestation can cause a substantial impact (Sigsgaard, 2002; Schmidt *et al*., 2003; Thies *et al*., 2003); however, in seasons with bad synchronization of parasitoid occurrence and

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aphid immigration and high rates of hyperparasitization (Höller *et al*., 1993; Sigsgaard, 2002; Holland *et al*., 2012), parasitoids have little impact. Their limited mobility, as well as their complex nutritional requirements and high specialization, makes parasitoids sensitive to many environmental factors. High habitat diversity at a small spatial scale seems to favour parasitoids more than mobile aerial predators, which are more affected by the large-scale attributes of the surrounding landscape (Tscharntke *et al*., 2007; Thies *et al*., 2011).

Aphid-specific predators, especially syrphids and coccinellids, are often closely synchronized in time and space with cereal aphids, and because of excellent prey exploration abilities and numerical and functional responses, they can reduce aphid population increase greatly (Chambers and Adams, 1986; Hemptinne *et al*., 1992; Tenhumberg, 1995; Tenhumberg and Poehling, 1995; Elliott *et al*., 2000; Scholz and Poehling, 2000; Freier *et al*., 2001; Almohamad *et al*., 2009).

However, despite a huge body of data, a proper and reliable forecasting of the efficacy of these predator guilds still remains unsatisfactory.

Biocontrol approaches

The classical biocontrol approach with inundative releases of natural enemies in cereals has been limited to a few attempts, such as the release of parasitoids (Levie *et al*., 2005). All have proved uneconomical. The biological strategy of choice in the complex cereal ecosystem is 'conservation biocontrol'; that is, aiming to stabilize or improve the naturally available regulation potential of aphid antagonists. Under the headlines of 'habitat manipulation', 'ecological engineering', 'functional biodiversity', or agri-environmetal schemes', several practical guidelines have been published (Kleijn and Sunderland, 2003; Boller *et al*., 2004; Gurr *et al*., 2004; Kleijn *et al*., 2006; Holland *et al*., 2008, 2012; Jonsson *et al*., 2008). Most such agri-environment measures focus on habitat management techniques at different scales to increase predator and parasitoid densities in the cereal ecosystem. On the crop scale, for instance, organic systems with reduced weed control and tillage can favour ground-dwelling predators (Moreby *et al*., 1994; Baguette and Hance, 1997; Andersen and Eltun, 2000). At the farm and landscape level, semi-natural refuges such as grass strips ('beetle banks') or flower-rich strips within fields or as crop boundaries (Fig. 24.3) can provide attractive habitats with food resources or hibernation sites and promote diversity of predators and parasitoids (Nentwig, 1992; Dennis *et al*., 1994; Lys *et al*., 1994; Hickman and Wratten, 1996; Frank, 1999; Landis *et al*., 2000; Collins *et al*., 2002; Lemke and Poehling, 2002; Boller *et al*., 2004; Tylianakis *et al*., 2004; Rossing *et al*., 2006; Holland *et al*., 2008, 2012; Haaland *et al*., 2011; Thies *et al*., 2011; Laubertie *et al*., 2012).

Recent studies, from many sites across Europe and including comparisons at small and larger spatial scales such as the landscape level, clearly demonstrate the importance of regional diversity for conservation biocontrol of cereal aphids (Östman *et al*., 2001; Thies *et al*., 2005; Tscharntke *et al*., 2005; Haenke *et al*., 2009). These studies show that species groups in different natural enemy communities vary, and identify a need to consider region-specific landscape management (Thies *et al*., 2011). Obviously, complex landscapes are better buffered against fluctuations in natural enemy efficacy and provide better conditions for long-term conservation biocontrol in cereals.

Cultural control

Options for cultural control of cereal aphids are limited. Reducing the proportion of winter cereals in the rotation is an option, but is not economically realistic. Later sowing of winter cereals can be effective, strongly reducing the establishment of aphid populations as vectors of BYDV. A rule of thumb is that winter cereals sown later than 20 September in central Europe are safe from intensive aphid colonization and virus spread (Dedryver *et al*., 2010).

Various studies indicate a strong positive relationship between nitrogen fertilization and aphid development. High amounts of nitrogen can escalate the intrinsic rate of increase of cereal aphids (Hanisch, 1980; Honěk, 1991; Hasken and Poehling, 1995; Gash *et al*., 1996; Duffield *et al*., 1997). Hence, limiting nitrogen fertilization to moderate levels can lower aphid densities.

Host-plant resistance

Some success has been achieved in breeding for aphid resistance in cereals, but until now more for *S. graminum* and *D. noxia* than for *R. padi* or *S. avenae*. Resistance to these species is typical partial (horizontal) resistance, with only reduced growth rates of populations (Dewar, 1977), a prolonged

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Fig. 24.3. Flower strips, Lower Saxony, Germany. Top: flower strips in cereal fields, containing different annual and perennial typical wild flowers of field boundaries (June); bottom left: same strip later in the season (July); bottom right: detailed view. (Photographs courtesy of A. Lemke.)

developmental period to adulthood, or both these traits. Potential sources of host-plant resistance to *R. padi* have been found in rye (Hesler, 2005; Hesler and Tharp, 2005; Hesler *et al*., 2007), rye-derived wheat lines and triticale. The potential for *R. padi* resistance was also identified in seedlings of *Thinopyrum elongatum*, *Thinopyrum intermedium*, *Elmus repens* and *Leymus angustus* and its wheat hybrids (Tremblay *et al*., 1989); however, so far no resistance genes have been identified properly or introgressed into elite wheat cultivars (Porter *et al*., 2009).

Variation in resistance to *S. avenae* has been found in diploid wheat relatives such as *Triticum monococcum* (Einkorn), *Triticum monococcum* subsp. *aegilopoides*, *Triticum dicoccoides*, *Triticum timopheevii* and *Triticum urartu* (Migui and Lamb,

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2003, 2004; Di Pietro *et al*., 1998), and also in winter wheat (Havličková, 1993), as well as in the durum wheat line C273 (Liu *et al*., 2011), but these sources of resistance have not yet been exploited in practice.

Conclusions

Aphids are still the most important pests of cereal crops in central Europe. Research has provided very detailed knowledge on the biology and interactions with host plants and natural enemies. The ecology of aphid antagonists has been widely researched; in particular, the importance of small- as well as large-scale habitat diversity for the efficacy of antagonists has been evaluated by many basic studies across Europe. As a consequence, the emphasis for sustainable control strategies for cereal aphids is on conservation biocontrol and the improvement of natural regulation, and the aim is to achieve implementation by specific agri-environmental schemes in different European regions. However in practical agriculture, cereal aphid control is still widely performed with synthetic pesticides, which is highly economic and can be based on relatively simple but reliable threshold systems. An important requirement, however, is prudent management of impending pesticide resistance.

Executive Summary

The chemical control of cereal aphids is still a viable option, and recommended simple economic thresholds for cereal aphids are available and accepted by farmers, because of their reliability. Less used are monitoring protocols that also involve some estimate of the abundance of natural enemies. Sophisticated forecasting systems based on population and migration modelling are being developed to warn farmers.

The release of natural enemies is not practised and, instead, the biological control emphasis is increasingly on conserving indigenous natural enemies by using softer insecticides and habitat manipulations, such as improving small- and large-scale biodiversity, providing refuge areas and alternative host/prey habitats for natural enemies. Indeed, agri-environmetal schemes may greatly reduce, or even eliminate, the need for insecticide application in the future. Financial incentives to support biodiversity, such as set-aside and country stewardship schemes in Europe, have made the provision of such refuges acceptable to farmers.

Although the greenbug and Russian wheat aphid are managed largely through resistant varieties, plant resistance is not deployed against other cereal aphids, since it has proved to be only partial. More promising sources of resistance found in ancient wheats and some grasses have not yet been exploited.

Cultural control is limited to the late sowing of winter cereals and avoiding excessive nitrogen fertilization.

There is no manipulation of the behaviour of aphids/natural enemies with semiochemicals.

The only implemented interaction between biological and chemical control methods is to seek selectivity in the choice of pesticides and the timing of application.

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25 IPM Case Studies: Sorghum

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Introduction

Sorghum, *Sorghum bicolor* (Fig. 25.1), is a cultivated grass species also known as great millet, Guinea corn, Kafir corn and milo. Native to North Africa, it is cultivated throughout tropical, subtropical and warm temperate regions. There are generally two types of sorghum, forage varieties and grain varieties. Both are grown mostly for animal feed and, more recently, for biofuel. In developing countries, grain varieties are grown for human consumption. Worldwide, 45.6 million ha of sorghum were harvested in 2014 (FAOSTAT, 2016).

There are four aphid species that commonly attack sorghum: *Schizaphis graminum* (greenbug), *Rhopalosiphum maidis* (corn leaf aphid), *Melanaphis sacchari* (sugarcane aphid) and *Sipha flava* (yellow sugarcane aphid) (Fig. 25.2). Beginning in the late 1960s, the greenbug became the key aphid pest of sorghum on the High Plains, USA (Young and Teetes, 1977), although damage receded significantly after 2000. In 2013, an apparently novel strain of *M. sacchari* began developing large populations on sorghum in Mexico, Texas and southern Oklahoma, reaching epidemic status on the High Plains by 2015 and becoming the primary aphid pest. Feeding by *S. graminum* causes severe chlorosis on sorghum foliage, and uncontrolled colonies will reduce grain yield and even kill plants. Feeding by *M. sacchari* produces similar damage (Fig. 25.3), but requires more aphids feeding for a longer period. Whereas greenbugs do not feed past flowering, *M. sacchari* can feed through the seed-filling stage, reducing grain quality, fouling panicles with honeydew and mould and causing physical problems with harvesting.

History of *Schizaphis graminum* on Sorghum

The greenbug first attracted attention in Bologna, Italy, in 1852 when large clouds of alates descended on the city in numbers sufficient to cause a public nuisance (Hunter, 1909). At the time, the primary host plants were thought to be grasses in pastures and meadows, but subsequent damage to maize, sorghum and other small grains was reported from northern Italy and Hungary in the 1880s (Hunter, 1909). However, it was not until the 1960s that significant economic damage to sorghum was again reported in Europe (Barbulescu, 1964) and South Africa (Matthee, 1962). On the High Plains of the USA, *S. graminum* had been a serious problem of wheat since the late 1880s (Hunter, 1909), but only began causing significant and widespread damage to sorghum in 1968 (USDA, 1968). Over 400,000 ha of sorghum were infested in Kansas in 1968, and the pest destroyed over 100,000 ha of the crop (Harvey and Hackerott, 1969). This sorghum-damaging greenbug was designated 'biotype C', based on its ability to damage 'Piper' Sudan grass (*Sorghum* × *drummondii*). Leaf feeding causes chlorotic lesions that can reduce yield and kill plants, and flower feeding can cause sterility and blasted heads (Fig. 25.4).

By 1981, the greenbug was estimated to cause 2.5% annual grain loss in sorghum, ranking it second only to sorghum midge, *Contarinia sorghicola*, as the most damaging insect pest of the crop in the USA (USDA, 1981). As late as 1992, almost one-third of the sorghum acreage in the USA was treated with insecticides to control greenbugs (Webster *et al*., 1995). More recent data from the six primary sorghum-producing states, however, indicated that only 6% of the sorghum acreage received insecticide

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Fig. 25.1. Healthy, maturing heads of grain sorghum.

treatment for any pest in 2011 (National Agricultural Statistics Service, 2011). The target of most applications in southern regions is sorghum midge, whereas to the north it is a complex of lepidopteran larvae that feed on ripening grain, collectively called 'headworms' by farmers (primarily *Helicoverpa zea* and *Spodoptera frugiperda*). The scale of greenbug problems on sorghum has diminished so dramatically since the turn of the century that rigorous screening of new sorghum varieties for greenbug resistance has been largely abandoned. Although the reasons for this decline remain uncertain, multiple factors, cultural, environmental and biological, appear implicated.

Greenbug Management Practices

Broadcast insecticide applications are typically the first response of farmers seeking to protect their crop from a new pest. The extent to which initial reliance on chemical controls impeded the establishment of natural biological control of greenbugs in sorghum fields cannot be determined in retrospect, but must have been considerable given the level of control currently provided by the natural enemy complex. Fortunately, the development of commercial varieties with resistance to greenbug quickly became a research priority and, once released, these varieties facilitated higher treatment thresholds and reduced application frequencies, although 'rescue' treatments with insecticides continued to be relied upon for decades.

Chemical control

Initially, foliar formulations of organophosphates, carbamates, and even one organochlorine (endrin), gave excellent control of greenbugs (DePew, 1971; Cate *et al*., 1973). Soil-applied granules of systemic materials such as disulfoton and carbofuran also provided control, and increased yields under greenbug pressure (DePew, 1974). Within a few years, however, greenbugs evolved resistance to organophosphates, specifically disulfoton (Peters *et al*., 1975; Teetes *et al*., 1975). New organophosphates and carbamates soon became available, and chlorpyrifos emerged as the

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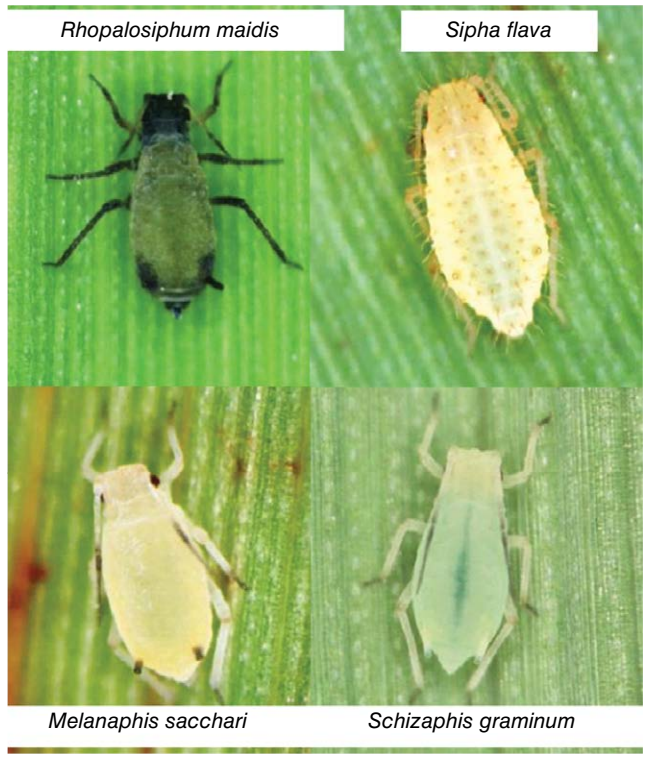

Fig. 25.2. The four aphid species regularly occurring on sorghum. (Photograph courtesy of R.T. Villanueva.)

Fig. 25.3. Unsprayed block of sorghum showing chlorosis due to feeding by *Melanaphis sacchari*.

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Fig. 25.4. Flower sterility caused from greenbug feeding results in blasted grain. Note chlorotic lesions on pannicle sheath. (Photograph courtesy of J.P. Michaud.)

chemical of choice in the 1980s. Resistance to chlorpyrifos soon evolved as well (Niemczyk and Moser, 1982; Sloderbeck *et al*., 1991), although there was substantial variation among greenbug genotypes in levels of insecticide resistance (Shufran *et al*., 1996, 1997a,b; Rider *et al*., 1998). The most prevalent strain appeared to lack the reproductive disadvantages often associated with insecticide resistance (Shufran *et al*., 1997b; Stone *et al*., 2000). Combinations of chlorpyrifos and malathion were recommended to improve control when resistant greenbugs were present (Archer *et al*., 1999). However, Buschman and DePew (1990) showed that organophoshate mixtures (e.g. chlorpyrifos + parathion) sprayed for greenbug control on sorghum could cause outbreaks of Banks grass mite, *Oligonychus pratensis*. Outbreaks of spider mites, *Tetranychus urticae*, are also associated with insecticide use in sorghum, probably because their primary natural enemies, predatory mites and thrips, are negatively affected by many insecticide treatments.

Since 2000, the treatment of seed with systemic neonicotinoid insecticides (e.g. imidacloprid and thiamethoxam) has become a ubiquitous practice in the production of sorghum and most other row crops on the High Plains. These factory-applied treatments provide emerging seedlings with 2–3 weeks of protection from damage by seedling pests. However, the regional decline in greenbug populations was already well under way before the use of seed treatments became widespread, and greenbugs rarely establish on seedlings in most regions of the High Plains because nascent colonies lack sufficient shelter from the elements.

Host-plant resistance

The breeding of greenbug-resistant sorghum hybrids began shortly after the advent of biotype C (Hackerott *et al*., 1969; Wood, 1971; Teetes and Johnson, 1974), and the first lines became commercially available in 1976 (Morgan *et al*., 1980). However, greenbug resistance in sorghum, as in wheat, has been based primarily on antibiotic traits that impede greenbug feeding, and consequently aphid growth and reproductive rate. The evolution of biotypes immune to particular resistance traits has occurred repeatedly (Puterka and Peters, 1995), resulting in the designation of greenbug biotypes E (Hackerott *et al*., 1983), I (Harvey *et al*., 1991; Bowling *et al*., 1994) and K (Harvey *et al*., 1997), which successively overcame resistance traits effective against all biotypes preceding them (intervening letters were used to designate biotypes virulent to wheat resistance traits or resistant to insecticides). However, biotype K never displaced biotype I (Kindler *et al*., 2001), and has not been found in any greenbug samples from sorghum in central Kansas since 2002, based on reactions to the discriminant line PI 550610 (J.P. Michaud, unpublished). The disappearance of biotype K coincided with area-wide decline in greenbug populations overall, so it could be inferred that virulent biotypes ceased to evolve when antibiotic traits were adequately supported by biological control. There are likely fewer rare mutation events when natural enemies hold aphids at low densities and 'top-down' mortality becomes a stronger selective force on the population than 'bottom-up' plant defences.

High temperatures have been observed to interact with some resistance traits to exacerbate developmental delay and fecundity reduction of greenbugs on resistant hybrids compared to the values observed on the same hybrids at lower temperatures (Harvey *et al*., 1994; Thindwa and Teetes, 1994). High temperatures alone can be a significant impediment to

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greenbug establishment prior to canopy closure. In the 1980s, Dharmaratne *et al*. (1986) carried out a survey and economic analysis on the use of resistant hybrids and insecticides to control greenbugs over 5 years of sorghum production in the Texas Blacklands; the results suggested that farmers were better off planting resistant hybrids and foregoing insecticide treatments entirely.

Research continues to develop new sources of greenbug resistance in sorghum cultivars (Wilde and Tuinstra, 2000; Kofoid and Harvey, 2005; Kofoid *et al*., 2012). Antibiosis, antixenosis and tolerance mechanisms have all been identified, and many resistant lines express combinations thereof (Bowling and Wilde, 1996; Dogramaci *et al*., 2007). It has been argued that tolerance mechanisms should be prioritized in breeding programmes (e.g. Reese *et al*., 1994), because they are not expected to result in selection for new virulent biotypes. However, tolerance is usually measured only in relative terms in greenhouse 'flat' tests (some cultivars survive and yield better than others, despite similar aphid loads) that do not control properly for antibiotic effects. Given the large numbers of genes determining plant compensatory productivity, and their likely independent interactions with environmental conditions, tolerance is more a property of phenotype than genotype, and thus probably not a valid breeding objective. Although antibiotic traits provide only partial resistance, they can usually be linked to specific genes that can then be moved into agronomically desirable lines (Burd and Puterka, 2009).

Rice and Wilde (1989) observed that *Hippodamia convergens* fed greenbugs reared on antibiotic sorghum showed slightly delayed development and reduced pupal survival, although these effects probably had little impact on field populations of this important aphid predator. Similarly, Figueira *et al*. (2005) concluded that greenbugs reared on resistant sorghum genotypes were suitable as food for *H. convergens* in Brazil, despite a slight negative impact on larval weight gain. In a laboratory study, Dogramaci *et al*. (2005) showed that the parasitoid *Lysiphlebus testaceipes* was more effective at controlling greenbugs on resistant sorghum hybrids than on susceptible ones, confirming earlier work by Starks *et al*. (1972). In fact, resistance traits that slow greenbug development and reproduction are more likely to synergize than impede the efficacy of biological control. The timely arrival of natural enemies in the sorghum crop is critical, and must occur before aphid colonies achieve exponential growth, otherwise biological control will fail. By delaying the growth rate of aphid colonies, antibiotic resistance serves to extend the period during which natural enemies can prevent greenbugs from either establishing colonies or exceeding their economic threshold.

Biological control

The important role of predators and parasitoids in regulating greenbug populations was recognized in wheat long before sorghum was infested (Hunter, 1909). Initial efforts to improve biological control in sorghum were largely misguided attempts to introduce and establish exotic parasitoids and predators, despite the presence of a multitude of congeneric, locally adapted species with more than 100 years of history feeding on this pest (Jackson *et al*., 1971; Cartwright *et al*., 1977; Gilstrap *et al*., 1984; Michels and Bateman, 1986). Earlier, Fenton and Dahms (1951) had attempted inundative releases of *H. convergens* against greenbug in wheat, with poor results. Ironically, this coccinellid is the key greenbug predator in the central High Plains, but 'mail order' *H. convergens* are usually collected from overwintering aggregations in the Sierra Nevada mountains of California. These beetles are now known to have strong post-hibernation dispersal tendencies (e.g. Dreistadt and Flint, 1996), low fecundity (Bjornson, 2008) and almost certainly lack the specialized adaptations needed to cope with the severe climatic conditions prevailing on the High Plains (Michaud and Qureshi, 2006; Michaud, 2012). There is also the attendant risk of distributing parasitoids and diseases. Despite the sometimes significant role of naturally occurring entomopathogenic fungi in suppressing aphid populations under humid conditions (Pell *et al*., 2001; Chapter 11, this volume), these contribute no apparent greenbug mortality, as they do not become epizootic under the generally arid conditions prevailing on the High Plains.

Between 2000 and 2015, very few fields of wheat or sorghum in Kansas required treatment for greenbug, largely due to effective natural biological control. Working in Arkansas and Kansas, Kring *et al*. (1985) and Rice and Wilde (1988) demonstrated convincingly that early season suppression of greenbug on sorghum was provided by indigenous coccinellids (*H. convergens*, *Hippodamia sinuata*, *Coleomegilla maculata* and *Scymnus* spp.), the first

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species being of primary importance. The most abundant parasitoid, *L. testaceipes*, had little impact in these field experiments, typically appearing late in the season. In contrast, work in Oklahoma has indicated much greater parasitoid impact on greenbugs, especially in wheat, to the point where IPM decisions for greenbug include counts of mummified aphids (Elliott *et al*., 2004). It is now understood that neither the greenbug nor its parasitoid can overwinter much further north than the Kansas–Oklahoma border, whereas to the south, both the greenbug and its parasitoid can remain active on wheat throughout the winter (Jones *et al*., 2007). The parasitoid is able to remain active attacking its host at temperatures below the aphid's threshold for reproduction, thus gaining an early advantage on the aphids in spring. Harvey *et al*. (1982) documented two annual peaks of alate greenbug activity in Kansas, roughly coinciding with greenbug population peaks on wheat and sorghum at lower latitudes. Because both the greenbug and its parasitoid must migrate annually to colonize northern regions, the impact of the parasitoid is much lower at higher latitudes. Most native coccinellid species, by contrast, have excellent cold tolerance, and overwinter successfully throughout the entire summer range of the greenbug.

There is convincing evidence that biocontrol of greenbugs by predaceous coccinellids on the High Plains is enhanced when *R. maidis* infests sorghum early in the growing season. Kring and Gilstrap (1986) noted that corn leaf aphids served to retain *Hippodamia* spp. in sorghum, and Michels and Behle (1992) found that greenbugs did not reach economic thresholds in 2 years when corn leaf aphids were present early in the season, but severely damaged sorghum in the year that *R. maidis* populations failed to develop. Field data obtained from 31 irrigated and dry land sorghum fields in the Texas panhandle from 1988 to 2000 showed that peak greenbug density did not reach damaging levels provided that corn leaf aphid densities reached 100 or more per plant prior to sorghum reaching the boot stage (G.J. Michels, unpublished; Fig. 25.5). Peak coccinellid density was correlated significantly with corn leaf aphid density rather than greenbug

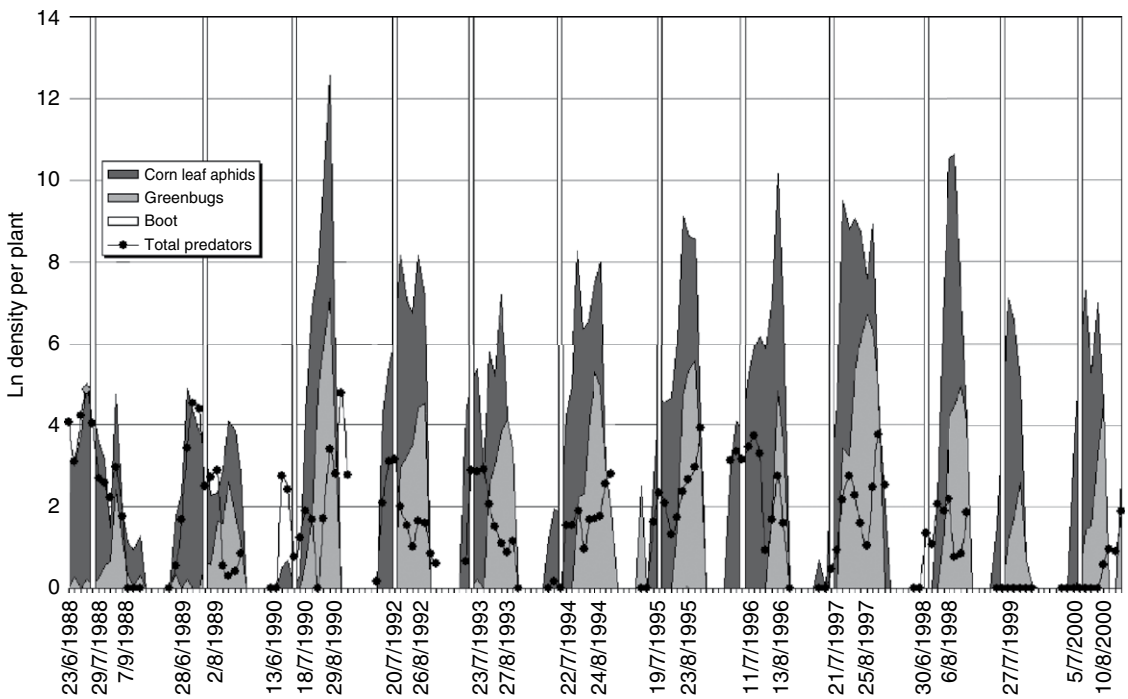

Fig. 25.5. Seasonal periodicity of corn leaf aphids (*Rhopalosiphum maidis*), greenbugs (*Schizaphis graminum*) and predaceous coccinellids in irrigated grain sorghum from 1988–1990 and 1992–2000, Texas Agricultural Experiment Station, Bushland, Texas.

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density. Corn leaf aphids do not cause economic damage to sorghum in vegetative stages, even in large numbers, and controlling them does not increase yield (Wilde and Ohiagu, 1976). Thus, their net agricultural impact in whorl-stage sorghum is beneficial, as they serve to support a complete generation of aphid natural enemies prior to the arrival of greenbugs on the crop. However, later flights of *R. maidis* can compound problems with more damaging aphid species, especially if they enter heads, although this is rare. It is also likely that the virtually complete adoption of Bt maize since 2005 has improved this crop as a source of corn leaf aphids to infest later-planted sorghum, since Bt maize requires few, if any, insecticide treatments. Consequently, outreach efforts emphasize the importance of distinguishing *R. maidis* from *S. graminum* to ensure farmers avoid misguided insecticide applications that could disrupt biological control.

Cultural control

Like most crop-feeding insects, greenbugs and other aphids respond to plant condition and agronomic practices. Aphids are usually nitrogen limited (Dixon, 2000), and Schweissing and Wilde (1979) observed that greenbug densities were higher on plants that received N than on those that did not. Archer *et al.* (1982) noted that greenbugs responded positively to increasing N (up to 225 kg N/ha) and the increase in plant biomass was accompanied by increasing damage. It was concluded that higher rates of N should not be used to try and raise sorghum tolerance to greenbug infestation.

Harvey and Thompson (1988) reported that greenbug populations were reduced when sorghum was sown at higher densities, and Burton *et al.* (1987) demonstrated decreased greenbug populations and reduced plant damage under reduced tillage that increased plant residues on the soil surface. A similar effect has been observed in wheat and appears to result from crop residues functioning as a reflective mulch that reduces the sharp contrast between green plants and bare soil, thus reducing the landing rate of alate aphids (e.g. Burton and Krenzer, 1985). For example, Burton *et al.* (1990) found that greenbug densities on a resistant hybrid were lower in no-till plots compared with those tilled conventionally. The widespread adoption of no-till practices on the central Great Plains over the past 15 years has been driven primarily by the benefits of moisture conservation and improved 'soil health', but has probably had area-wide impacts on greenbug ecology. Drought stress serves to lower the economic injury level for greenbug in sorghum because it reduces the plant's ability to compensate for damage (Kindler and Staples, 1981). However, Michels and Undersander (1986) demonstrated that greenbug reproduction was influenced negatively when water potential in sorghum fell below –0.3 MPa. In a 3-year study comparing the effects on greenbug of plant populations and irrigation regimes, Michels *et al.* (2002) found that peak densities of the aphid were highest in well-watered fields with low plant populations, and significantly lower in well-watered fields with high plant populations. These results indicated that low plant populations coupled with heavy irrigation created more greenbug problems than higher plant populations with moderate amounts of irrigation. High summer temperatures are often a limiting factor for greenbug colonies, since reproduction is diminished significantly when thermal maxima exceed 23°C (Pendleton *et al.*, 2009). Until recently, much of the sorghum grown in the southern plains was irrigated by flooding the furrows between the plants, a practice that created a cool microclimate underneath the canopy and around the lower leaves, the preferred location for greenbug establishment (Fig. 25.6). Overexploitation of the Ogallala aquifer, the primary underground reservoir of the central High Plains (Colaizzi *et al.*, 2008), has reduced flow rates from many wells in recent years. This has resulted in reduced irrigated sorghum acreage in the panhandle regions of Texas and Oklahoma and has driven widespread conversions to more efficient irrigation methods. The use of drip lines and drop nozzles has improved water-use efficiency by reducing evaporative loss, with attendant reduction in the microclimatic effects that favour greenbug colony establishment. Lower greenbug populations in these regions correlate with reduced numbers of migrant alates colonizing later-planted sorghum in more northerly latitudes, much of which is rain fed.

The Big Picture

It must be emphasized that the analysis presented here applies specifically to greenbugs and other aphids on sorghum in the southern and central Great Plains. The unique geography and climate of this region combine to generate a virtual superhighway of insect migration during summer months. The repeated convergence of cold, dry air masses

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Fig. 25.6. For many years, flood irrigation was widespread in southern latitudes, a practice that lowered subcanopy temperatures in sorghum fields, benefitting the establishment and growth of greenbug colonies.

from the north with warm, moist air masses from the Gulf of Mexico generates the 'low-level jet' – a strong, southerly wind flow that carries overwintered aphids (and many other pests) from subtropical regions northward with seasonal regularity. The combination of winter cold with generally sparse and ephemeral snow cover largely precludes the winter survival of the greenbug in the northern half of its range, and limits the impact of *L. testaceipes* north of the Oklahoma border with Kansas. Even moderate levels of greenbug resistance in sorghum cultivars improve the efficacy of biological control agents by slowing aphid development and diminishing their reproductive rate. The most important predator of greenbugs is probably *H. convergens*, populations of which appear highly adapted to local conditions throughout the High Plains; they are very drought tolerant compared to other coccinellid species (J.P. Michaud, unpublished) and are able to survive severe weather conditions by virtue of reproductive diapause in summer and hibernation in winter (Michaud and Qureshi, 2006). The recent invasion of *M. sacchari* creates new challenges for sorghum pest management; although unable to overwinter as far north as the greenbug, it can also colonize Johnson grass, *Sorghum halepense*, a ubiquitous subtropical weed. Fortuitously, many existing commercial hybrids appear to express considerable levels of resistance against *M. sacchari*. (Armstrong *et al*., 2015; Bayoumy *et al*., 2016): the aphid attracts virtually all key natural enemies present in the region (Colares *et al*., 2015a) and is a generally suitable prey item once consumed (Colares *et al*., 2015b).

Conclusions

After 30 years of causing serious economic losses to sorghum on the High Plains, greenbug problems have diminished to the point where they rarely require treatment. The degree to which improved IPM strategies have contributed to lower populations is unclear, but area-wide phenomena require explanations based on area-wide processes. Contributing factors probably include the planting of resistant varieties, the use of seed treatments to

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protect seedlings, and better farmer education with respect to the dynamics of natural enemies. However, even taken together, these are probably insufficient to explain the regional demise of large greenbug populations. Effective management clearly rests on a foundation of biological control contributed mostly by coccinellid and lacewing predators, with variable contributions from *L. testaceipes*, raising the question: Why did these indigenous species require 30 years to achieve their biocontrol potential? Many agronomic practices with the potential to affect greenbug populations have also changed over this period. These include the adoption of no-till and reduced tillage systems, the advent of Bt maize that favours higher populations of corn leaf aphid earlier in the season, and the reduction of acreage under flood irrigation. It seems plausible that the original host shift by greenbug to sorghum created an ecological disconnect from a guild of natural enemies adapted to exploiting them on wheat. Aphid natural enemies may require multiple generations to evolve the new responses required to track prey in a novel host-plant complex that presents a different olfactory profile and a different seasonal phenology of prey availability. Furthermore, outbreak populations initially drove heavy pesticide use that would have exerted high mortality on natural enemy 'first responders', greatly delaying the evolution of biological control processes and the final suppression of greenbug populations to sub-economic levels. The recent explosion of the sorghum-infesting strain of *M. sacchari* in the southern plains states provides a unique opportunity to observe directly another cycle of damaging aphid outbreaks on this crop, and most probably the gradual evolution of natural biological control once again.

Executive Summary

The IPM of aphids on sorghum, particularly greenbugs, has changed dramatically since the turn of the century, in concert with agronomic changes in the production of the crop. By 2000, insecticide use had declined precipitously and remained negligible until 2013, when the sugarcane aphid became invasive. Although greenbug biotypes resistant to insecticides, and those virulent to antibiotic varieties, have largely disappeared, the biological control of aphids in sorghum is once again threatened by insecticide use targeting epidemic populations of sugarcane aphids. The thresholds for treatment of sugarcane aphids are still being determined, and will probably be region specific. Fortunately, new classes of insecticides, primarily sulfoxamines and butenolides, show improved levels of safety for natural enemies, and should not delay the evolution of natural biological control to the same extent as did older, broad-spectrum materials.

Neither importation nor augmentative releases of natural enemies are justified, given the broad range of established aphid natural enemies in the system.

Semiochemicals are not exploited.

Host-plant resistance remains a key component of aphid IPM, but without adequate support from biological control to keep aphid populations low, resistant sorghum varieties remain vulnerable to the evolution of virulent aphid biotypes.

The complementary interaction between plant resistance traits and conservation biological control is key to the IPM of aphids in sorghum and can generally preclude the need for insecticide treatments.

Although cultural control is not practised explicitly, many agronomic practices (tillage, fertilization, irrigation, weed control, etc.) likely have a significant region-wide impact on aphid populations; improved understanding of these interactions will foster more holistic and sustainable IPM programmes into the future.

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26 IPM Case Studies: Leafy Salad Crops

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Introduction

What are leafy salad crops?

Leafy salads across the world show great diversity, dependent on local cultures and plant biodiversity, and include both species that are cultivated intensively and those that are gathered from the wild. For the purposes of this review, discussion will be confined to the commercial production of the Asteraceae, which include many varieties of lettuce, *Lactuca sativa* (Fig. 26.1).

However, the principles developed here can be applied to any vegetable with a short growing season and leaves that are harvested and eaten raw. These crops may be grown outdoors or under different degrees of protection, ranging from fleece or polythene covers to glasshouses. The different levels of environmental protection are used both to extend cropping seasons and to protect crops from invasion by aphids, as well as by moths and leaf miners (Ester *et al*., 1994). The greatest areas of these crops are outdoors. Nearly all species and varieties are characterized by a short growing period, sometimes only 3 or 4 weeks. The species of aphid encountered on crops will differ between plants from different families and regions of the world.

The IPM challenge

Leafy salad crops are very different from many other food crops as they are eaten fresh and raw, with little or no processing. The rapidly expanding market for 'bagged salads', often containing a number of different plant species that are labelled 'Washed and prepared', illustrates the extreme of such products. The consequence of this development is that the total yield is of little relevance; rather, it is the proportion of harvested units (usually heads) that are free from insects that is key to market success. The challenge to the grower of leafy salads is to deliver to retailers and the food service industry a continuous supply of product that is free from contamination from insects, pest or vagrant, and other foreign bodies, and with minimum insecticide residues. Such contamination can be eliminated only by attention to detail.

Year-round supply is achieved by growing crops in different regions of the world and freighting them to the areas of consumption. Growers that produce on a large scale may transfer their own production activities to different climatic regions in different seasons to achieve a continuous supply of product to their own processing plants and markets; they sometimes also transfer the processing activity. For example, farmers growing lettuce crops in southern England in summer will move their production to southern Spain in winter. Similarly, production in the USA focuses on the Central Coast areas of Salinas and Santa Maria in California from May to September, but shifts to the Imperial and Yuma Valleys on the California and Arizona border from November to March. In different locations, growing conditions and the pest spectrum will differ. The delivery of crops free from pests under such circumstances requires high skill levels.

Leafy salads are grown on a small land area and, as such, constitute a small market for the sale of agrochemicals. The consequence is that the armoury of agrochemicals available for use is more limited than that available to the producers of broad acre

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Fig. 26.1. Lettuce grown in beds maximizes crop uniformity and enables access by machinery. (Original colour photograph courtesy of G.M. Tatchell.)

crops, so alternatives to agrochemicals need to be developed and deployed if the quality of produce demanded by retailers and consumers is to be delivered routinely.

The Aphids

Twenty-one species of aphid have been recorded from lettuce (Blackman and Eastop, 2000). However, only a few of these are the focus for control on leafy salads. In Europe, *Pemphigus bursarius* (lettuce root aphid) may colonize the roots of lettuce, while the specialist *Nasonovia ribisnigri* (currant–lettuce aphid) (Fig. 26.2) and the generalists *Myzus persicae* (peach–potato aphid) and *Macrosiphum euphorbiae* (potato aphid) may colonize the foliage (Reinink and Dieleman, 1991). The infestation of the heart of the lettuce by *N. ribisnigri* is of greatest economic concern (Forbes and Mackenzie, 1982; Mackenzie and Vernon, 1988). In North America, similar spectra of aphid species are pests (Alleyne and Morrison, 1977; Forbes and Mackenzie, 1982), though *N. ribisnigri*, along with

Fig. 26.2. The currant–lettuce aphid (*Nasonovia ribisnigri*) colonizes the hearts of lettuce and is therefore very difficult to control. (Original colour photograph courtesy of Universtiy of Warwick, UK.)

Aulacorthum solani (glasshouse and potato aphid), was only introduced to California in 1998 (Palumbo, 1999). In South America (Brazil), *M. persicae* has been identified as the most important species (dos Santos *et al*., 1992).

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Components for Aphid IPM

Chemicals and resistance to insecticides

The intolerance of consumers in many regions of the world to any contamination of fresh, unprocessed food by pest insects has led growers to minimize the risk of downgrading or rejection of their crops by the frequent use of prophylactic applications of insecticides. The consequence of this unsustainable approach, both on lettuce and other crops, has been the development of resistance to insecticides in at least three species of aphid that infest lettuce. *Myzus persicae* is exposed to insecticides on a wide range of crops and has shown resistance to different classes of insecticides for many years (reviewed by Field *et al*., 1997, Foster *et al*., 2000; Chapter 19, this volume), with at least seven different mechanisms of resistance identified so far (Bass *et al*., 2014). The frequency of different insecticide-resistant genotypes varies between years (Foster *et al*., 2002b). Broad-spectrum resistance to the organophosphate acephate and the cyclodiene endosulfan has been identified in *N. ribisnigri* in southern France and Spain (Rufingier *et al*., 1997, 1999). Resistance to pirimicarb, and to a lesser extent pyrethroids and organophosphates, in *N. ribisnigri* has also been identified in the UK (Barber *et al*., 1999, 2002). Interestingly, insecticide-resistant *N. ribisnigri* were less aggregated on plants than susceptible aphids, so a greater proportion of plants were infested, with the potential for a greater rejection rate of plants at harvest (Kift *et al*., 2004). Limited resistance to pirimicarb and lambda-cyhalothrin has been identified in *M. euphorbiae* in the laboratory (Foster *et al*., 2002a). The complexity of controlling three species of aphid with different mechanisms of resistance to insecticides on a single crop is bound to drive the approach to aphid management towards more biologically based approaches. This direction is further driven by the impact of insecticide-based control strategies for *M. persicae* on the wide range of crops that are also hosts for this aphid and over which the manager of leafy salad crops has no control.

Chemical control – reducing insecticides

More careful, and therefore selective, placement of insecticides in space and time has been achieved by the use of insecticide seed treatments. Until recently imidacloprid has been used successfully on lettuce in many regions, including the UK for the control of aphids (Parker and Blood Smyth, 1996; Parker *et al*., 2002), and this is thought to have contributed to a reduction in the overall quantities of insecticide applied to lettuce (Garthwaite *et al*., 2013). However, imidacloprid seed treatments are no longer approved for lettuce in the UK and have been replaced by thiamethoxam. Thiamethoxam can be applied to leafy salad seed via traditional film coat methods or phyto-drip technology in a number of European countries, including the UK. Phyto-drip is a new seed treatment technology that applies a single drop of insecticide to each seed. In addition, insecticide applications to lettuce foliage can be timed better through the use of day-degree forecasts that predict immigration to crops (Collier *et al*., 1994, 1999), though in practice these may be of greater use in strategic planning than for the tactical control of aphids in a single crop.

Biological control

The very short growing season of leafy salad crops does not allow for the development of classical approaches to biological control in single crops, though those natural enemies that occur outdoors undoubtedly do achieve some reduction of aphid numbers, particularly where insecticide usage is limited (Nunnenmacher and Goldbach, 1996). The opportunity for using biological control increases with sequential cropping. For example, producers are experimenting with the release of the aphid parasitoid, *Aphidius colemani*, into field-grown organic crops, though improved control of aphids is yet to be substantiated (Bennison, 2013). Growers of organic lettuce in California rely on conservation biological control by hover flies to manage aphids, particularly *N. ribisnigri*, by planting strips of sweet alyssum, *Lobularia maritime* (Gillespie *et al*., 2011). The experimental deployment of wild-flower strips in the UK led to a reduction in the numbers of lettuce aphids on adjacent lettuce crops during June and July, but the effect decreased with distance from the strips (Skirvin *et al*., 2011).

The biological control of aphids has, by contrast, been very successful on pepper and cucumber grown in glasshouses, where aphids are particularly troublesome, although increased instances of hyperparasitism are threatening the success of IPM programmes (Jacobson, 2011). Effective control of *Aphis gossypii* (melon aphid) on cucumber has been achieved by either the weekly release of small numbers of the parasitoid *A. colemani* or by rearing the

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parasitoid on *Rhopalosiphum padi* (bird cherry–oat aphid) living on cereal plants as banker plants grown in pots in the glasshouse, from which the parasitoids disperse to attack the aphids on cucumber (Jacobson and Croft, 1998; Chapter 28, this volume). *Myzus persicae* is the primary pest aphid on pepper and can be controlled by the repeated release of *A. colemani* (Foster *et al*., 2003) or by the larvae of the common green lacewing, *Chrysoperla carnea* (Kift *et al*., 2005). It should be noted that the fruit of pepper and cucumber are not infested directly and that the plants have a long growing season, which provides sufficient time for equilibrium to be established between predator and prey. Efforts have been made to transfer these approaches to the control of aphids on glasshouse-grown lettuce crops, but as yet with limited success. In Germany, the parasitoid *Aphidius matricariae* was of little use for aphid control on lettuce because its main host, *M. persicae*, was less abundant than *N. ribisnigri*, *M. euphorbiae* and *A. solani*, all of which were seldom, if ever, parasitized by this species. However, repeated applications of *C. carnea* eggs did give good control (Quentin *et al*., 1995). The parasitoid *Aphidius hieraciorum* has been identified from *N. ribisnigri* in the UK and its potential as a biological control agent explored (Anon., 2005). *Aphelinus abdominalis,* a commercially available parasitoid, is also effective against *N. ribisnigri.* However, this aphid's preference to feed in the centre of lettuce heads may restrict the parasitoid's access (Shrestha *et al*., 2014). Despite this, the use of arthropod biological control agents on lettuce has as yet proved uneconomic for large field crops. Additionally, customers do not discriminate between a pest aphid and its natural enemies (including aphid mummies), with the presence of either resulting in rejection at the point of sale. Some biological control agents also require warm temperatures, which only occur for a few months a year, and the maintenance of minimum temperatures for frost protection in protected lettuce crops is insufficient for biological control agents.

Opportunities do, however, arise for the inundative release of biological control agents as biological insecticides. To date, fungal pathogens have shown the greatest potential for aphid control, particularly for the smaller areas of salad crops grown under protection. A formulation of the fungus *Lecanicillium lecanii*, which is available commercially for the control of a number of different pests of glasshouse crops, has been shown to reduce the numbers of *M. persicae*, *M. euphorbiae* and *N. ribisnigri* on lettuce foliage in laboratory and glasshouse experiments, though the relative efficacy against each aphid species differed between experiments, and the level of control achieved did not satisfy market requirements alone (Fournier and Brodeur, 2000). This example amply illustrates the challenges of using biological approaches where only complete elimination of aphids and cadavers on the marketable parts of the plants is acceptable. For market, whole head products are generally not washed, but it is recommended to do so in the kitchen. Bagged salads are washed, but cadavers may remain on the cut leaves. This contrasts with infestations of *P. bursarius* on the roots of lettuce, where effective control does not require elimination. Adequate control of *P. bursarius* can be achieved by raising lettuce plants in modules in which the potting mix contains conidia of the fungus *Metarhizium anisopliae* (Chandler, 1997), although this has never been developed as a commercial product.

Host-plant resistance

Resistance to both diseases and aphids in lettuce has been the target of many plant-breeding programmes, and resistant varieties hold much promise for the future. As yet, only a few cultivars with resistance to aphids are available commercially. A single dominant gene (*Nr* gene) conferring resistance to *N. ribisnigri* has been identified in accessions of the wild species *Lactuca virosa* and introgressed into *L. sativa* by backcrossing (Eenink *et al*., 1982a,b; Eenink and Dieleman, 1983; van Helden *et al*., 1993). This resistance has been deployed successfully in integrated control programmes (Aarts *et al*., 1999; Parker *et al*., 2002). The number of varieties carrying this resistance gene has increased gradually, and these have been deployed widely. Around 2009, a breakdown in resistance was reported from some locations in Europe, including the UK (Thabuis *et al*., 2011). Aphid biotypes able to overcome the resistance and develop and reproduce equally well on resistant and susceptible varieties were relatively widespread. This has further stimulated the search for genetic material that contains different mechanisms of resistance (VeGIN project, for example). Two new and potentially unique sources of resistance against *N. ribisnigri* have been identified in *Lactuca serriola* and *Lactuca virosa* accessions in the USA (McCreight and Liu, 2012). The investigation of

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varieties with resistance to the new *N. ribisnigri* biotype that broke down existing host-plant resistance is also in progress (Thabuis *et al*., 2011; ten Broeke *et al*., 2013). More than one source of resistance to *P. bursarius* has also been identified in the old lettuce varieties 'Avoncrisp' and 'Lakeland' (Dunn, 1974; Ellis *et al*., 1994) and in *L. virosa* (Ellis *et al*., 2002). Lettuce is a less suitable host for *M. persicae* than brassicas. Apart from any total resistance, there is a range of varietal susceptibility of lettuce to *N. ribisnigri* (R. Collier and B. Torevasei, unpublished).

Modifying aphid behaviour

A surprising number of unconnected studies have explored aspects of aphid behaviour to improve control on lettuce. For example, Ester *et al*. (1993) was able to reduce the amounts of carbamate and organophosphate insecticides to one-tenth of the recommended dose and yet achieved successful control when the alarm pheromone (*E*)-β-farnesene was included with the insecticides.

Volatile plant chemicals known to be involved in the process of plant colonization by aphids include chemicals from an aphid's primary host plant that seem to interrupt colonization by the aphid of its secondary host (Pettersson *et al*., 1994). *cis*-Jasmone has been isolated from *Ribes nigrum*, the primary host of *N. ribisnigri*, and shown to be electrophysiologically active to *N. ribisnigri*. *cis*-Jasmone is also a well-known plant volatile produced in response to insect herbivory. In olfactometer studies, *cis*-jasmone repelled *N. ribisnigri* in the presence of lettuce (Birkett *et al*., 2000) and, when included in a mixture of other electrophysiologically active compounds from *R. nigrum*, reduced the numbers of *N. ribisnigri* alatae colonizing lettuce in field-cage experiments (G.M. Tatchell and L.J. Wadhams, unpublished). The production and deployment of such plant volatile chemicals could provide components for a novel strategy that manipulates behaviour and limits crop colonization, though control has not been demonstrated in the field.

IPM in Practice

Assurance and accreditation schemes

Broad principles of IPM have been established by organizations such as the International Organisation for Biological Control (IOBC) that include crop-specific recommendations (Malavolta *et al*., 2005). Such guidelines have been developed into accreditation and assurance schemes of crop production in many countries, driven by the requirement of retail organizations to control the standards of production by their suppliers. In the UK, the individual crop protocols of the Red Tractor Assurance Fresh Produce Standards (RTAFPS) are an industry-wide initiative that addresses the key issues of production, including aphid control, on fruit, salads and vegetables through the promotion of Integrated Crop Management. Some retail organizations have developed their own but related standards. It is a prerequisite that producers in the UK be accredited to these schemes if they are to supply the multiple retailers and major players in the food services industry. GlobalGAP has established the Integrated Farm Assurance Standard for suppliers to European retailers and the Harmonized Produce Safety Standard for suppliers to North American markets. Individual country standards, such as RTAFPS, may be benchmarked to GlobalGAP to help facilitate international trade. However, these standards provide very little detail of how aphids should be controlled beyond the safe use of approved insecticides. This perhaps reflects the tensions between growers, who do not wish to be constrained in the approaches available to them to deliver insect-free produce to their markets, and the retailers, who need to demonstrate to customers that the food purchased in their stores is safe.

Practical control

Outlined above is a fairly traditional list of individual approaches to aphid control developed for the pest aphids of leafy salads, but which could be combined in any number of ways to achieve effective season-long control. Yet it is the dichotomy between season-long control and the often very short season of an individual salad crop that now needs to be resolved. In practice, a series of crops is planted sequentially throughout the growing season, but each crop will be present only for a few weeks of the whole annual cycle of climatic seasons, and will be exposed to a different risk of aphid infestation (driven by changes in the seasonal abundance of aphids). IPM is therefore considered on two different temporal scales, i.e. that of a single crop and that of the season. The season effect will vary between different climatic regions and will require identification for each region.

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In the UK, low temperature and light in the winter months confine outdoor lettuce production to the period from February to October. The earliest crops may be grown under fleece, primarily to protect them from frosts, but also to prevent aphid infestation once aphids begin to fly in spring.

The monitoring of aphid numbers in the UK over a number of years on plots of lettuce planted sequentially throughout the growing season, and in water traps, has identified two periods of peak abundance. These two periods of high risk are characterized by different aphid species. In midsummer (late June and July), the three species that infest the foliage, *N. ribisnigri*, *M. persicae* and *M. euphorbiae*, as well as the root-infesting *P. bursarius*, are all abundant. In contrast, in early autumn (September), only *N. ribisnigri* is abundant. These two periods of high risk are separated by a period of low risk, irrespective of the growth stage of the plants (Fig. 26.3) (Parker *et al*., 2002). A similar pattern identified in Switzerland stimulated the application of control measures when 10% of plants were infested during the high-risk period compared with 40% during the low-risk period (Fischer and Terrettaz, 1999).

Growers are aware of the seasonality of risk, though perhaps not as precisely as research monitoring programmes have identified, and seasonal control strategies are modified accordingly. The effort devoted to crop walking to assess aphid populations on crops is modified through the season.

The IPM strategies adopted within the UK are focused around the optimum use of effective insecticides. Since the mid-1990s, imidacloprid and, more recently, thiamethoxam seed treatments have been used almost ubiquitously. However, seed treatments do not protect the crop for its duration and further aphid control is required as harvest approaches. In the UK, the number of active ingredients available for use on leafy salads is limited, due to the small commercial market for use on specialist crops and recent reviews of registrations. The tactical selection of any one chemical for use is related to previous applications and concerns over control failures associated with insecticide resistance.

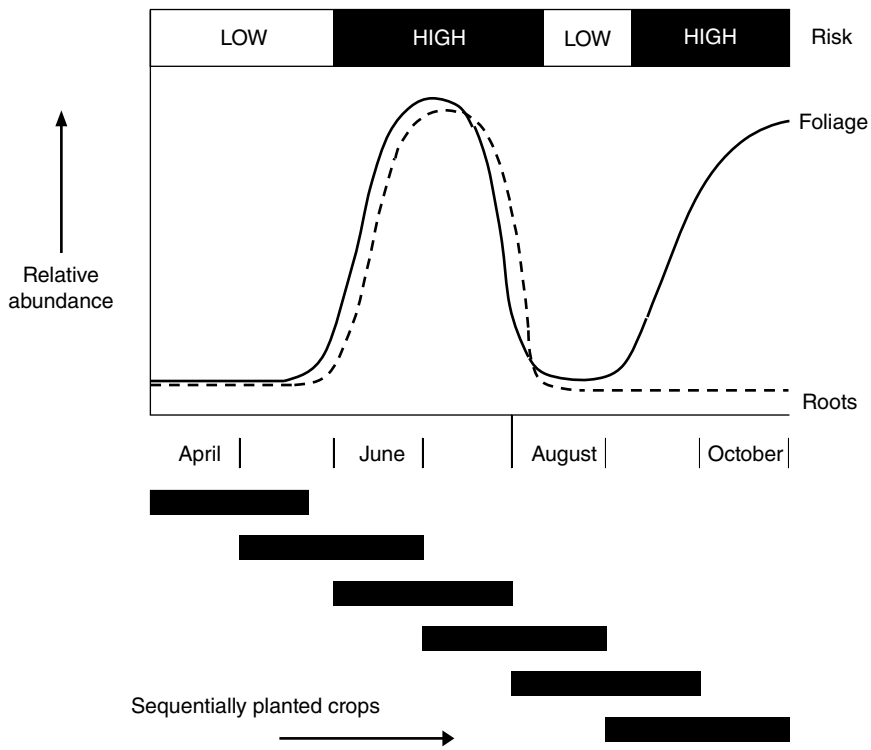

Fig. 26.3. The risk of infestation by aphids of leafy salad crops alters with planting date. The relative risk to foliage and the roots informs strategic IPM decisions. (Adapted from Parker *et al*., 2002.)

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Growers have also become increasingly aware of selecting chemicals that are safer to natural enemies, which newer chemistries, such as spirotetramat, offer. Information on the side effects of pesticides on natural enemies is now widely available to support such decision making.

Varieties resistant to aphids are in practical use, particularly where there is a history of aphid infestation. However, their cost is high. Not all lettuce varieties remain available, and the heads produced do not always meet the quality requirements of retailers and processors. As improved resistant varieties become available, their use may become more widespread. Additionally, where more than one lettuce crop is grown on the same ground within the same season, the use of imidacloprid may be restricted to a single crop, due to the maximum dose of imidacloprid that can be applied per hectare per year. In such circumstances, seed treatments are applied only to crops grown during the high-risk period in summer, when more than one aphid species is present. Varieties resistant to *N. ribisnigri* are deployed in late summer and autumn, when it may be the only species present.

The increasing number of plant species being grown as leafy salads for inclusion in bags of prepared salads has increased the IPM challenge. Some of these species are grown for very short periods prior to harvest, and the approved harvest intervals for insecticides may restrict their use. Many growers are adapting the IPM methods they have developed on lettuce for the novel crops as best they can.

Aphid-transmitted viruses occur in leafy salads but are not usually the target for control. Occasionally, virus infections cause significant losses; for example, in 2015 in the UK, significant losses occurred in part of the season that was associated with large numbers of migrant *M. persicae*, although the causal virus has yet to be confirmed. IPM strategies may require modification to account for virus spread.

Executive Summary

A feature of these short-season crops is that any individual crop is 'exposed' to a different component of the aphid life cycle. Therefore, an IPM approach across the annual periodicity of aphid life cycles involves a different range of control options for each crop.

The growers of leafy salads that supply major retailers and food processors have taken significant steps towards the use of effective IPM compared to the prophylactic application of chemicals adopted in the past. However, aphid control remains chemically based, though resistance is a current and future problem. Growers, especially those supplying for 'bagged salads', cannot risk the presence of any insects (whether pests, natural enemies, or cadavers) for fear of crop rejection. Seed treatments reduce the need for foliar applications, which can sometimes damage natural biological control, although newer chemistry, such as spirotetramat, is reported to be safer to natural enemies. Applications of foliar insecticides are applied only in response to the results of detailed crop monitoring.

Biological alternatives may become more attractive should the availability of insecticides be limited still further. However, there have been releases of the parasitoid *A. colemani* into organic field-grown lettuce crops, and the fungus *L. lecanii* has also been used commercially on protected crops.

The use of resistant varieties is currently limited, but is likely to increase considerably as more varieties with good agronomic and processing characteristics become available.

Cultural control is limited to the use of crop covers to protect crops from insect infestation, particularly early in the season, or those crops harvested as 'baby leaf'.

Semiochemicals have potential for manipulating aphid behaviour, perhaps in the form of a 'push–pull' strategy involving sacrificial or less valuable plants, but much further research is required before commercial implementation.

Interaction between control methods is represented by the use of lettuce varieties resistant to aphids and the use of novel chemistries applied to the seed or the foliage that reduce the need for foliar applications of broader spectrum insecticides, so preserving natural enemies.

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27 IPM Case Studies: Brassicas

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Introduction

All members of the family Brassicaceae (formerly Cruciferae), which includes the genus *Brassica*, contain specific secondary plant compounds known as glucosinolates. Although plants containing these chemicals are toxic to most aphids, some species have overcome the toxins and feed exclusively on such plants (Finch, 1980). The aphid species that have adapted in this way can colonize many species in the 220 genera of Brassicaceae found throughout the world. Hence, many wild plants and garden flowers in this Family are sources of pest aphids of *Brassica* crops. Until about 25 years ago, cultivars of *Brassica oleracea* (e.g. cabbage, cauliflower, Brussels sprout) and *Brassica napus* var. *napobrassica* (swede) were the commonest crucifers grown on a field scale in the UK. However, following the expansion in the area of land drilled with oilseed rape during the mid-1970s, the oil-bearing cultivars of *Brassica napus* and *Brassica rapa* have become the commonest (Finch and Thompson, 1992). Not only are such plants grown at a much higher density (80–120 plants/m) than the *B. oleracea* cultivars (2–20 plants/m), but also they are grown on an area of about 650,000 ha, approximately 20 times the area used for growing brassicaceous vegetable crops.

The main aphids found on *Brassica* crops (e.g. cabbage and mustard) worldwide are the foliage-feeders *Brevicoryne brassicae* (cabbage aphid), *Lipaphis pseudobrassicae* (mustard aphid), *Myzus ascalonicus* (shallot aphid), *Myzus persicae* (peach–potato aphid), *Macrosiphum euphorbiae* (potato aphid), *Protaphis middletonii* (corn root aphid) and the root-feeders *Pemphigus populitransversus* (poplar petiole gall aphid) and *Smynthurodes betae* (bean root aphid) (Blackman and Eastop, 2000). Of these, *B. brassicae*, *M. persicae* and *L. pseudobrassicae* are the species of most economic importance. This chapter will focus on IPM strategies used for aphid control in the UK, drawing comparisons with strategies employed in other countries where information is available.

Biology of Pest Aphids in the UK

In the UK, *B. brassicae* (Fig. 27.1) often causes severe crop damage. This aphid infests the leaves and shoots of many *Brassica* crops and remains on herbaceous cruciferous plants throughout its life cycle. In most northern areas of its distribution, *B. brassicae* overwinters as an egg on the stems of crop plants that are in the field during the winter period (e.g. autumn-drilled rape and overwintering vegetable *Brassica* crops). The eggs hatch in February/March and the resulting aphids colonize nearby host plants. Although *B. brassicae* still overwinters in the egg stage in the UK (N. Kift, unpublished), overwintering eggs have been hard to find during the past 30 years (Chua, 1977; P.R. Ellis, unpublished). It appears that the overwintering population of *B. brassicae* is now made up largely of anholocyclic nymphs and adults (Harrington *et al.*, 1990; R. Collier, unpublished). During late spring and early summer, alate *B. brassicae* leave their overwintering sites and, after dispersing (Finch and Thompson, 1992), some find new host plants. Once the aphids colonize horticultural *Brassica* crops, aphid numbers increase rapidly. This increase is usually followed by a mid-season 'crash', in which the aphid population is often nearly annihilated (Fig. 27.2). It is not known whether environmental conditions per se, host-plant maturation, natural biological control agents, aphid biology (e.g. a decline in fecundity), or a combination of the four, contribute most to this

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mid-season crash. Following the crash, aphid numbers increase again in early autumn and then decline at the onset of winter. The early peak in *B. brassicae* numbers usually occurs between mid-July and mid-August, and the late peak between mid-September and mid-December.

Myzus persicae infestations can also require control in *Brassica* crops, although this species is usually less damaging than *B. brassicae* in the UK. As with *B. brassicae*, there is often a mid-season crash, and this appears to occur at about the same time as the decline in numbers of *B. brassicae*, if both species are present in a crop.

There are considerable variations in the levels and patterns (Dixon, 1998) of aphid infestations from year to year. For example, although *M. persicae* numbers were low in most *Brassica* crops grown during the 10 years from 1992 to 2001, and most of the years subsequently, large infestations were found during the autumns of 1996 and 2001. Unfortunately, it is often difficult to destroy large infestations of aphids in the autumn, even with insecticides that are highly effective earlier in the year (in some cases, because low temperatures do not favour the activity of certain insecticides). Therefore, late infestations cause major problems for growers of horticultural *Brassica* crops, as retailers and consumers have an extremely low tolerance to the presence of aphids or aphid damage in the marketed produce. In addition to direct damage (distortion of the foliage and, in extreme cases, reduced plant growth) and crop contamination (the presence of aphids, honeydew and sooty mould), *B. brassicae* and *M. persicae* can cause further problems by transmitting viruses including *Turnip mosaic virus* and *Cauliflower mosaic virus* (Kennedy *et al.*, 1962). *Lipaphis pseudobrassicae* is not a major pest in UK *Brassica* crops.

Fig. 27.1. Cabbage aphid – *Brevicoryne brassicae*.

Integrated Crop Management

In the UK, most *Brassica* crops are grown according to standards described in the Red Tractor Assurance scheme, a scheme supported by both the major supermarkets and the major vegetable processors.

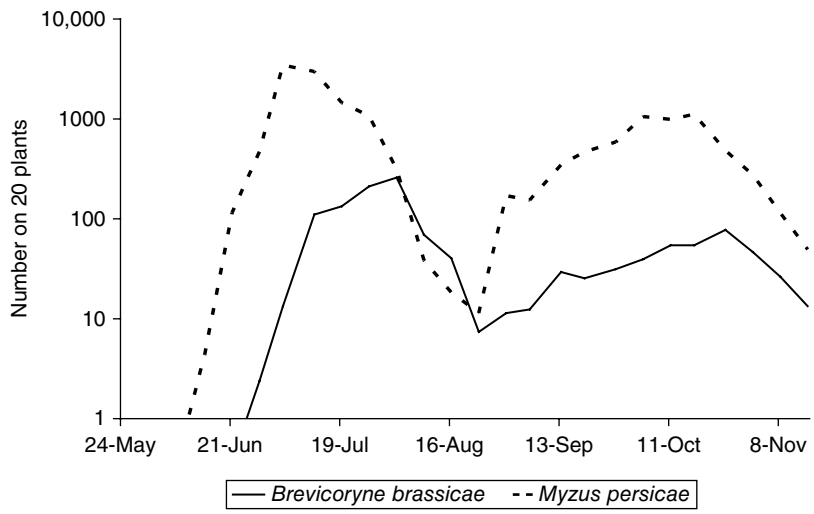

Fig. 27.2. Numbers of *Brevicoryne brassicae* and *Myzus persicae* found on insecticide-free Brussels sprout plants at Kirton, Lincolnshire, UK, in 2001. The mid-season crash occurred during August. (From Collier *et al.*, 2003.)

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The aim of the scheme is to promote the production of 'safe and environmentally responsible' crops. The Red Tractor Assurance scheme provides assurance to internationally recognized standards, and is a fundamental link in an integrated chain of assurance throughout the food chain from farm to retailer. It has been developed over the years to address legislative requirements, scientific evidence, good practice in the industry and consumer concerns. Each year, the participating growers of the Red Tractor Fresh Produce scheme are provided with updated, crop-specific protocols that describe 'best' practice. In addition, each grower is required to make his or her premises available for inspection by an independent auditor. The Assured Produce protocols are not prescriptive; it is simply to advise growers of the best practice and to provide useful sources of information. A similar set of standards and procedures is being used worldwide and is known as GLOBALG.A.P. This scheme has the objective of facilitating safe, sustainable agriculture worldwide. Voluntary standards are set for the certification of agricultural products around the globe, and increasing numbers of producers, suppliers and buyers are harmonizing their certification standards to match. There are additional schemes to which growers can subscribe, including several organic certification schemes.

Control Methods

Chemical control

In the UK, aphids in commercial *Brassica* crops are controlled exclusively with insecticides. The insecticides can currently be applied as foliar sprays or as a 'phytodrip' treatment, where a single droplet of a solution containing insecticide is applied to a preseeded cell block. In the recent past, UK growers have relied heavily on organophosphorus (OP), carbamate (particularly the selective aphicide pirimicarb) and pyrethroid insecticides. However, the use of OP insecticides and pirimicarb has ceased, and they have been replaced by neonicotinoids (the first of these marketed being imidacloprid as a seed treatment) and more recently by several other insecticides with different modes of action, including pymetrozine and spirotetramat. Seed treatments (such as the phytodrip treatment) with neonicotinoids, which have systemic activity, can be very effective and can reduce the number of foliar sprays required later in the season (R. Collier, unpublished). However, approval for the use of neonicotinoids on rape has recently been withdrawn in countries belonging to the European Union because of concerns about their effect on pollinators, especially bees. Further new active ingredients, with different modes of action, may become available in the next few years.

To date, no population of *B. brassicae* has developed resistance to any insecticide in the UK or elsewhere. In contrast, populations of *M. persicae* have become resistant to various carbamate, OP, pyrethroid and neonicotinoid insecticides (Foster *et al*., 2000; Chapter 19, this volume). Some *M. persicae* populations in the UK have lower susceptibility to imidacloprid, which in most cases has been correlated with an increased tolerance to nicotine (Devine *et al*., 1996). However, there is no firm evidence that neonicotinoids such as imidacloprid are failing to control *M. persicae* effectively under field conditions in the UK (Nauen and Denholm, 2005; S.P. Foster, unpublished).

With the plasticity exhibited by *M. persicae* populations, it is important to adopt strategies that will prevent the build-up of resistance. Consequently, the UK Insecticide Resistance Action Group has published resistance management guidelines for *M. persicae* on *Brassica* crops. Although no formal system exists for testing aphids for their resistance to insecticides, *M. persicae* populations are tested regularly by insecticide manufacturers and by some research organizations.

There is increasing interest in the use of biopesticides (based on entomopathogens, plant extracts or semiochemicals) to control the pest insects infesting horticultural crops, and a wide range have been evaluated in a recent multi-organization project in the UK (the SCEPTRE project). Some of these have aphicidal activity, and a role may be identified for them in the production of edible *Brassica* crops in the UK.

Monitoring and forecasting

Brevicoryne brassicae and *M. persicae* are both caught in the network of suction traps run by the Rothamsted Insect Survey (Chapter 16, this volume). The current information from this network is available on the Rothamsted Insect Survey website and also forms part of two weekly e-bulletins for farmers and growers supported by the Agriculture and Horticulture Development Board (AHDB) – a statutory body responsible for collecting an

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'industry levy' used to fund research/development of direct benefit to UK farmers and growers.

Analyses of long-term data sets from the Rothamsted Insect Survey have shown that, for several aphid species, there is a negative correlation between the date the first alate of a given species is trapped and winter temperature (Harrington *et al*., 1990). The relationship with winter temperature is particularly pronounced for *M. persicae*, (Harrington *et al*., 1990) and for *B. brassicae* (R. Harrington, unpublished), both species being largely anholocyclic in the UK. There is also often a strong positive correlation between winter temperature and aphid abundance up until early July. This information is used to alert growers to the likely need for, and timing of, control of *M. persicae* in sugar beet (*Beta vulgaris*) crops. Similar forecasts, produced by the Rothamsted Insect Survey, now help growers of vegetable *Brassica* crops to decide when it is worthwhile looking for both species, and are disseminated as part of the two bulletins described above. Day-degree models for *B. brassicae* and *M. persicae* are available online from the University of California Statewide Integrated Pest Management Program. Although such models are based on published data and are supported by a comprehensive list of references, they have not been validated in the UK.

In the UK, local information on the development of aphid infestations is provided by crop consultants and representatives of pesticide companies, who walk and inspect the *Brassica* crops under their jurisdiction on a regular basis ('scouting'). Between 1996 and 2001, growers in south Lincolnshire (the area of eastern England in which a large area of vegetable *Brassica* crops are grown) were supplied with information on aphid infestations by scientists from Horticulture Research International (now Warwick Crop Centre, The University of Warwick). Such information was collected by taking weekly records of the numbers of aphids found on insecticide-free *Brassica* plots. Although the information collected was faxed weekly to subscribers, the service ceased after 2001 because of insufficient grower funding. In Germany, members of the extension service warn growers, by fax, telephone or e-mail, as soon as large numbers of aphids start to migrate into *Brassica* crops (M. Hommes, unpublished). In the USA, control advice and information about crop scouting are available on a number of websites managed by the extension services (e.g. University of California (UC IPM Online)).

Sampling and decision making

In the UK, vegetable *Brassica* growers spend considerable time inspecting their crops for aphids. The information collected is used to make decisions about applying sprays to their crops, and is also documented carefully. Unfortunately, no standard method has been developed for estimating aphid numbers in commercial crops. Therefore, the spray thresholds used by growers vary from place to place, as they are based on the method used there for estimating aphid numbers.

Systems of supervised control, based on spray thresholds for pest aphids of vegetable *Brassica* crops, were developed in northern Europe (Ellis *et al*., 1988; Hommes *et al*., 1988; Theunissen, 1988; Freuler *et al*., 1991; Blood Smyth *et al*., 1992, 1994; Paterson *et al*., 1994; Hildenhagen and Hommes, 1997) but uptake was limited, partly because they were complicated and time-consuming. Some of the methods developed were subsequently revisited in the UK (Perry *et al*., 1998; Collier, 1999; Collier and Mead, 1999; Collier *et al*., 2003) in the hope that they could be made more user-friendly. Obviously, the reliability of the spray thresholds on which any new system is based is of paramount importance. Hence, the major thrust of the research was to ensure that the sampling methods used to obtain the underlying data were as robust as possible. While the research indicates that such approaches could be used to optimize pesticide use, they continue to be unappealing to growers in the UK.

No figures have been published to indicate how many commercial growers of vegetable *Brassica* crops use spray thresholds in northern Europe. In Germany, although the extension service circulates spray thresholds (Hildenhagen and Hommes, 1997) to most growers, only 10–25% use them (M. Hommes, unpublished); spray thresholds are not used in Switzerland. Therefore, despite considerable inputs into the development of sampling and decision-making systems, uptake by growers has been poor, possibly because the original systems were too inflexible and/or too time-consuming. Research has been done also to develop an action threshold for *B. brassicae* in rape in the UK (Ellis *et al*., 1999), and information is available in publications for farmers produced by the AHDB.

In the USA, the major pests of *Brassica* crops are the caterpillars of Lepidoptera, and aphids are regarded only as sporadic pests. Nevertheless, information on crop walking ('scouting') and treatment

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thresholds for aphids is available. For example, the University of California Pest Management Guidelines, which are available online, include a presence/absence sequential sampling programme for deciding how best to control *B. brassicae* infestations in Brussels sprout crops.

Research has been done in Asia to establish treatment thresholds for the pest aphids of *Brassica* crops (e.g. Singh and Malik, 1998; YongNian *et al*., 2000 – both for *L. pseudobrassicae*). However, how widely such thresholds are used in practice cannot be determined.

The thresholds used vary depending on the species of pest aphid, size of infestation, the crop type and its closeness to harvest. In Germany, when *Brassica* plants are infested with less than 100 aphids/plant, sprays are applied only when 20% of the plants have become infested. However, when more than 100 aphids are found on any plant, the spray threshold is lowered to 10% infested plants (M. Hommes, unpublished). The University of California Pest Management Guidelines indicate that Brussels sprout crops can tolerate 40% infested plants up to 2 weeks before harvest, but advise treatment at 15% infested plants. The same guidelines indicate that broccoli and cauliflower crops can tolerate up to 100 aphids/plant up to heading, but that once heads begin to form, cabbage aphids must be controlled even if only a few are present. They suggest that cabbage crops have less tolerance for aphids and should be treated as soon as 1–2% of plants are infested with one or more aphids. In the midwest USA, treatment for *B. brassicae* infestations was suggested if 1–2% of the plants were infested. If *M. persicae* was the infesting species, then populations of 100 aphids/plant could be tolerated (Eastman *et al*., 2005).

Biological control

Aphid infestations on *Brassica* crops are reduced by specific predators and parasitoids (Hafez, 1961; Dunn and Kempton, 1971; Raworth *et al*., 1984; Hart *et al*., 1997), by a range of polyphagous predators (Sunderland *et al*., 1987) and by entomopathogenic fungi (Dunn and Kempton, 1971; Milner, 1997; McLeod *et al*., 1998; Chapter 11, this volume). Most pest management guidelines recognize the importance of natural enemies and propose that natural enemies should be considered when making treatment decisions. However, nobody has indicated how the application of insecticide sprays against aphids should be modified to take account of the contribution from natural enemies to control.

In addition, there is no concerted effort to conserve natural enemies by: (i) ensuring that only selective insecticides are sprayed; or (ii) altering the cropping system to provide predators and parasitoids with additional sources of food and shelter. The latter is normally achieved by growing flowering plants alongside crop plants. For example, van Emden (1965) showed that growing flowers alongside a Brussels sprout crop increased the hover fly (Syrphidae) population on the crop plants adjacent to the flowers, giving a 15–20% reduction in aphid numbers. Similarly, in New Zealand, fewer aphids (*B. brassicae* and *M. persicae*) were recorded in plots of cabbage surrounded by phacelia (*Phacelia tanacetifolia*), a plant grown specifically to provide hover flies with a plentiful supply of pollen (White *et al*., 1995). In both cases, however, aphid numbers were not reduced sufficiently to give commercially acceptable levels of control. To date, no detailed research has been done in the UK on the biological control of aphids in field *Brassica* crops. Although some potential arthropod biological agents have been considered elsewhere in the world (Raworth, 1984; Makhmoor and Verma, 1989; Nirmala Devi *et al*., 1996), the control of aphids using arthropods has not been demonstrated in any field *Brassica* crop. However, biopesticides based on entomopathogenic fungi are now approved for use on field *Brassica* crops in certain countries (e.g. 'Botanigard' containing *Beauveria bassiana*).

Host-plant resistance

Certain species and cultivars of *Brassica* are more resistant to aphid infestation than others (Singh and Ellis, 1993; Ellis *et al*., 1998). Unfortunately, the current levels of resistance to aphids of such cultivars are not sufficient to ensure that the 'partially resistant' crops remain aphid free. Therefore, insecticides still have to be applied. It has been suggested that the benefits from partially resistant cultivars, natural enemies and insecticides could be combined to improve overall aphid control (Verkerk *et al*., 1998; Chapter 23, this volume). However, such an approach has not been tested in the field. There is no evidence that growers select cultivars because of their resistance to pest aphids.

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Cultural control

Crop covers (Fig. 27.3)

Fine-mesh covers can be used to keep aphids off most crop plants (Bedford *et al*., 1994; Evans *et al*., 1997). In the UK and in Switzerland (R. Baur, unpublished), crop covers are considered too expensive for large-scale use. However, a significant proportion of the UK swede crop used for human consumption is already covered in fine-mesh netting to exclude *Delia radicum* (cabbage root fly), for which, since the withdrawal of chlorfenvinphos, there is no effective approved insecticide. Crop covers may be used in Germany on cauliflower, Chinese cabbage (*Brassica rapa* subsp. *pekinensis*), swede and radish crops, as the plants command a high price at market (M. Hommes, unpublished). In contrast to crop covers, reflective mulches (supposed to deter aphids from landing on *Brassica* crops) have not been effective anywhere in Europe.

Increasing crop diversity

Many researchers have shown that the numbers of aphids found in *Brassica* crops are reduced considerably when the crop background is allowed to become weedy (Smith, 1969; Dempster and Coaker, 1974), when the crop is intercropped with another plant species (Altieri *et al*., 1985; Andow *et al*., 1986), or when the crop is undersown with clover (Finch and Kienegger, 1997). In field experiments, Finch and Kienegger (1997) showed that undersowing cabbage plants with clover (Fig. 27.4) reduced *B. brassicae* infestations by 78–95% when compared to cabbage grown in bare soil. The clover simply disrupted host-plant colonization by the aphids (Finch and Edmonds, 1994; Finch and

Fig. 27.3. Crop covers being used to exclude pest insects in a field trial a Warwick HRI, Wellesbourne, UK.

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Fig. 27.4. Cabbage plants undersown with clover to reduce colonization by pest insects.

Collier, 2000). However, such approaches have not been used in commercial practice.

Executive Summary

Insecticides are still the sole tool used by the vast majority of UK brassica growers, Although spray thresholds for the two main pest aphids, *B. brassicae* and *M. persicae*, are available to growers, and they receive help from extension services about when spraying is likely to be necessary, many treat prophylactically.

Several of the older insecticides have now been replaced by newer compounds such as the neonicotinoids, though recently the use of neonicotinoids has become restricted and resistance to them has appeared in some *M. persicae* populations. In the UK, guidelines for managing resistance in this aphid have been published. Except in some supermarket and trade protocols, insecticides are rarely selected on the basis of being less harmful to natural enemies.

No predatory arthropods are released to reduce aphid numbers in brassica crops. Biopesticides based on entomopathogenic fungi are now approved for field use in certain countries.

Although plant cultivars are available that are partially resistant to aphids, the resistance levels are still not high enough as a sole control measure to induce producers to grow them.

Of the methods of cultural control available, crop covers are used by some growers, but commerce has not embraced other cultural methods with established potential, such as the provision of nectar sources for natural enemies and intercropping/undersowing

At present, semiochemicals are not applied to disrupt pest aphids or to manipulate natural enemies in brassica crops.

The only interaction between the control measures considered is the choice of insecticides to limit damage to biological control.

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28 IPM Case Studies: Cucurbits

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Introduction

Cucurbits (family *Cucurbitaceae*) were among the earliest cultivated plants, dating back to 10,000 BC or earlier (Robinson and Decker-Walters, 1997). Today, watermelon (*Citrullus lanatus*), cucumber (*Cucumis sativus*), melon (*Cucumis melo*, including muskmelon, cantaloupe and honeydew melon), squash and pumpkin (*Cucurbita pepo*, *Cucurbita moschata* and *Cucurbita maxima*) are the most commonly grown cucurbits on a worldwide basis (FAOSTAT, 2013) (Fig. 28.1).

Aphids attack cucurbits wherever they are grown. *Aphis gossypii* (melon aphid) is by far the most important of the direct pests, but *Myzus persicae* (peach–potato aphid) and *Aphis craccivora* (cowpea aphid) also attack cucurbits. The leaves of watermelon, melons and cucumber become crumpled and distorted when the melon aphid feeds on them (Goff and Tissot, 1932) and heavy infestations can result in yield losses (Webb, 1996). Sooty mould develops on leaves and fruit coated with honeydew excreted by aphids. For cucurbit crops throughout the world, aphids are most damaging as virus vectors (Dahal *et al*., 1997; Luis-Arteaga *et al*., 1998; Abou-Jawdah *et al*., 2000; Sevik and Arli-Sokmen, 2003).

There are relatively few published IPM programmes for cucurbits. Multiple tactics are generally recommended for the control of aphids and the viruses they transmit. This chapter will focus primarily on aphid pest management in the USA, but will also refer to strategies used in other countries, particularly for the management of aphids on cucumbers under protected cultivation.

Aphid-vectored Viruses Affecting Cucurbits

Lecoq and Desbiez (2012) list 14 aphid-transmitted viruses that affect cucurbits. All but three are non-persistently transmitted potyviruses. The others include the non-persistently transmitted *Cucumber mosaic virus* (CMV) (genus *Cucumovirus,* family *Bromoviridae*), and the persistently transmitted *Cucurbit aphid-borne yellows virus* (CABYV) and *Melon aphid-borne yellows virus* (MABYV), both poleroviruses (family *Luteoviridae*). Of the potyviruses, the watermelon strain of *Papaya ringspot virus* (PRSV-W), *Zucchini yellow mosaic virus* (ZYMV) (Fig. 28.2) and *Watermelon mosaic virus* (WMV) are the most common worldwide. PRSV-W is found in subtropical and tropical regions and WMV more often in temperate and Mediterranean climates (as is CMV). Other potyviruses cause economic damage on a more regional basis, such as *Moroccan watermelon mosaic virus* in Africa and the Mediterranean basin and *Zucchini yellow fleck virus* in the Mediterranean basin. More aphid-transmitted potyviruses of unknown economic importance continue to be found and described wherever cucurbits are grown; for example, *Watermelon leaf mottle virus* (Purcifull *et al*., 1998) in Florida and *Algerian watermelon mosaic virus* in Algeria (Yakoubi *et al*., 2008). Most recently, a virus that was first discovered in 1982 in Guadeloupe and described as PRSV-Tigré, a strain of PRSV-W (Quiot-Douine *et al*., 1986), was further characterized and found to be a genetically distinct species. The virus, now called *Zucchini tigré mosaic virus*, has been found in widespread locations, including Réunion Island, Mauritius, Venezuela, the French West Indies and Myanmar (Romay *et al*., 2014).

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Fig. 28.1. Field of young watermelon (*Citrullus lanatus*) plants in north central Florida, USA.

Many species of aphids that do not reproduce on cucurbits are capable of transmitting the above viruses. The important vector species will vary from region to region (Adlerz, 1987; Castle *et al*., 1992; Basky *et al*., 2001). Understanding which aphids are important in virus spread in a particular region may help in management decisions, such as when to apply oils or whether to remove aphid host plants around the crop.

Management Options for Aphids and Aphid-Vectored Viruses in Cucurbits

Chemical control

Aphis gossypii has become resistant to organophosphate, carbamate, organochlorine (O'Brien *et al*., 1992), pyrethroid (Sun *et al*., 1994) and neonicotinoid insecticides (Koo *et al*., 2014) in various parts of the world, particularly in cotton, but also in field-grown (Hollingsworth *et al*., 1994, Koo *et al*., 2014) and glasshouse cucurbits. In field-grown cucurbits in Hawaii, resistance levels can vary from one field to another, depending on their history of insecticide use (against all insect pests) (Hollingsworth *et al*., 1994). The use of pirimicarb can actually stimulate reproduction in populations of melon aphid that are resistant to this carbamate (Rongai and Cerato, 1996).

Where resistance to insecticides is not a problem, the melon aphid has been relatively easy to manage as a direct pest of cucurbits. More selective insecticides such as neonicotinoids (imidacloprid, thiamethoxam, clothianidin and dinotefuran are registered for use on cucurbits in the USA) and pymetrozine give long-lasting control and increased yields (e.g. Webb, 1996) (Fig. 28.3). Additional active ingredients specific for aphids (flonicamid and flupyradifurone) are also registered for use in the USA.

In the USA, neonicotinoids are used mainly to control *Bemisia tabaci* (sweet potato whitefly), with aphid control a secondary benefit. No experimental evidence exists for the reduction of secondary spread of non-persistent viruses in cucurbits from using these insecticides. In general, little effect on the spread of these viruses has been found for

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Fig. 28.2. *Zucchini yellow mosaic virus* symptoms in cantaloupe (*Cucumis melo*).

any of the older insecticides (Loebenstein and Raccah, 1980), and some evidence exists that residues increase virus spread in cucurbits, presumably by causing increased aphid movement (Ullman *et al*., 1991; Webb and Linda, 1993). Bees are essential for the pollination of cucurbits (except for parthenocarpic varieties of cucumber grown under protected cultivation) and their preservation must be considered in any pest management programme that makes use of insecticides.

Oils

In Florida, Georgia and South Carolina, where much of the spread of aphid-transmitted viruses in cucurbits is from plant to plant within a field (secondary spread), the use of a highly refined mineral oil (JMS Stylet Oil, Vero Beach, Florida) is recommended to reduce virus spread in squash (Kucharek and Purcifull, 1997; Smith, 2001; Boyhan, 2004), although it does not control aphids on the plants (Webb and Linda, 1993). Mineral oil has been shown to interfere with the retention of virus in the aphid's stylets (Wang and Pirone, 1996). Finding additional chemicals that interfere with transmission would be of great benefit.

Sampling and thresholds

Little information is available about the actual use of specific sampling schemes and thresholds for aphids on field-grown cucurbits. The New York State IPM Program publishes scouting procedures for cucurbits (Zitter *et al*., 2000). Sampling patterns such as a V, W, or X are suggested, with a choice of five sites, varied from week to week, along the path chosen through the field. Early in the season, five whole plants are examined at each site. As vine crops grow and it becomes impossible to distinguish separate plants, ten leaves and five fruits are examined in areas 3.1 m × 3.1 m. For aphids, the number of leaves with five or more aphids is recorded, and if more than 20% of the leaves have aphids, an insecticide treatment may be needed. If many aphids are parasitized or infected with a fungal pathogen, treatment may not be necessary.

Lam and Foster (2002) recommend flagging areas of the field where natural enemies are present in aphid colonies and returning in several days to see if the population of aphids is increasing or decreasing before making a decision to use an insecticide.

In Hawaii (Johnson *et al*., 1989), density treatment levels (DTLs) were estimated for watermelon, based on the type of injury, the potential for aphid population increase and the grower's judgement regarding the amount of damage that could be tolerated. The DTL for *A. gossypii* was set at 20 aphids/leaf in the absence of viruses and zero aphids/leaf in their presence. The lower threshold was not practical, however, and later work in Hawaii showed that it was rarely effective in reducing virus spread (Ullman *et al*., 1991).

Under protected cultivation, growers use yellow sticky traps to monitor for melon aphid. Action must be taken as soon as aphids are found, because of their reproductive capacity. Within a week, populations can increase 10- or 12-fold on glasshouse-grown cucumber (Wyatt and Brown, 1977).

Biological control

Under field conditions, naturally occurring coccinellid beetles, hover-fly larvae and braconid parasitoids

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Fig. 28.3. (a) Cantaloupe, 'Athena', treated with pymetrozine; (b) untreated cantaloupe showing severe crumpling of leaves due to a heavy infestation of melon aphid. (From 1996 field trial at the University of Florida, IFAS, Research and Education Center, Leesburg, USA.)

reduce the number of aphids on cucurbit crops (summarized by Capinera, 2001, for the USA). Most recommendations point to the need to conserve these natural enemies. With more selective insecticides available for managing other pests (USA), this is currently feasible.

The introduction of insect predators and parasitoids to control aphids is limited to crops grown under protected cultivation and is most common in The Netherlands and British Columbia (Ramakers and Rabasse, 1995; Shipp, 2004). The braconid *Aphidius colemani* is used to control melon aphid (Shipp, 2004). It can be introduced by weekly releases of parasitized aphid mummies or reared in a banker plant system, using *Rhopalosiphum padi* (bird cherry–oat aphid) on cereal plants. The predatory midge *Aphidoletes aphidimyza* is also recommended for aphid control in cucumber (Shipp, 2004).

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Host-plant resistance

Resistant and tolerant varieties can provide excellent control of aphid-vectored viruses (e.g. Clough and Hamm, 1995; Tricoli *et al*., 1995; Webb and Tyson, 1997; Walters, 2004). McGrath (2012) has listed the commercially available cucumber, muskmelon or cantaloupe, pumpkin, courgette and yellow summer squash varieties that have resistance or tolerance to one or more viruses, including genetically modified varieties that contain the coat protein genes of one or more viruses (Fuchs and Gonsalves, 1995; Tricoli *et al*., 1995). A cantaloupe variety, 'Hannah's Choice', developed in the USA by M. Jahn, a plant breeder formerly at Cornell University, has resistance to WMV, PRSV-W and ZYMV (Henning *et al*., 2005). Harris Moran released the first pumpkin (*C. pepo*) variety, 'Magician F1', with tolerance to ZYMV (Anon., 2004). In Australia, two 'Jarrahdale'-type pumpkins (*C. maxima*), 'Dulong QHI' and 'Redlands Trailblazer', are highly resistant to ZYMV, PRSV-W and WMV (Herrington *et al*., 2001). There are as yet no commercially available virus-resistant or virus-tolerant varieties of watermelon grown in the USA.

Resistance to *A. gossypii* and its transmission of viruses has been identified in muskmelon germplasm from India (Kishaba *et al*., 1971) and Korea (Pitrat and Lecoq, 1980). However, examples of the practical use of this resistance are lacking. In Bangladesh, local genotypes of ash gourd (*Benincasa hispida*), also known as wax gourd or winter melon, are relatively resistant to *A. gossypii* (Khan *et al*., 2000). The density of trichomes on leaves was correlated negatively with the number of aphids per leaf.

Cross-protection

Cross-protection, the inoculation of plants with a mild strain of a virus to protect against a severe strain (Fletcher, 1978; Fulton, 1986), is another strategy that has been used with some success to control ZYMV in cucurbits (Lecoq *et al*., 1991; Wang *et al*., 1991; Perring *et al*., 1995). In Israel, since 1996, over 2500 ha of cucurbits have been protected from infection with ZYMV by inoculation with a mild strain (Yarden *et al*., 2000). Rezende and Pacheco (1998) reported control in Brazil of PRSV-W in courgette by cross-protection and developed practical methods that growers could use for inoculating plants. The disadvantages of cross-protection include the potential mutation of the mild strain of the virus to a severe form and possible synergistic effects with other viruses (Fulton, 1986).

Cultural control

The role of weeds in the control of aphid-vectored viruses

Two cucurbitaceous weeds have been shown to be sources of PRSV-W in south Florida. Creeping cucumber (*Melothria pendula*) is often heavily infected with PRSV-W. A perennial, it grows back quickly after relatively brief periods of freezing weather and is present as a source of virus for aphids as soon as crops are planted (Adlerz, 1969, 1972a, 1974). A second wild cucurbit, balsam-apple (= balsam-pear) (*Momordica charantia*), also serves as a source of PRSV-W in south Florida (Adlerz, 1972b). The removal of either *M. pendula* or *M. charantia*, however, has been ineffective in reducing incidence of the virus on the cultivated crop (Adlerz, 1981).

In contrast to the importance of weed virus sources in Florida, it is the crops in a desert region in Israel that are the major source of aphids and the viruses they transmit (Ucko *et al*., 1998). Regulations in the Arava region stipulate the removal of vegetable crops and all weeds growing in vegetable crop fields at the end of the growing season. All perennial crop-growing areas must also be kept free of weeds during a 1-month crop-free or phytosanitary period. Instituting this 1-month phytosanitary period during the latter half of June and the beginning of July eliminates virus epidemics in melons and other vegetables in the Arava region.

Mulches

Work by Smith *et al*. (1964) and Kring (1964) first demonstrated the repellent effects of reflective aluminium. Reflective mulches have been improved in the intervening years and are more widely available to growers. More recent studies (Stapleton and Summers, 2002) continue to show the benefits of reflective mulches for reducing early season virus spread, and their use is being recommended except in situations where the use of reflective mulch would delay warming of the soil in spring.

Floating row covers

Floating row covers act as a physical barrier to aphids, both those that colonize cucurbits and

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those that land temporarily and transmit virus. Lightweight covers can be left on squash and cantaloupe plants until flowering, when they must be removed for pollination (Natwick *et al*., 1988; Perring *et al*., 1989; Webb and Linda, 1992), and have the added advantage of excluding all insects, not just viruliferous aphids (Fig. 28.4). Heavier row covers, used for frost protection, allow earlier planting in temperate climates. Earlier planting and delaying the removal of covers may help the crop escape infection with aphid-transmitted viruses. However, cost and disposal problems may limit the use of covers in commercial plantings to situations in which cold protection makes possible earlier harvest and higher prices for the crop.

Living mulches and intercropping

Aphids may be less likely to land on a crop grown with a living mulch because the mulch eliminates the contrast with bare ground that aphids respond to when locating host plants (Kennedy *et al*., 1959, 1961). Living mulches (yellow mustard – *Sinapis alba*, or buckwheat – *Fagopyrum esculentum*) have been tried in Hawaii with courgette (a *Cucurbita pepo*) (Hooks *et al*., 1998). Aphids, both apterae and alatae, were greatly reduced and infection with PRSV-W delayed in mulched plots.

Increased plant diversity may increase the abundance of insect predators and parasitoids (Andow, 1991). Marcovitch (1935) found that the number of melon aphids was much reduced on watermelon when it was grown in a mixed planting with turnips. Turnips were planted a month before the watermelon and became heavily infested with *Lipaphis pseudobrassicae* (mustard aphid). Natural enemies became very numerous on the turnips and presumably kept melon aphids from becoming abundant enough to damage the watermelon. *Aphis gossypii* severely affected a solid planting of watermelon only 110 m away.

Although research continues (Frank and Liburd, 2005; Damicone *et al*., 2007; Nyoike and Liburd, 2010), the use of living mulches and intercropping

Fig. 28.4. Floating row covers over courgette (*Cucurbita pepo*). (From field trial at the University of Florida, IFAS, Research and Education Center, Leesburg, USA.)

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has been difficult to implement in commercial cucurbit production.

Sanitation and removal of infected plants

Additional cultural recommendations for managing aphid-vectored viruses include destroying plants showing symptoms in the early stages of an epidemic (Blancard *et al*., 1994), ploughing-in the crop immediately after harvest, removing volunteer cucurbits in the vicinity of production fields and avoiding sequential plantings when virus is a problem (Kucharek and Purcifull, 1997).

For glasshouse crops, recommended practices include screening vents and keeping nearby areas free of weeds (Gilkeson, 1994).

IPM Programmes for Cucurbits that Include Aphid Management

In the USA, recommendations to growers for managing aphid-borne viruses include multiple tactics, as either a list of possible measures or a specific combination. Smith (2001) recommended that South Carolina squash growers used a combination of virus-resistant varieties (depending on what their buyers would accept), reflective mulch for early season control and the application of highly refined mineral oils to interfere with transmission. In Arizona and southern California (Palumbo and Kerns, 1996), both *M. persicae* and *A. gossypii* attack cucurbits. Recommendations include eliminating alternate host plants such as mustards for *M. persicae*, using row covers over the seedbed until first bloom and using reflective mulches. Monitoring flight activity and aphid species composition with yellow sticky traps is recommended. It is suggested that melons planted in January or February, before peak aphid flights occur in California, be treated at planting with a soil-applied systemic insecticide such as imidacloprid or thiamethoxam. The same tactics are suggested for *A. gossypii*. The conservation of naturally occurring predators and parasitoids may keep this aphid under control if foliar insecticides are avoided.

The University of California cucurbit IPM guidelines for insect pests (Coviello *et al*., 2005) provide no threshold for aphids, but note that naturally occurring predators and parasitoids can limit populations. Reflective mulches, row covers and weed control are suggested. Growers are encouraged to plant sweet alyssum (*Lobularia maritima*) around the field as a nectar source for parasitoids. Delaying planting until the spring aphid flight is over is another option. Growers are cautioned not to apply excess nitrogen fertilizer.

In Western Australia, recommended cultural controls for managing aphid-transmitted viruses include destroying volunteer cucurbits and weeds that could be a source of virus, removing infected plants (roguing) during the growing season and avoiding planting near older cucurbit crops (Coutts and Jones, 2005). Virus-resistant varieties are a good option, even when resistance is incomplete. Other measures found useful in multi-year field studies included planting upwind of virus sources and using tall barriers of millet (a non-host for the virus). Planting to avoid peak aphid flights when crops were young was also helpful (Coutts *et al*., 2011). How many of these tactics growers will employ is not known.

Shipp (2004) outlines an IPM programme for cucumber grown in protected culture. Components of this programme include monitoring with yellow sticky traps, releases or banker plant production of *A. colemani*, physical exclusion of pests, sanitation and selective use of pesticides when pests increase too quickly for biological control to work. In The Netherlands, practices have been developed that allow growers to use an IPM label for their crop (Ramakers and Rabasse, 1995). Specialized advisors are seen as essential for the success of biologically based IPM programmes in protected cultivation (Shipp, 2004).

Executive Summary

Especially where virus transmission is the major problem of aphid presence, chemical control with newer products such as imidacloprid is normal, particularly as many *A. gossypii* populations are resistant to older compounds. Thresholds and monitoring protocols for aphids are available in some situations, though the threshold varies from place to place. Monitoring with sticky traps is common practice in protected cultivation.

Biological control by releasing parasitoids or establishing them on banker plants is the main form of aphid control on cucurbits in glasshouses, where *A. gossypii* has frequently developed resistance to insecticides. There is no release of natural enemies on field crops, though many growers aim to conserve local natural enemies from damage from foliar sprays as far as possible. Cross-protection (inoculating plants with a mild strain of a virus) has shown some success.

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Highly resistant varieties are available (not commercially available for watermelon), usually as tolerance to virus rather than resistance to aphids. In the USA, courgette varieties with virus resistance transferred by traditional plant breeding are gaining in acceptance. However, in other parts of the world, aphid- or virus-resistant varieties are little used, as susceptible varieties have more desirable agronomic properties.

Cultural control involves the use of reflective mulches and crop covers, with some growers promoting biological control by providing nectar plants. The removal of weed sources of cucurbit viruses is also recommended. There are many other cultural measures available for inclusion in IPM programmes, such as delaying planting and limiting nitrogen applications.

There is no use of semiochemicals.

Several IPM programmes are available to growers. They involve a combination of control methods, though such combinations do not seem to be designed intentionally to exploit any synergism between them.

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29 IPM Case Studies: Seed Potato[1]

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Introduction

As potato is predominantly vegetatively (clonally) propagated; viruses that are systemic within the plant can be transmitted from one generation to the next through the planting of infected tubers. The resulting virus-infected plants provide a source of inoculum during the growing season. Approximately 40 viruses infect cultivated potatoes, of which 13 are primarily transmitted by aphids (Valkonen, 2007). The most widely distributed and common viruses, and therefore the most economically important viruses, are the aphid-transmitted polerovirus *Potato leaf roll virus* (PLRV), the potyviruses *Potato virus Y* (PVY) and *Potato virus* A (PVA) and the carlaviruses *Potato virus M* (PVM) and *Potato virus S* (PVS) (Gopal and Khurana, 2006). In Scotland, aphid-transmitted viruses are responsible for over 75% of the virus symptoms seen in classified seed potatoes.

PVY is considered to be the most economically damaging virus in cultivated potatoes, having superseded PLRV in recent decades. Economic losses caused by potato viruses may be quantitative (yield reduction from fewer and/or smaller tubers) or qualitative (effect on tuber appearance and/or processing quality – Fig. 29.1). The level of loss depends on the virus, the virus strain, the cultivar, the growing conditions and whether the infection is primary (current-season infection) or secondary (passed on from the mother tuber following infection in previous seasons). Viruses can affect quality by producing external symptoms, e.g. potato tuber necrotic ring disease caused by the PVY strain PVY^{NTN}, or internal tuber symptoms, e.g. net necrosis caused by PLRV.

Potato Viruses and their Aphid Vectors

Virus transmission by aphids is traditionally categorized by the duration of the period over which the virus is retained by the vector (Chapter 15, this volume). PLRV is circulative in the insect and is transmitted in a persistent manner, whereas PVY and most other aphid-transmitted potato viruses are stylet-borne and transmitted non-persistently. Because of the length of the acquisition phase and the latent period before the aphid is able to transmit PLRV, the important vector species are those that colonize and reproduce on potato (Ragsdale *et al*., 2001). Worldwide, *Myzus persicae* (peach–potato aphid) is generally the most economically important aphid vector as a consequence of both its abundance and efficiency as a vector of PLRV (Hille Ris Lambers, 1972; Beemster and de Bokx, 1987; Raman and Radcliffe, 1992; Robert and Bourdin, 2001).

PVY is now considered to be the potato virus responsible for the greatest economic losses worldwide (Valkonen, 2007). PVY is responsible for a range of foliar and tuber diseases, depending on virus strain, cultivar, environment and whether the infection is primary or secondary. The rings of swollen/sunken necrotic tissue characteristic of potato tuber necrotic ringspot disease (PTNRD) make tubers unmarketable, and are among the most extreme symptoms of PVY infection. PVY exists as a diverse range of strains or variants, and recombination events between these strains are relatively common (Karasev and Gray, 2013). For PVY, the helper component proteinase (HC-Pro) acts as a molecular 'bridge' between the virus and the aphid stylet and is believed to determine the specificity of the virus–vector relationship. While most aphid species are

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Fig. 29.1. Investigation of tuber cracking in potato plants showing virus symptoms. Potato tubers cv. Estima showing symptoms with (right) and without (left) virus. (Photograph courtesy of SASA.)

understood not to be able to transmit PVY, a large number of species (more than 50) have been reported to transmit PVY (Harrington *et al*., 1986; Sigvald, 1987, 1989; Heimbach *et al*., 1998; Ragsdale *et al*., 2001). Most of these species are considered transient, never colonizing potato. *Myzus persicae* is widely considered to be the most efficient vector of PVY (MacGillivray, 1981), but the greater abundance of some less efficient vector species can make them more important in PVY epidemiology (Piron, 1986; Sigvald, 1987; Boiteau *et al*., 1988; Weidemann, 1988; Harrington and Gibson, 1989).

Monitoring Aphids

Aphids transmit viruses when they move from an infected plant to an uninfected plant; assessments of the risk of transmission are therefore best made by monitoring aphid flight activity. The association of virus spread with aphid flight activity is well documented (Hille Ris Lambers, 1972; van Harten, 1983). The two most frequently used techniques are: coloured water pan traps, which attract and trap alate aphids, and suction traps, which sample alates flying at a set height by the suction and filtration of air at a set rate (Chapter 16, this volume).

Each technique has its own characteristics, benefits and drawbacks. An awareness of potential bias should always be considered when assessing the risk of virus transmission based on aphid monitoring data. For example, water pan traps monitor aphids in crops at the foliage level, but may not reflect the true pattern of aphid abundance across the whole field. Suction traps are less likely to be influenced by positional effects on a macro scale, but will not reflect the exact abundance and composition of aphid populations at field level.

In the UK, a network of 16 suction traps is operated by the Rothamsted Insect Survey. A network of approximately 100 yellow water pan traps sited in growers' fields is operated by the Food and Environment Research Agency (Fera). This provides a standardized continuous means of aphid monitoring (the suction traps), supplemented with data collected at field level with a wide coverage over the majority of the potato-growing area of the country. Data are made available to growers showing when aphid populations are on the increase, or when populations begin to exceed the long-term means for any specified week; for example, Fig. 29.2 from the Science and Advice for Scottish Agriculture (SASA) website.

Mathematical Modelling

Developing epidemiological models for aphid-vectored viruses in potato production requires the incorporation and evaluation of many variables,

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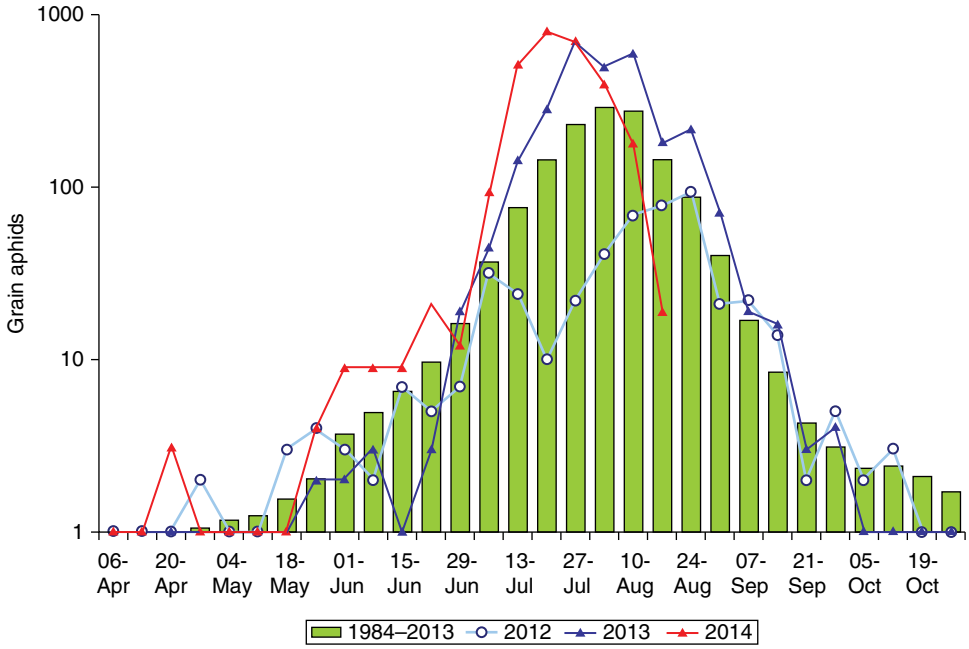

Fig. 29.2. Weekly total catches of the grain aphid *Sitobion avenae* in three suction traps located close to the main areas of potato production in Scotland. The catches for recent years, 2012–2014, are compared with a 30-year mean 1984–2013. From SASA website: http://www.sasa.gov.uk/wildlife-environment/aphid-monitoring/cereal-aphids

including the relative efficiency factor (REF) of each aphid species as a vector of a specific virus, relative to the vectoring efficiency of *M. persicae*. The REF values published from different studies (e.g. van Harten, 1983; De Bokx and Piron, 1990; Verbeek *et al*., 2010) have been variable. This may have resulted from the use of different virus strains or isolates, variation between the biotypes, or clones of aphids used, as well as the method used to evaluate transmission efficiency. Verbeek *et al*. (2010) defined new REF values for PVY strains, PVY^{N}, PVY^{NTN}, $PVY^{N\text{-}Wi}$, for a wide range of aphid species. They found differences in transmission efficiency between different clones of *M. persicae*, an effect already known for persistently transmitted viruses, e.g. *Barley yellow dwarf virus* (Smyrnioudis *et al*., 2001). They also showed that, for some aphids, the REFs were higher for the recombinant strains of PVY.

Coupled with aphid monitoring data, REFs are used in the UK to compare the risk of virus transmission between seasons and between locations. A vector pressure index for each species of aphid is calculated by taking the catch of that species over a specific period and multiplying this by the REF. The overall vector pressure index for a site over a period is the sum of the respective pressure indices for all vector species. Information of this nature is published on the Fera website for the UK yellow water pan traps and on the SASA website for suction traps located in Scotland (Scottish Agricultural Science Agency, 2016). In general, action thresholds for the vector pressure index are not established, as the risk of virus transmission varies according to the levels of inoculum both within the crop and in the vicinity of the crop, the susceptibility of the potato variety to the virus and the maturity of the potato crop and the end use of the crop, e.g. high grade seed, ware consumption. This same variation presents a considerable challenge for evaluating the effectiveness of any models based on REFs in assessing the risk of virus transmission. One approach is to collect extensive information on changes in virus incidence, such as the data recorded during crop inspections in a seed potato classification scheme. These data can then be related to aphid vector pressure index data collected within the area covered by that classification scheme.

Data collected during inspections of the Scottish seed potato crop (*c*.5000 crops planted over 11,000 ha *per annum*) show changes in the incidence of the

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Fig. 29.3. Potato cv. Pentland Dell showing foliage symptoms of leaf roll caused by PLRV. (Photograph courtesy of SASA.)

symptoms produced by PLRV to be correlated strongly with the abundance of *M. persicae* in three suction traps during the preceding year (only symptoms of secondary infection are seen at crop inspection). In Scotland, 87% of the variance in year-to-year changes in the incidence of leaf roll symptoms (Fig. 29.3) during the period from 1969 to 1992 can be accounted for by the annual catch of *M. persicae* in the Scottish aphid suction traps (Brewer and Pickup, 1996). This study found no evidence to suggest that other aphid species might play a significant role in PLRV transmission in Scotland. Fig. 29.4 shows that the relationship found by Brewer and Pickup still holds for PLRV transmission in Scottish seed potato crops.

A similar approach has been taken for modelling changes in the incidence of the symptoms attributed to PVY in the Scottish seed potato crop. In this case, the pattern of changing incidence of PVY closely follows the abundance of three species of cereal aphid, *Metopolophium dirhodum* (rose–grain aphid), *Sitobion avenae* (English grain aphid) and *Rhopalosiphum padi* (bird cherry–oat aphid) (Fig. 29.5). As with PLRV, the relationship only holds if the incidence of PVY is predicted using aphid and virus data in the preceding year, again indicating that symptoms of secondary infection are seen at crop inspection.

A similar approach was taken by Kirchner *et al.* (2011), who investigated the transmission of PVY in the high-grade seed production region of Finland in relation to yellow water pan trap catches of alate aphids from several fields. Changes in PVY incidence were modelled on counts of aphid vector species, their REF values, varietal resistance and the initial infection rate in the seed crops. While initial virus levels and early-season vector flight activity were the most important factors, only the models that included *Aphis fabae* (black bean aphid) improved the fit of the model with the incidence of PVY in the harvested tubers. The explanatory power of the models was lost if this species was omitted. Steinger *et al.* (2015) compiled virus incidence data, dominated by PVY, from three susceptible varieties within the Swiss seed certification programme over the period 1989–2012. They concluded that early migrating *Brachycaudus helichrysi* (leaf-curling plum aphid), rather than *M. persicae*, was the main vector of PVY in Switzerland.

Integrated Pest Management

Approaches to the management of virus spread in potato can be categorized as preventive or therapeutic (Ragsdale *et al.*, 2001). Prevention focuses on reducing inoculum, a primary objective of all seed potato certification programmes, with therapeutic action focused on vector reduction. Because PLRV and PVY differ in their transmission characteristics, different approaches are required to manage them. Aphicides to control vectors often limit the spread of PLRV effectively, although insecticide resistance is an increasing problem. Aphicides are less effective for the control of PVY where virus acquisition and transmission may occur before aphicides can act (Ragsdale *et al.*, 1994; Radcliffe and Ragsdale, 2002) and where management tends to rely on a wider range of tactics.

Cultural Control

Seed potato certification

Many countries have established official seed potato certification schemes to provide quality control of

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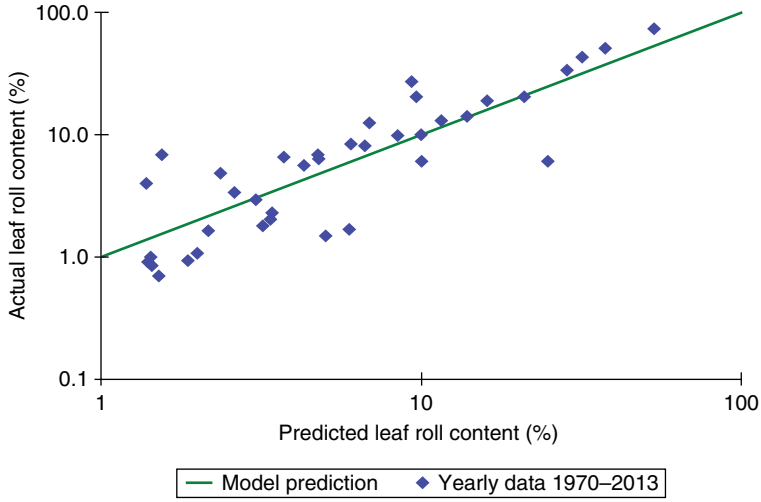

Fig. 29.4. The relationship between the area of the Scottish seed potato crop containing plants exhibiting symptoms of potato leaf roll virus (PLRV) and the catches of the peach–potato aphid, *Myzus persicae* (MP), in the Dundee 12.2 m aphid suction trap in the previous year (t–1). The relationship for the model: PLRV(t) = 0.89PLRV(t–1) + 0.34MP(t–1) – 1.36 (adjusted $r^2 = 0.79$, $p = 7.7\ E^{-15}$).

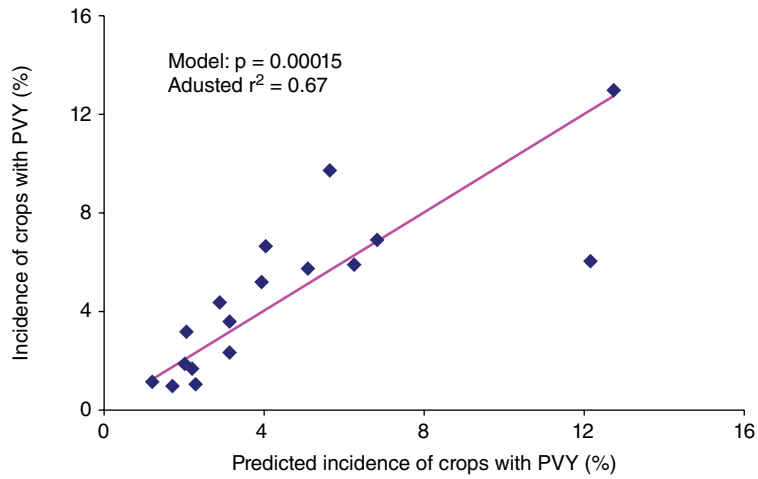

Fig. 29.5. The relationship between the area of the Scottish seed potato crop containing plants exhibiting symptoms of PVY and the catches of three cereal aphids, *Metopolophium dirhodum*, *Sitobion avenae* and *Rhopalosiphum padi* (CA), in three Scottish aphid suction traps (Elgin, Dundee and Edinburgh) in the previous year (t–1). The relationship for the model: PVY(t) = 0.78PVY(t–1) + 0.28CA(t–1) – 2.33 (adjusted $r^2 = 0.67$, $p = 0.00015$).

propagation material and minimize the virus inoculum. Tolerances are usually relaxed incrementally with successive generations of propagation, and seed lots are downgraded or rejected outright if infection exceeds tolerance for the grade. In most schemes, the initial planting material should be free of virus infection. Although field propagation preferably takes place in areas of low vector (aphid) pressure, the risk of introducing virus into the seed crop inevitably increases with successive generations, so a maximum of seven field generations is a typical limit. As the initial planting material should be virus free, any virus has first to enter the potato crop from an external source. Following initial infection, further proliferation will be a combination of amplification of the inoculum now present within

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the crop and the acquisition of further infection from external virus sources. Effective management of virus within the crop requires an assessment of the relative risks presented by the virus introduced with the parental stock and the virus inoculum within the environment of that crop. Virus management depends on the ability to intervene to minimize the chance of transmission from either source.

During seed multiplication, roguing can limit the extent of the inoculum available for transmission. Pesticides may be used to control virus vectors and, in some countries, the use of official dates of haulm destruction has proved an effective tool in controlling virus spread in seed potato crops. Forecasting the arrival of aphid vectors (Chapter 16, this volume) may improve the timing of pesticide application and haulm destruction.

Crop isolation from virus sources

Ideally, the propagation of seed potatoes should occur in localities isolated from potential sources of inoculum. Many US states and Canadian provinces have established seed farms in geographically isolated areas or designated growing regions where potato production is limited to seed (Slack, 1993). However, in most countries, there is little isolation of late-generation seed and commercial potato production.

An analysis of the horizontal transmission (clean parent crop, infected daughter crop) of virus, based on the presence of mosaic symptoms (Fig. 29.6) in Scottish seed crops from 2009 to 2011 demonstrated that crops grown within districts (administrative areas within counties) with a high area of potato production (both seed and ware crops) were more likely to acquire virus infection from external sources (Fig. 29.7). This suggests that, in Scotland, other potato crops and not weeds are the main sources of virus inoculum. Seed potato growers generally have limited flexibility in locating their fields, and thus other cultural control methods and vector management assume greater importance.

Roguing

Physical removal of rogues from seed potato fields, in particular plants exhibiting symptoms of virus infection, has long been an important virus management tactic (Thresh, 1988). The goal of roguing is to remove all infected plants before winged aphids arrive and virus transmission occurs. Latent infection and varieties that do not exhibit clear symptoms of infection limit the effectiveness of roguing, as infected plants are missed and high levels of inoculum remain in the field.

Groundkeepers and volunteers

Groundkeepers (potato plants growing from non-harvested potato tubers) or volunteer plants (potato plants originating from true potato seed) can be a significant source of virus inoculum, particularly when present in a field used to produce higher-grade seed crops. Surveys of the incidence of virus in groundkeepers typically show higher infection rates than in potato crops in the region, largely because they may have been present for many more generations. Jones *et al.* (1996) found infection levels of 60–97% in harvested tubers when an uninfected seed crop was planted in fields in which

Fig. 29.6. Potato cv. Shepody showing foliage symptoms of severe mosaic caused by PVY. (Photograph courtesy of SASA.)

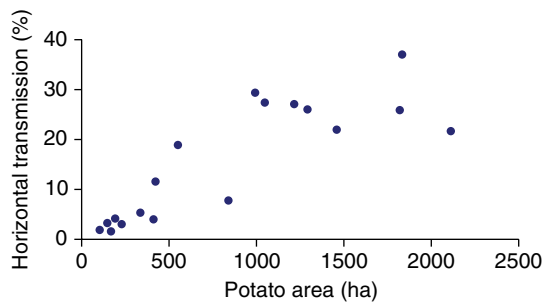

Fig. 29.7. The effect of the total area of potato production within a district on the incidence of horizontal transmission of mosaic-causing viruses to daughter seed crops.

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groundkeepers accounted for 4–8% of potato plants present, of which 31–93% were found to be infected, predominantly by PVY^N.

Chemical control

Insecticides

Managing persistently transmitted viruses by controlling aphid populations with insecticides is generally far more effective than the management of non-persistent viruses. Among the reported successes in controlling virus spread with insecticides (all crops and insect vectors), 94 of 119 cases involved persistent and semi-persistent viruses, whereas most failures, 32 of 48 cases, involved non-persistent viruses (Perring *et al*., 1999).

By suppressing the development of colonizing aphids within the crop, insecticides are the most practical means of interrupting the spread of PLRV from within-field sources. This has been attributed to the extended post-acquisition latent period before an aphid can transmit (DiFonzo *et al*., 1995). Insecticide resistance has become an increasing problem, particularly in the control of *M. persicae*. Genetic characterization of clones of *M. persicae* using microsatellite markers has identified a turnover of insecticide resistance mechanisms in the UK (Kasprowicz *et al*., 2008; Fenton *et al*., 2010). Insecticide usage in commercial crops favours those new immigrant clones that possess a greater selection of insecticide resistance mechanisms (Chapter 19, this volume) and the capacity to survive in field conditions. Clones carrying super-knock down resistance to pyrethroid insecticides and resistance to dimethyl carbamates, through a modified acetylcholinesterase (MACE), are now dominant in intensive agriculture across northern Europe (Fontaine *et al*., 2011). The development of resistance to neonicotinoid insecticides in populations of *M. persicae* in southern Europe has also been reported (Slater *et al*., 2012).

For non-persistent viruses like PVY, where the acquisition and inoculation periods can be as brief as a few seconds, the potential for insecticides to limit virus transmission is much reduced (Perring *et al*., 1999). To be effective, an insecticide would have either to kill an aphid or prevent it from feeding with immediate effect. While the rapid 'knock-down' ability of pyrethroids has been shown to reduce PVY transmission in the laboratory, less success has been found with field trials (Collar *et al*., 1997; Gibson *et al*., 1982; Perring *et al*., 1999).

Mineral oils

There is now a considerable body of evidence that mineral oils can reduce the transmission of potyviruses, with reductions in the range of 30–60% compared to untreated controls (Al Mrabeh *et al*., 2010). Mineral oil has been demonstrated to be more efficient than plant vegetable oil (Martin-Lopez *et al*., 2006; Wróbel, 2012). Evidence for oil-based treatments performing significantly better than control plots has been demonstrated for both PVA and PVY^N (Dawson *et al*., 2015). The actual mode of action of mineral oils in inhibiting the transmission of non-persistent viruses is not fully understood; one hypothesis suggests that oil affects the interaction between the HC-Pro of the virus and the aphid mouthparts or alimentary tract (Qiu and Pirone, 1989). Phytotoxic effects and consequent reduction in yields have been reported in many mineral oil studies when applications exceed concentrations of 1% (Al Mrabeh *et al*., 2010).

Biological control

The contribution of parasitoids, predators and fungal entomopathogens to the suppression of aphid populations can be overlooked easily by potato growers. It might seem unlikely that biological control agents could be effective given the intensive use of pesticides in many potato production systems. However, outbreaks can be induced by the inappropriate application of insecticides, particularly if the resistance status of the aphids is overlooked so that the insecticides have greater impact on natural enemies (ffrench-Constant *et al*., 1988; Harrington *et al*., 1989; Lagnaoui and Radcliffe, 1998).

Host-plant resistance

Modern potato varieties are tested routinely for resistance to virus, usually by setting up field trial plots containing infected potato plants and comparing the acquisition of virus by a candidate variety with that by standard control varieties of known resistance levels (Chapter 15, this volume). This can be a costly method for assessing resistance, and the results can be dependent on the strain of virus selected for the trial. Historical data on resistance may no longer be valid if that strain is no longer prevalent in commercial crops.

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Executive Summary

The aphid problem in potatoes is principally a virus problem. Potato growers rely on sophisticated and complex multi-tactic pest management programmes to limit the spread of potato viruses in propagation material. Tight tolerances for viruses in seed potato certification schemes provide the primary defence against virus proliferation in the production system.

Cultural control is important. The presence of groundkeepers/volunteer potatoes can introduce virus infection into a crop. Thorough roguing to remove any infection at the earliest opportunity is a key element in an effective virus management programme. Where potato crops are grown in proximity to other crops, the risk of the crop acquiring virus from external sources increases. Weeds are unlikely to be a major source of virus in many temperate areas of potato production.

Worldwide, the most important vector of PLRV is *M. persicae*. The virus is spread by both apterae and alatae. Growers rely heavily on aphicides, which, if the necessary knowledge of the incidence of insecticide resistance is available, are effective in limiting current-season spread.

Worldwide, PVY is now the most economically important potato virus. Due to the speed of transmission of PVY, insecticides generally have minimal effect in reducing virus spread, although the rapid 'knock-down' of pyrethroid insecticides may provide some protection. Mineral oils are increasingly used and are well documented to reduce transmission rates (typically reductions of up to 60%).

Natural enemies do play a role in the regulation of aphid populations, and the prophylactic application of insecticides may lead to uncontrolled aphid outbreaks, particularly when target aphid populations are resistant. However, efficacy in relation to resistance in the aphid population takes precedence over selectivity in choice of insecticide.

Varietal resistance should be considered when establishing virus management programmes, but the emphasis is on resistance to the virus rather than on aphid resistance.

There is no use of semiochemicals to manipulate aphid or natural enemy behaviour.

The regional nature of potato virus management problems presents a compelling argument for industry-wide cooperation between seed potato growers, seed certification agencies, growers of potatoes for fresh market and processing, the processing industry and all parties involved in potato pest management decisions to effect the reduction of virus inoculum and vector abundance.

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30 IPM Case Studies: Cotton[1]

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Introduction

Cotton is an industrial crop of prime importance in numerous producer and consumer countries such as Australia, Brazil, China, India, Pakistan and the USA (ICAC, 2013). The main cultivated species worldwide is *Gossypium hirsutum*. Crop profitability depends on both yield and fibre quality. Cotton production includes a wide range of farming systems, from rainfed, low-input agriculture in developing countries to irrigated, high-input agriculture with high levels of mechanization in Australia, Brazil, or the USA (Fig. 30.1). Among cotton pests, aphids have a special status because of the wide range of damage they can cause to crops, from disease transmission and yield reduction through feeding activities, to honeydew deposition that contaminates the fibre when bolls are open. The resultant 'sticky cotton' is an important limitation to cotton processing.

The cotton or melon aphid, *Aphis gossypii*, is by far the species of greatest economic importance (Leclant and Deguine, 1994; Deguine *et al*., 2007). Several other aphid species can be found on cotton leaves, including *Acyrthosiphon gossypii*, *Aphis craccivora*, *Brachyunguis plotnikovi*, *Macrosiphum euphorbiae* and *Myzus persicae* (Leigh and Goodell, 1996; Williams *et al*., 2011; Bagwell and Baldwin, 2014) and *Aphis medicaginis* in China (Wu and Guo, 2005; Luo *et al*., 2014). The bean root aphid, *Smynthurodes betae*, has been reported on cotton roots (Williams *et al*., 2011).

Damage and Economic Impact

The cotton aphid *A. gossypii* causes three types of damage to cotton (Fig. 30.2): disruption of plant growth by phloem sap feeding, diseases through virus transmission and contamination of cotton fibre by honeydew, resulting in 'sticky cotton'.

Disruption of plant growth

Cotton aphids usually feed on the abaxial leaf surface, and sometimes on plant stems or petioles. Cotton plants infested by phloem-sap-feeding aphids early in the season develop typical 'leaf roll' symptoms. Prolonged aphid infestations can lead to premature leaf abscission and defoliation. Disruption of plant growth by reduction of the leaf area and photosynthesis results in lower fruiting positions (shorter plants), lower fruit retention and delayed harvesting (Deguine *et al*., 1994). Subsequent yield losses are amplified when drought occurs before flowering. During the fruiting stage, sap feeding by aphids has little impact on yield.

[1] Material from the first edition of this chapter has been included, and the contributions of the late François Leclant and Maurice Vaissayre are gratefully acknowledged.

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Fig. 30.1. Diversity of cotton cropping systems: from smallholders in Paraguay (left) to highly mechanized farms in Mato Grosso, Brazil (right). (Photographs courtesy of Pierre Silvie.)

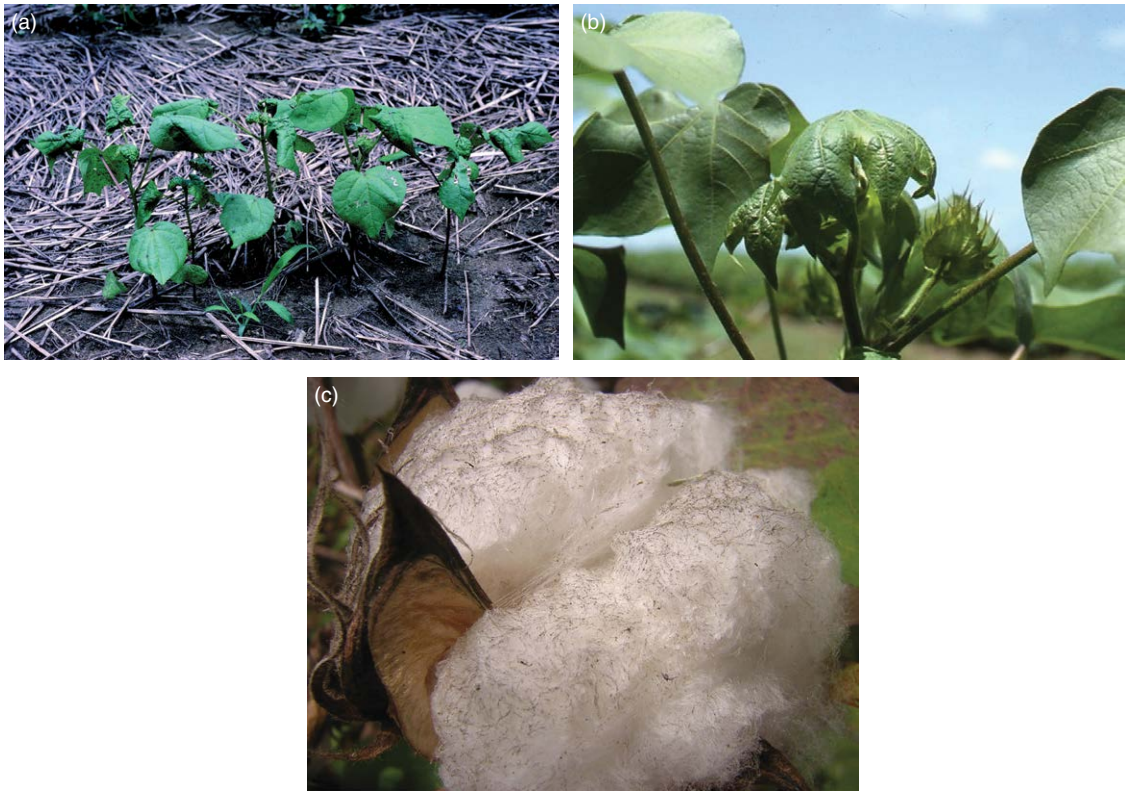

Fig. 30.2. Damage caused by *Aphis gossypii*. From left to right: (a) general stunting as a result of sap feeding. (Photograph courtesy of Pierre Silvie.) (b) Cotton blue disease symptoms on young leaves. (Photograph courtesy of Pierre Silvie.) (c) Sticky cotton. (Photograph courtesy of Thierry Brévault.)

Vector-borne diseases

The cotton aphid can transmit diseases as a vector of viruses (Table 30.1). In Brazil, the characterization of a new luteovirus within the genus *Polerovirus* was published in the 2000s (Corrêa *et al*., 2005), and inheritance studies showed that resistance was conditioned by one dominant gene in CD 401 and Delta Opal varieties (Pupim Junior *et al*., 2008).

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Table 30.1. Diversity of cotton diseases transmitted by *Aphis gossypii*.

Disease	Continent or country	Reference
Cotton blue disease (CBD)	Africa	Cauquil and Vaissayre (1971)
	Asia	Lacape *et al*. (2002)
Cotton leaf roll dwarf virus (CLRDV)	South-east Asia	Cauquil and Follin (1983)
Mosaïco-das-nervuras forma Ribeirão Bonito	Brazil	Cauquil and Follin (1983)
Cotton vein mosaic virus (CVMV)	Brazil	Michelotto and Busoli (2003)
Doença azul	Brazil	Papa *et al*. (2001)
Cotton anthocyanosis virus (CAV)	Brazil	Costa (1957)
	India	Mali (1978)
Cotton bunchy top (CBT)	Australia	Ali *et al*. (2007)

The viral genome was completely sequenced in Argentina by Distéfano *et al*. (2010). Detection of an atypical form with different symptoms has recently been reported in Brazil (Silva *et al*., 2008; Galbieri *et al*., 2010), as well as in Argentina (Distéfano, 2013).

Screening of cotton genotypes for resistance and breeding disease-resistant cultivars, in some cases with the help of marker-assisted selection, is a common approach to manage cotton diseases.

Sticky cotton

Cotton quality can be affected dramatically by end-of-season aphid infestations, due to contamination of the fibre with honeydew (30–40% melezitose). Cotton stickiness caused by sugars is a serious problem for the textile industry, including ginning and spinning. Sticky cotton entails special handling and processing requirements, because honeydew spots adhere to working surfaces and cause residues to build up on textile equipment, leading to losses in productivity and quality (Héquet *et al*., 2007). For growers, sticky cotton means higher costs for pest control and reduced cotton marketability.

The risk of sticky cotton can be minimized by carefully managing late-season aphid populations (using an action threshold) and reducing the period of lint exposure (by accelerating defoliation). In developing countries, cotton topping (i.e. removal of plant terminals) is a way to limit end-of-season aphid populations (Deguine *et al*., 2000; Shwetha *et al*., 2009). In mechanized crops, the use of a defoliant is an alternative.

Economic impact

The economic impact of *A. gossypii* varies with environmental conditions, including seasonal temperatures and rainfall patterns. Yield losses strictly due to aphids are not easy to measure in the field because of the wide range of pests attacking cotton. Some references are given by Kerns *et al*. (2015) in the USA.

In Africa, losses of up to 6.5% seed cotton were reported by Matthews and Tunstall (1994). An average per cent yield loss of 0.15% across the USA was estimated by Hagenbucher *et al*. (2013a) from 2006 to 2012. Also in the USA, aphids reduced yields by 0.04% on average in 2012 compared to 0.7, 0.4 and 0.2% for *Lygus* spp., thrips and bollworms/budworms, respectively (Williams, 2013).

In China, total crop losses due to cotton aphids were estimated globally to decrease from 1.0% to 0.5% following the commercial release of Bt cotton (Wu and Guo, 2005). In South-east Asia, particularly in Vietnam, the aphid-vectored cotton blue disease (CBD) leads to 10–30% yield reduction (Lê Quang *et al*., 2008).

Main Biological and Ecological Traits of the Cotton Aphid

Life cycle

The cotton aphid, *A. gossypii*, is a cosmopolitan and polyphagous species widely distributed in tropical, subtropical and temperate regions (Chapter 1, this volume, describes its taxonomic status and host-associated forms). The aphid displays a wide morphological variability, including pterous (winged) and apterous (wingless) forms (Fig. 30.3). Apterae have a very variable colour, from light yellow to dark green (Nevo and Coll, 2001).

Apomictic parthenogenesis is the main or unique mode of reproduction of *A. gossypii* in the tropics (Leclant and Deguine, 1994). However, in areas with very cold winters in Japan, China, Korea, India and the USA, *A. gossypii* is considered a holocyclic

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Fig. 30.3. Apterous forms and winged adults of *Aphis gossypii* on cotton leaf. (Photograph courtesy of Thierry Brévault.)

species, with a sexual reproduction event on a limited number of primary hosts. The species is characterized by strictly clonal reproduction all year round throughout most of its range in Africa (Ebert and Cartwright, 1997). Under suitable environmental conditions (temperature 26–28°C), it takes only 4–5 days to complete one generation, which allows 50 generations per year. Successive apterous generations can develop on cotton until winged forms are produced in response to environmental changes such as competition for host resources.

Host plants and host races

Hundreds of host plants have been recorded worldwide. In Africa, Deguine *et al.* (1999) listed 658 species of potential secondary host plants belonging to 420 genera and 103 different botanical families. Inaizumi (1980) listed 912 plant species worldwide belonging to 116 different botanical families. This aphid species is considered a pest on cultivated Cucurbitaceae (melon, marrow, courgette, watermelon), Malvaceae (cotton, okra, ornamental hibiscus) and Solanaceae (potato, chilli pepper, sweet pepper, aubergine), and it is also found in abundance in citrus orchards and on many ornamental plants, including chrysanthemums and hibiscus (Ebert and Cartwright, 1997). However, the analysis of genetic diversity by molecular markers has shown that the clonal diversity is structured by the host plant (Carletto *et al.*, 2010). Five host races dominated by asexual clones were unambiguously identified (Cucurbitaceae, cotton, aubergine, potato and chilli or sweet pepper). In cotton-producing regions of sub-Saharan Africa, low genetic diversity was reported, with mainly two genotypes (*Burk* and *Ivo*) detected on cotton. The frequency of one clone (*Burk*) in cotton crops increased significantly throughout the course of the growing season, especially when cotton fields were sprayed with insecticides (Brévault *et al.*, 2008).

Biological regulation

At the beginning of the growing season, populations of *A. gossypii* colonizing cotton seedlings are often regulated by mechanical factors such as the reflection of raindrops from the ground to the underside of the leaves. When relative humidity is high, mainly at night, the epizootics of entomopathogenic fungi can reduce aphid populations significantly. In these conditions, *Neozygites fresenii* can cause 75% mortality of *A. gossypii* populations (Steinkraus *et al.*, 1991, 1995, 2002; Abney *et al.*, 2008). This fungus is relatively active in 'dry' conditions: more than 70% of aphids were infected at the peak of the fungus infection in 1987 in southern Chad, Africa (Silvie and Papierok, 1991).

Natural enemies including predators, parasitoids and entomopathogens play an important role in regulating aphid populations on cotton, especially in the absence of insecticides (Lu *et al.*, 2015; Chapter 11, this volume). The multicoloured Asian ladybird *Harmonia axyridis* is a predator that has spread naturally in many regions of the world, displacing local coccinellids (Koch, 2003). Probably coming from Brazil or Argentina, where it had been introduced for biological control in greenhouses, this species has eliminated all aphids and other coccinellids on cotton plants in south Paraguay (Silvie *et al.*, 2014). Parasitoids such as *Lysiphlebus testaceipes*, which is a very common species, are able, in unprotected cotton, to parasitize the majority of the aphid population at the end of the growing season (Fig. 30.4). In western and central Africa, high rates of *A. gossypii* parasitism by *Aphelinus albipodus* have been observed at the end of the cropping season when insecticides are no longer sprayed on cotton (S. Nibouche, unpublished) (Fig. 30.4).

Tools for IPM

Conventional IPM tools can be appropriately combined for the management of *A. gossypii* populations: host-plant resistance (to aphids or aphid-borne

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Fig. 30.4. Aphids mummified by (left) *Lysiphlebus testaceipes* (photograph courtesy of Pierre Silvie) or (right) *Aphelinus albipodus* (photograph courtesy of Thierry Brévault) on cotton leaves at the end of the growing season.

diseases), cultural practices and conservation or enhancement of biological control of aphids. When necessary, insecticide spraying based on action thresholds is recommended. Seed treatments with neonicotinoids are generally applied as a preventive measure to protect seedlings.

Host-plant resistance

Resistance to aphids has been demonstrated in *Gossypium arboreum* (Reed *et al*., 1999). Regarding *G. hirsutum*, some traits such as red foliage (El-Zik and Thaxton, 1989), high gossypol content (Du *et al*., 2004), or 'okra' leaf have been identified as conferring resistance to aphids. Nibouche *et al*. (2008) showed that leaf hairiness increased cotton susceptibility to *A. gossypii*, confirming earlier work (Weathersbee *et al*., 1995; Zarpas *et al*., 2006). However, these traits are not necessarily considered by cotton breeders, who focus mostly on resistance to virus-borne diseases.

Cultural practices

Numerous cultural practices are known to limit the development of aphid populations, including planting date and plant density. Early planting is generally recommended in regions where low temperatures or drought occur in the late season. Early harvesting is also recommended to prevent sticky cotton.

Cotton volunteers and ratoon plants have to be eliminated immediately after harvesting to avoid the risk of aphid multiplication and virus transmission. In Brazil, this is done especially in regions where the soybean–cotton rotation is adopted. Cotton volunteers can be hidden by soybean plants and only seen after the harvest of soybean (Fig. 30.5).

Several authors have noticed the generally positive role for the limitation of aphid population at the beginning of the cropping season of a mulch background or cover crops (Jones *et al*., 2001; Döring and Chittka, 2007).

Suitable fertilization is also important. Nitrogen excess, particularly late season, may delay leaf senescence and extend the cotton plant cycle, leading to favourable conditions for aphid population growth and a higher risk of sticky cotton (Cisneros and Godfrey, 2001). Similarly, late-season irrigation can favour aphid outbreaks and honeydew production (Slosser and Parajulee, 2001).

Biological control

Biological control of cotton aphids by predators, parasitoids and pathogens has been studied extensively. Cotton aphids have a number of predators and parasitoids, but these are usually suppressed by insecticide sprays. Action of these aphidophagous species can be enhanced in different ways (Table 30.2).

In northern China, relay intercropping winter wheat with cotton (Fig. 30.6) was described by Ma *et al*. (2006) and Zhang *et al*. (2007). Winter wheat serves as a reservoir of the aphid *Sitobion avenae*, a good prey for arthropod predators but also a host of *Aphidius gifuensis*, which parasitizes both cotton aphids and wheat aphids.

In north-eastern Brazil, recent studies have encouraged the adoption of a strip intercropping system based on the association of cotton with *Foeniculum vulgare* (Ramalho *et al*., 2012) (Fig. 30.6). This crop hosts the fennel aphid, *Hyadaphis foeniculi*, prey of

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Fig. 30.5. Cotton volunteers grown inside a soybean field (observed after harvest of the soybean) in Mato Grosso, Brazil. (Photograph courtesy of Pierre Silvie.)

Table 30.2. Techniques for conserving or enhancing numbers of natural enemies of *Aphis gossypii*.

Action	Objective	Reference (year, country)
Planting cotton field margins with maize, sorghum or cowpea	To conserve predators	Mohan *et al*. (2014, India)
Spraying yeast-based food formulations	To attract and/or to enhance predators	Mensah *et al*. (2012, Benin)
Intercropping cotton with:		
– safflower (*Carthamus tinctorius*)	To increase predation	Lê Quang *et al*. (2008, China)
– leguminosous plants	To conserve and enhance coccinellids and syrphids populations	Mohan *et al*. (2014)
– maize		Ouyang *et al*. (2012)
Relay intercropping with wheat	To increase predation by coccinellids	Ma *et al*. (2006, China) Zhang *et al*. (2007, China)
Strip intercropping with *Foeniculum vulgare*	To preserve coccinellids on alternate host and to enhance predation	Ramalho *et al*. (2012, Brazil)

the coccinellids *Cycloneda sanguinea* (L.), *Scymnus* spp. and the lacewing *Chrysoperla carnea*. By contrast, in Oklahoma, Phoofolo *et al*. (2010) reported no effect of a relay intercropping sorghum system with cotton, wheat and lucerne as sources of coccinellids.

Augmentative biological control is another option offered to cotton growers (Knutson and Tedders, 2002).

Cotton aphid management in organic cotton

Intercropping cotton with other useful crops to promote biological control is widely recommended by NGOs promoting organic cotton production by small-scale farmers. Some other methods, including cultural practices and the use of natural plant

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Fig. 30.6. Cotton intercropping systems (left) in relay with winter wheat in northern China and (right) in strip with fennel in north-eastern Brazil. (Photographs courtesy of Lizhen Zhang, China Agricultural University, and Dr Francisco Ramalho, EMBRAPA Algodão, Brazil.)

compounds (e.g. neem extracts), are used to keep pests under control. In India, for example, a 'Top Ten' mixture is recommended with the adoption of an action threshold of 20% infested plants (Eyhorn *et al*., 2005).

Chemical control

Insecticides can be applied as seed treatments or foliar sprays. They should be selected carefully, as many populations of cotton aphid are resistant to particular insecticides, and because most predators and parasitoids are killed by broad-spectrum compounds.

Seed treatment

Seed treatment is a good way to control sucking pests at the beginning of the season. Active ingredients most frequently used today belong to the class neonicotinoids. As an example, in India, imidacloprid or thiametoxam are used at the rates of 5–7 g/kg and 10g/kg of seeds, respectively (Mohan *et al*., 2014).

Foliar insecticides

Insecticides recommended to manage cotton aphid populations include organophosphates (malathion, methyl parathion), carbamates (carbosulfan, carbaryl), neonicotinoids (imidacloprid, acetamiprid, thiametoxam), organochlorines (endosulfan) and pyrethroids. More recent active ingredients include pymetrozine or flonicamid. The use of IPM-compatible insecticides, such as neonicotinoids (acetamiprid) or flonicamid, should be encouraged on cotton and relay crops to control aphids. Spraying paraffin oil is an option currently proposed to Australian growers for aphid control (Najar-Rodríguez *et al*., 2007; Leven *et al*., 2015), either used alone or mixed with a reduced (½) rate of chloronicotinyl (R. Mensah, unpublished). In any foliar treatment, the spraying technique plays an important role in the efficacy of the application, and can explain some failures in aphid control. Ultra low volume (ULV) and very low volume (VLV) sprays do not provide satisfactory coverage of the aphids located on the undersides of leaves (Deguine *et al*., 2004).

Insecticide resistance (see Chapter 19, this volume, for resistance mechanisms)

The cotton aphid emerged as a major cotton pest in the late 1980s, when many recommended insecticides failed to provide satisfactory control. Since the first chemical failure was reported in 1928 with hydrocyanic acid, resistance to organophosphates, carbamates, pyrethroids (Chapter 19, this volume) and, more recently, neonicotinoids has also developed. Resistance to insecticides in field populations of *A. gossypii* has been documented worldwide, including Africa (Gubran *et al*., 1992; Nibouche *et al*., 2002), Asia (Sun *et al*., 2005; Ahmad and Arif, 2008), Australia (Herron *et al*., 2001), Europe (Foster *et al*., 2007) and the USA (O'Brien *et al*., 1992). In a recent study, Carletto *et al*. (2010) showed that insecticide resistance traits differed among and within host races in *A. gossypii*. Of the

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two main genotypes detected on cotton in sub-Saharan Africa, *Burk* showed multiple resistance to cypermethrin (pyrethroid) and profenofos and monocrotophos (organophosphates), while *Ivo* remained fully susceptible to these commonly used insecticides (Brévault *et al*., 2008). This could explain the low diversity and prevalence of the multi-resistant genotype *Burk* observed in cotton fields. These findings have implications for improving aphid control and resistance management by using appropriate insecticides according to the genotypes occurring in the field and their insecticide-resistance traits.

Action thresholds

Chemical control targeting cotton aphids can be chosen to prevent potential yield loss and honeydew contamination during boll opening. To implement IPM, monitoring the *A. gossypii* population by trapping winged aphids, field sampling and scouting for nymphs and adults is required. Researchers and consultants have recommended sampling methods and action thresholds for the two types of cropping system, small-scale farms or large mechanized farms. The variation among thresholds can be attributed to the lack of research on the impact of aphids on cotton yields. Basic information is available in publications and illustrated guides.

In small African fields (0.2–5 or 10 ha) or cotton blocks (>50 ha) made of several small plots, cotton plants are sampled weekly, usually 25–40 plants/plot. In Brazil, Fernandes *et al*. (2011) have recently proposed a sequential sampling method for *A. gossypii* based on an economic injury level (EIL) of 0.4 (40% of plants infested).

Action thresholds or economic threshold levels (ETL, the pest density at which control measures must be taken to prevent a rising population from reaching the EIL) have been built using various criteria (Table 30.3).

In intensive cotton farming systems, scouting is used routinely for assessing pest incidence. For aphids, observations are made at least weekly on >100 ha of cotton considered as homogeneous units. In Brazil, thresholds are based on cultivar susceptibility to viral diseases. In Australia, the physiological stage of cotton or the presence of honeydew on fibre are considered (in Maas *et al*., 2013). In the USA, more complete studies by Kerns *et al*. (2015) have recently confirmed the established action threshold of 50 aphids/leaf in Texas and California. Aphid counts can be used directly, or in a kind of 'wait and see' approach, to allow for the short-time dynamics of aphids. Most authors recommend that thresholds should be lowered when there is a risk of plant stress.

The Case of Bt Cotton

Nowadays, most varieties of cotton (70%) deployed worldwide are genetically engineered. Some varieties have been modified to produce insecticidal Cry proteins from *Bacillus thuringiensis* (Bt) that target major lepidopteran pests. During 2010–2012, Bt cotton accounted for 79–95% of cotton planted in Australia, China, India and the USA. An effect of Bt toxins on aphids is quite unlikely because of the mode of feeding of the aphid in the phloem. However, Zhang *et al*. (2006) detected trace amounts of Bt toxins (4.0–6.0 ng/g fresh mass) in *A. gossypii* feeding on Bt cotton. Uptake of toxin at the extremely low level detected in aphids (Romeis and Meissle, 2011) may explain why a majority of field or laboratory tritrophic studies on the non-target effect of Bt toxin on natural enemies through ingestion of their aphid host or prey have not as yet revealed major concerns (Zhao *et al*., 2013). A bivalent transgenic cotton encoding both a Bt toxin and a protease inhibitor gene (a cowpea trypsin inhibitor gene) was reported to affect the survival, fecundity, longevity and feeding behaviour of aphids negatively in the first two generations, but aphid fitness soon increased in the third generation (Liu *et al*., 2005).

Bt cottons have provided several benefits, including reduced insecticide use, regional suppression of key pest species, protection of natural enemies and

Table 30.3. Action thresholds currently used to help decisions on control of *Aphis gossypii* on cotton.

Action threshold	Location (country)	Reference
30% infested plants	Sub-Saharan countries	Silvie *et al*. (2013)
10% affected plants	India	Mohan *et al*. (2014)
>50 aphids/leaf	Texas	Parajulee *et al*. (2011)
>10 aphids/leaf	India	Udikeri *et al*. (2012)

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increased or less variable yields. Some field studies reported that Bt cotton crops did not increase aphid populations significantly compared to conventional cotton plots treated with insecticides for the control of bollworms (Mann *et al*., 2010; Sujii *et al*., 2013), probably because the natural enemies of aphids were preserved (Wu and Guo, 2003; Han *et al*., 2014). In contrast, other studies have observed increased populations of sap-feeding herbivores, such as aphids in Bt cotton (Naranjo, 2011). Such resurgence of secondary pests in Bt cotton could be explained partly by the reduced use of broad-spectrum insecticides to control Lepidoptera. In a recent study, Hagenbucher *et al*. (2013b) proposed that the absence of damage by lepidopteran herbivores, leading to a lack of induction of secondary metabolites (particularly terpenoids) in Bt cottons, could benefit non-target herbivores such as *A. gossypii*.

Perspectives

Multi-scale research is needed to improve the integrated management of aphids in cotton crops.

At the plant scale, breeding new cultivars tolerant or resistant to aphid-borne diseases could be achieved by a better understanding of the genetic basis of the mechanisms involved in virus–aphid–plant interactions. Genetic engineering of aphid-resistant cultivars should be better explored (Wu *et al*., 2006; Chougule *et al*., 2013). Emerging research on endophytic microorganisms might also generate new kinds of insecticides against aphids (Shi *et al*., 2013; Castillo Lopez *et al*., 2014). The induction of herbivore-induced plant volatiles, such as the ones released by aphid-infested cotton plants (Hedge *et al*., 2011), is another potential field of research.

At the field scale, the incorporation of natural enemy prevalence into the action threshold is under way (Luo *et al*., 2014; Zhou *et al*., 2014). Plant extracts are another option currently being explored in many countries, particularly for organic crop systems (de Andrade *et al*., 2012). However, the impact of such extracts on aphid populations has to be assessed correctly if used in conventional cotton crops, because generally the control they give cannot compete with neonicotinoids (Pinto *et al*., 2013).

At the landscape scale, remote sensing is a promising way to detect high aphid infestations (Reisig and Godfrey, 2010). First results show the importance of semi-natural habitats and alternative resources for enhancing biological control (Taki *et al*., 2013). In the future, cotton aphid management should also become part of a multi-pest approach including multitrophic interactions.

Executive Summary

Cotton is known as the 'entomologist's crop' because of the diversity of insect pest problems it is prone to, and aphids are usually considered among the most important. The Bt toxin involved in cotton genetically engineered for resistance to Lepidoptera is not effective against aphids, but the reduction in insecticide use on GM cotton does not necessarily result in increased aphid numbers where indigenous natural enemies (which also are little affected by the toxin) are abundant.

Although *A. gossypii* transmits several viruses of cotton, control is targeted mainly at preventing damaging effects on plant growth and the contamination of the cotton with honeydew, which reduces marketability as it disrupts processing. Keeping numbers below the economic threshold is therefore the goal, and action thresholds have been determined; as a result, monitoring by scouting is frequently practised in intensive cotton farming systems. Measures of natural enemy prevalence are likely to be included in action thresholds in the near future.

Crops untreated with insecticide are often free of problem aphid populations, and the important contribution to this of natural enemies (particularly parasitoids) is widely recognized when selecting pesticides. The choice of active ingredient is further limited by the widespread resistance of *A. gossypii* to particular insecticides. Specific recommendations are available in different regions.

There is little purposeful release of natural enemies against cotton aphids, with more emphasis on retaining reservoirs of predators and parasitoids on what are effectively 'banker plant' systems involving relay or strip intercropping of cotton with other crops rearing natural enemies of cotton aphid on other aphid species.

Currently, plant breeding efforts focus on tolerance to aphid-transmitted viruses, and not on aphid resistance.

Cultural practices have a long history of use against damage by cotton aphid, particularly early harvesting coupled with termination of irrigation. It has also long been recognized that excess nitrogen fertilization can exacerbate aphid problems.

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Semiochemicals are not in field use, although research on the attraction of natural enemies to plant volatiles released by aphid-infested plants is actively being researched

Interaction between control measures is limited to the choice of insecticide, to limit damage to biological control.

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31 IPM Case Studies: Berry Crops[1]

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Introduction

The perennial crops referred to as berries, soft fruit, or small fruit are grown throughout the world, with primary regions of production in Western and Eastern Europe, the Americas and Australasia. Economically significant berry crops include grape (*Vitis* spp.), strawberry (*Fragaria* × *ananassa*), blueberry (*Vaccinium* spp.), American cranberry (*Vaccinium macrocarpon*) and species and hybrids in the genus *Rubus*. These include European raspberry (*Rubus idaeus* subsp. *idaeus*), American red raspberry (*Rubus idaeus* subsp. *strigosus*), black raspberry (*Rubus occidentalis*), blackberry (*Rubus fructicosus* agg.), cut-leaved blackberry (*Rubus laciniatus*), California blackberry (*Rubus ursinus*) and loganberry and boysenberry (hybrids – both *Rubus loganobaccus* – between raspberry and blackberry). They are all high-value crops, often with a long establishment period incurring high capital costs. Increasingly, berry crops are grown under complete or partial cover to improve yields and quality, and to manipulate the timing of harvest. This change can bring about new pest challenges (Demchak, 2009), but it also provides environments more suitable for releasing natural enemies (Birch *et al*., 2011).

Aphids infesting berry crops (Blackman and Eastop, 2000) are rarely abundant enough to cause feeding damage, although live aphids and shed exoskeletons can contaminate fruit, and honeydew can encourage sooty mould infections. More often, their primary economic impact is as virus vectors, especially for perennial plantations. Infection with these diseases can cause debilitating losses of productivity, and infected plants must be removed, leading to increased replant costs. The demand for high-quality fruit has continued to drive the use of insecticides for aphid control, but pesticides are increasingly limited in these minor crops. Food safety concerns, increasing pre-harvest intervals for pesticides, and pest resistance to pesticides have all contributed to the development of integrated management strategies that minimize the use of toxicants and maintain fruit quality. This chapter provides a general overview of the strategies used for the management of aphids in berry crops, with a focus on aphid IPM programmes in raspberry and blueberry.

Aphid IPM in Raspberry

Raspberry (*R. idaeus*) is a high-value crop, grown commercially in Europe and temperate regions of the Americas and Australasia for the fresh and processing markets. World production has increased over the past decade and in 2012 was estimated to be 578,000 tonnes (FAO, 2015). In the North American literature, this crop is referred to as red raspberry to distinguish it from the black raspberry (*R. occidentalis*), a species indigenous to North America. Blackman and Eastop (2000) list 11 aphid species occurring on European, red and black raspberries, but only four cause economic damage (*Amphorophora idaei* (Fig. 31.1), *Amphorophora agathonica*, *Aphis idaei* and *A. rubicola*). Aphids can cause contamination of hand- and machine-harvested raspberries (Kieffer *et al*., 1983; Gordon *et al*., 1997a) and honeydew can encourage moulds

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Fig. 31.1. Apterous virginopara and nymph of the large raspberry aphid, *Amphorophora idaei*, feeding on a raspberry leaf. (Copyright James Hutton Institute, reproduced with permission.)

on fresh fruit, but aphids are more important as vectors of a number of viruses on perennially grown crops (Jones, 1986; Converse, 1987; Martin *et al*., 2013) (Table 31.1). These virus diseases reduce yield and fruit quality and produce a range of symptoms depending on the virus, virus complex and cultivar. European and North American red raspberry cultivars are susceptible to aphid-borne viruses (Table 31.1). However, many are tolerant and can be infected without showing clear symptoms. Mosaic diseases resulting from viruses transmitted by *Amphorophora* species are widespread, but viruses cause symptomless decline in most cultivars (Converse, 1987; Jones and McGavin, 1998; Martin *et al*., 2013). In container production systems with shorter plant lifespans, which have been adopted widely for improved yields and quality, such as in most European countries, the economic importance of aphid-borne viruses has decreased over the past decade.

The costs of establishing a raspberry plantation are high, but fruit can be harvested for many years if the crop remains free from virus diseases (Gordon *et al*., 1997b) and the soil is free from raspberry root rot pathogens (Maloney *et al*., 1993). Control depends on planting certified virus-indexed stocks and preventing them from becoming infected (Jones, 1986; Ellis *et al*., 1991), or growing new plants every few years. Conventional insecticides are now heavily restricted in the European Union (Hillocks, 2012) and have proved ineffective in preventing the introduction of the most important viruses, vectored by *Amphorophora* species (Taylor and Chambers, 1969; Freeman and Stace-Smith, 1970). Because these aphid-borne viruses are transmitted in a semi-persistent manner (Jones, 1986), they can be spread before immigrant viruliferous alates are killed. Although insecticides may limit virus spread within plantations, aphid control is not usually the primary reason for insecticide use in raspberry crops, due to a range of other key pests attacking the crop (e.g. raspberry beetle (*Byturus tomentosus*) and, more recently, spotted wing drosophila (*Drosophila suzukii*)). In addition, many insecticides cannot be applied at or close to harvest, when aphid populations usually peak, because of the risk of chemical residues on the fruit. However, with the increasing trend to grow raspberries under protected polytunnels, the extended season means that other aphid pests are now attacking the crop earlier in the season. One such example is the potato aphid, *Macrosiphon euphorbiae*, which colonizes protected raspberries before *A. ideai*. This has created a new challenge for growers, since many pesticides can only be applied a maximum number of times and often cannot be applied during flowering, to protect pollinators. To meet this challenge, the SCEPTRE research programme has developed biopesticide- and biocontrol-based alternative solutions to aphid control (O'Neill *et al*., 2015). Combining these approaches provides as good suppression of both potato and large raspberry aphid as the conventional neonicotinoid control treatment and reduces the negative impacts on pollinators and natural enemies (Mitchell *et al*., 2010).

In contrast to the methods employed in blueberries (see below), the removal of infected plants (roguing) is of little value in preventing the spread of aphid-transmitted raspberry viruses, because the viruses induce no symptoms in most modern cultivars in single infections. Fortunately, strong and heritable sources of resistance to *Amphorophora* species have been used by plant breeders to diminish the importance of viruses transmitted by these aphids. All modern commercial raspberry cultivars contain resistance to *A. idaei* and *A. agathonica*, provided by either major or minor genes (Keep and Knight, 1967; Daubeny, 1972; Jones, 1986). The existence of heritable resistance to colonization by *A. agathonica* was shown over 75 years ago in the USA (Huber and Schwartze, 1938). The resistance was derived from European raspberry cultivars (mainly cv. 'Lloyd George'), and results from a single dominant gene, Ag_1 (Daubeny, 1966). An additional benefit is that *A. agathonica* acquires virus less readily from raspberry genotypes resistant to that vector than from aphid-susceptible genotypes (Stace-Smith, 1960).

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Table 31.1. Vectors of the major aphid-borne viruses of berry crops. (From Converse, 1987; Blackman and Eastop, 2000; Martin *et al*., 2013.)

Natural vector	Crop	Virus	Disease
Amphorophora idaei	European red raspberry	*Black raspberry necrosis virus* (BRNV)	Symptomless decline
	(*Rubus idaeus* subsp. *idaeus*)	*Raspberry leaf mottle virus* (RLMV)	Raspberry leaf mottle
		Rubus yellow net virus (RYNV)	Yellow mosaic
		RYNV + other viruses	Raspberry mosaic
Amphorophora agathonica	North American red raspberry	BRNV	Symptomless decline
	(*Rubus idaeus* subsp. *strigosus*)	BRNV + RYNV	Yellow mosaic
		RLMV	Raspberry leaf mottle
		Raspberry latent virus	Enhance crumbly fruit with *Raspberry bushy dwarf virus*
Amphorophora agathonica	Black raspberry	BRNV	Tip necrosis
Aphis idaei	European red raspberry (*Rubus idaeus* subsp. *idaeus*)	Raspberry vein chlorosis virus (RVCV)	Vein chlorosis
Aphis rubicola	North American red raspberry (*Rubus idaeus* subsp. *strigosus*)	Raspberry leaf curl virus (RpLCV)	Leaf curl
	Black raspberry (*Rubus occidentalis*)	RpLCV	Leaf curl
	Blackberry (*Rubus fruticosus* agg.)	RpLCV	Leaf curl
Aphis gossypii	Strawberry	*Strawberry mottle virus* (SMoV)	Strawberry mottle
	(*Fragaria* × *ananassa*)		
Chaetosiphon fragaefolii	Strawberry	SMoV	Strawberry mottle
and other *Chaetosiphon* spp.	(*Fragaria* × *ananassa*)	*Strawberry crinkle virus*	Strawberry crinkle
		Strawberry latent C virus	Strawberry latent C disease
		Strawberry mild yellow-edge virus	Strawberry mild yellow-edge
		Strawberry vein banding virus	Strawberry vein banding
Illinoia pepperi	Blueberry (*Vaccinium* spp.)	*Blueberry shoestring virus* (BSSV)	Blueberry shoestring
Ericaphis fimbriata	Blueberry (*Vaccinium* spp.)	*Blueberry scorch virus*	Blueberry scorch

This resistance has been effective in controlling the spread of raspberry mosaic (a disease caused by mixed infection by up to four viruses) in the Pacific Northwest of North America for many decades (Daubeny, 1980). Populations of *A. agathonica* that overcome the Ag_1 gene were first reported in North America in the early 1990s (Daubeny and Anderson, 1993), and now six biotypes of this aphid have

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been identified in British Columbia (Dossett and Kempler, 2102). Efforts to identify additional sources of resistance to this aphid in native germplasm have been ongoing since the early 1980s in recognition of the risk of relying on a single dominant gene (Daubeny and Stary, 1982). Two genes for resistance have been identified in native *R. ideaus* subsp. *strigosus*, Ag_2 and Ag_3, but with a lack of markers to track these genes, progress on incorporating them into commercial cultivars has been slow. More recently, 132 wild populations of *R. occidentalis* from eastern North America were screened for resistance to *A. agathonica*. Three populations with resistance were identified (Dossett and Finn, 2010), with at least two of these genes, Ag_4 and Ag_5, being distinct from each other. These new sources of resistance to *A. agathonica*, along with the development of genetic tools to identify resistance genes (Bushakra *et al*., 2015) in seedlings, provide a bright future for the use of aphid resistance for virus control in red and black raspberry.

In Europe and North America, *Amphorophora* aphids are holocyclic and monoecious on *Rubus*, producing several parthenogenetic generations over the summer (Dicker, 1940; Kennedy and Schaefers, 1974; Lightle *et al*., 2014). Their taxonomic identity was confused for many years (Kennedy *et al*., 1962), and prior to the early 1970s the species *A. agathonica* was referred to as a North American race of *Amphorophora rubi* (Daubeny, 1972). However, whereas the British cultivar 'Lloyd George' was resistant to *A. rubi* in North America and remained free from mosaic, it was highly susceptible to *A. rubi* and virus infection in Europe (Hill, 1956, 1957; Rautapää, 1967; Jones, 1976). Blackman *et al*. (1977) showed that the species on European raspberry was *A. idaei* (2n = 18), and that it could be separated by morphological characters and cytology from *A. rubi* (2n = 20), a species largely confined to *R. fruticosus* agg. and other host plants in the blackberry group. They also confirmed that *A. agathonica*, which originated from native red raspberry, *R. idaeus* subsp. *strigosus*, was a distinct species with a chromosome complement of 2n = 14. Knight *et al*. (1959) identified a single dominant gene, A_1, from cv. 'Baumforth A' as a source of strong resistance to *A. idaei*. The ability to select resistant progeny plants accurately and rapidly led to a succession of aphid-resistant cultivars becoming available to European growers since the early 1970s. Twelve dominant resistance genes have been identified from these cultivars (Keep, 1989), although some of these genes are ineffective against virulent biotypes of *A. idaei* (Briggs, 1959, 1965). The 'universal' resistance gene, A_{10}, from *R. occidentalis*, cv. 'Cumberland', confers resistance to most large raspberry aphid biotypes and has been incorporated into most new cultivars (Keep, 1989; Birch *et al*., 2011).

Resistance to *Amphorophora* provides an outstanding example of the value of vector resistance for controlling aphid-borne virus spread in the field (Jones, 1987). Virus infection in the aphid-susceptible cultivar 'Malling Jewel' reached 100% in four growing seasons, compared with <20% in aphid-resistant genotypes (Fig. 31.2). Those with the highest resistance to *A. idaei* were infected least rapidly; almost half the number of plants containing A_1 or A_{10} resistance genes were still uninfected after seven growing seasons (Jones, 1976, 1979; Birch *et al*., 2003). Genotypes with minor gene resistance (Jennings, 1963) also became infected less rapidly than aphid-susceptible genotypes. Both forms of resistance to *A. idaei* have proved effective in limiting the spread of viruses transmitted by this vector in commercial crops (0.5–1 ha), with virus incidence rarely exceeding 5% after 10 years cultivation (Jones, 1987). Molecular analysis, using rDNA intergenic spacer region (IGS) markers, showed that UK populations of *A. idaei* contained a wide range of genotypes (Birch *et al*., 1994; Fenton *et al*., 1994). The widespread use of cultivars containing gene A_1 or A_{10} has imposed strong selection pressure on *A. idaei* (Jones, 1988). In a survey, 77% of *A. idaei* from plantations in England and Scotland were found to be virulent and capable of colonizing cultivars containing gene A_1, and a new virulent biotype was found on two cultivars containing A_1 (Birch *et al*., 1994; Jones *et al*., 2000) and an A_{10}-breaking biotype of *A. idaei* has recently been detected in England (Birch *et al*., 1997, 2002). In the past decade, selection pressure on the A_{10} gene in England (but not Scotland to date) has resulted in partial breakdown of this resistance; plant breeders in the UK are therefore combining A_{10} with other aphid resistance genes to increase durability.

The development of cultivars resistant to *A. idaei* has decreased the use of aphicides in raspberry plantations in the UK (Jones, 1988; Gordon *et al*., 1997b). However, the development of economic thresholds, a fundamental concept in the development of IPM (Kennedy, 2000), is inappropriate for aphids as virus vectors, since these must be controlled even at low population densities to prevent virus

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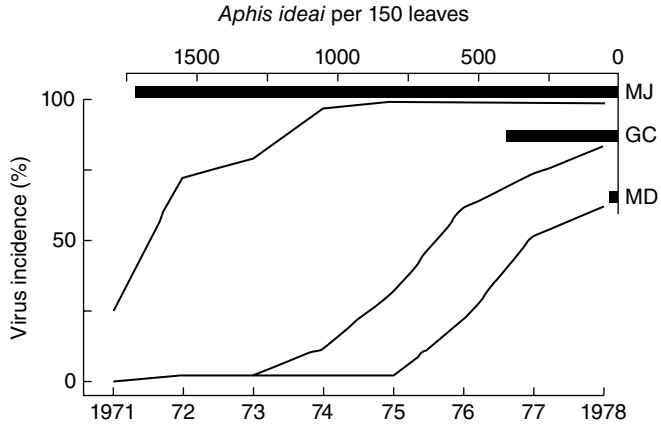

Fig. 31.2. Effect of resistance to *Amphorophora idaei* in raspberry on the incidence of viruses transmitted by this vector in Scotland during 1971–1978. Histograms indicate relative numbers of *A. idaei* found on 150 leaves during aphid population peaks, averaged across all years. Cultivars and their resistance to *A. idaei* are: MJ = 'Malling Jewel' (susceptible); GC = 'Glen Clova' (minor gene resistance); MO = 'Malling Orion' (A1 major gene resistance). (From Jones, 1976, 1979; courtesy of the Association of Applied Biologists.)

infection. Nevertheless, the use of aphid-resistant cultivars fits well into the overall management of the crop (Gordon *et al*., 1993; Birch *et al*., 2003, 2011) and frees growers from the need to make aphid control decisions for *A. ideai* (but not *M. euphorbiae*). It is likely that aphid-resistant raspberry cultivars will continue to contribute substantially to pest management strategies in the future, but will require additional tools (biopesticides, biocontrol) to ensure durability. The pressure on growers to meet the exacting standards set by supermarkets can dictate the cultivars produced (based largely on yield, berry size, shape, colour, flavour), as well as the need to have plants suitable for growing under protective cover to meet year-round consumer demand. Research to integrate pest and disease resistance and the use of natural enemies in raspberry plantations is under way to meet the requirements of consumers for high-quality fruit with a minimum of pesticide residues (Gordon *et al*., 1990; Mitchell *et al*., 2010; Birch *et al*., 2011). A recent development has included the addition of floral resource plants (e.g. buckwheat) in raspberry polytunnels to attract and retain aphid natural enemies, especially hover flies and parasitoids (Orre-Gordon *et al*., 2013; O'Neill *et al*., 2015).

Aphid IPM in Blueberry

Aphids recorded from blueberry include *Aphis fabae*, *Aphis gossypii*, *Aphis vaccinii*, *Ericaphis* (= *Fimbriaphis*) *scammelli*, *Ericaphis* (= *Fimbriaphis*) *fimbriata*, *Illinoia azaleae*, *Illinoia borealis* and the blueberry aphid, *Illinoia pepperi* (Fig. 31.3) in the northern hemisphere (Blackman and Eastop, 2000; Polavarapu and Peng, 2000a,b), and *A. gossypii*, *M. euphorbiae*, *Myzus persicae* and *Aphis spiraecola* in the southern hemisphere (Larraín Sanhueza *et al*., 2007; Rocca and Greco, 2011). In the past 30 years, aphid management programmes in the North American highbush blueberry industry have emphasized control of *I. pepperi*, due to its distribution

Fig. 31.3. Apterous virginopara of the blueberry aphid, *Illinoia pepperi,* feeding on a blueberry leaf. (Photograph courtesy of Rufus Isaacs.)

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throughout most of the major production regions and its role as a virus vector. *Blueberry shoestring virus* (BSSV) is circulative, persistently transmitted and causes a serious disease of highbush blueberry (Morimoto *et al*., 1985; Terhune *et al*., 1991) (Ramsdell, 1987; Martin *et al*., 2012). Infection leads to poor plant vigour (Fig. 31.4), and losses to the Michigan blueberry crop from this virus have been estimated at US$3 million/year (Ramsdell, 1979, 1987). BSSV has been reported from most regions of highbush blueberry production in North America (Ramsdell, 1987), but is rare outside of the Great Lakes region (Martin *et al*., 2012) and has been detected in wild highbush blueberry and lowbush blueberries (*Vaccinium angustifolium*) (Lockhart and Hall, 1962; Hancock *et al*., 1986, 1993). Symptoms include elongated reddish streaks on current-year and 1-year-old stems, and strap-like or crescent-shaped leaves (Stretch and Hilborn, 1970; Ramsdell, 1987). Petals may be reddened and fruit on infected bushes may become reddish-purple instead of the typical blue. Urban *et al*. (1989) showed that the virus spread slowly within plants, and field observations were consistent with a latent period of between 2 and 4 years before visible symptoms were observed. Through a combination of cultivar selection, regular monitoring, cultural controls and accurate timing of effective insecticides, blueberry growers can minimize the level of BSSV and protect their plantings.

Variation in the resistance of 16 highbush blueberry cultivars to *I. pepperi* revealed four cultivars with significantly lower aphid population growth than the others (Hancock *et al*., 1982). Some aphids were still present on these cultivars, however, suggesting that resistant cultivars were likely to provide only partial prevention of virus transmission. A more promising approach was the finding by Schulte *et al*. (1985) that some cultivars were resistant to infection by BSSV, either because the virus could not replicate or because the plant actively defended itself against development of the virus. The cultivars 'Bluecrop' and 'Atlantic' were found to have particularly effective field resistance and were recommended for planting where virus pressure was great.

Morimoto and Ramsdell (1985) used trap plants to show that infestation by apterous blueberry aphids started at around 700 day-degrees (base 3.4°C) after 1 March. Immigration was almost

Fig. 31.4. During bloom, highbush blueberry bushes show poor leaf and shoot growth indicative of shoestring virus infection. The plant on the right is infected and highly symptomatic, with thin, strap-like leaves and stunted shoots. (Photograph courtesy of Rufus Isaacs.)

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exclusively by apterae, and coloured water traps revealed that the primary source of infected aphids was from within infected fields. Movement of the vector within plantings is predominantly by local dispersal from plant to plant and, because aphids overwinter as eggs on blueberry bud scales (Elsner and Kriegel, 1989), removal of plants showing symptoms is recommended as an effective foundation of BSSV eradication programmes.

Soon after the relationship between *I. pepperi* and BSSV had been verified, Whalon and Elsner (1982) evaluated the effects of insecticides on the vector and its biological control agents. Pirimicarb and acephate provided the greatest control of *I. pepperi*, while methomyl, malathion and diazinon were less effective and were most damaging to biological control agents. In the past decade, the availability of selective insecticides that are highly effective on sucking pests without disrupting natural enemies has helped to reduce the importance of aphids in commercial blueberry production. For example, foliar and soil applications of these insecticides both provided complete control of *I. pepperii* and *E. fimbriata* (Polavarapu and Peng, 2000a,b). However, the rapid spread of spotted wing drosophila into most major berry production regions in recent years (Asplen *et al*., 2015) has resulted in greater use of broad-spectrum insecticides that are expected to lead to outbreaks of secondary pests such as aphids. Current IPM recommendations for the management of *I. pepperii* and BSSV include monitoring bushes annually for viral infection and aphid infestation. If virus symptoms are absent, minimal use of aphicides is recommended to maintain the activity of natural enemies, since these can cause significant aphid mortality in blueberry (Whalon and Elsner, 1982; Elsner and Kriegel, 1989). Bushes showing symptoms should be removed and disposed of away from the field. If BSSV and aphids were detected in the previous year, insecticides should be applied with thorough coverage beginning at 700 day-degrees (base 3.4°C) after 1 March and reapplied if needed to maintain a very low aphid population (Morimoto and Ramsdell, 1985). Aphid control prior to harvest is particularly important in fields with a history of BSSV, to prevent mechanical harvesters spreading the vectors. In Michigan, where 70% of the crop is machine harvested, rubidium-labelled aphids were spread at least 64 bushes along the row by a mechanical harvester (M.E. Whalon, unpublished). Washing harvesters before moving to the next field is a simple strategy to help reduce the spread of BSSV within and between blueberry farms.

Ericaphis fimbriata has emerged as a species of economic importance on highbush blueberries (*Vaccinium corymbosum*) in the eastern and western USA (Raworth, 2004; Raworth *et al*., 2008a), because it is a vector of the carlavirus *Blueberry scorch virus* (BlScV). This virus is spread by aphids in a non-persistent way (Bristow *et al*., 2000). There is a range of symptom intensity depending on the cultivar and the virus strain, but there can be blighting of leaves, flowers and shoots (Martin *et al*., 2012). Variability in the symptoms and the ability of infected bushes of some cultivars to remain productive for years has resulted in limited bush removal, except in cases where cultivars develop severe symptoms. This is complicated by the virus also being moved to other species of *Vaccinium* that remain symptomless by aphids (Martin *et al*., 2006). Establishing new fields with virus-tested plant material is essential since young plants do not reliably exhibit symptoms (Oudemans *et al*., 2011). As with BSSV, chemical control of the aphid vector is recommended in regions where this virus is present. Other approaches to managing aphid control have focused on biological control (Raworth *et al*., 2008b) and characterizing virus transmission dynamics (Bristow *et al*., 2000; Mathur *et al*., 2014). BlScV is transmitted inefficiently by aphids, and therefore reducing aphid populations can greatly reduce the rate of spread. Also, since BlScV is transmitted in a non-persistent manner, isolation from infected sources by as little as 1 km is very effective at preventing virus transmission into a healthy field.

Aphid IPM in Strawberry

Aphids are pests in most regions of strawberry production (Maas, 1998), due in part to the transmission of viruses (Table 31.1). Virus diseases remain a common threat to nurseries and perennial plantings (Tzanetakis and Martin, 2014), but have become somewhat less of a problem as annual strawberry production has increased (Hancock, 1999). In addition to the *Chaetosiphon* complex, *A. gossypii* has also become a direct pest in California, where aphids cause fruit contamination from cast cuticles and honeydew on which sooty moulds develop. The selection of insecticides that minimize the impact on predators in strawberry fields (Easterbrook, 1997) has been emphasized in the development of IPM programmes for strawberry (Zalom *et al*., 2001).

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The recommendations for southern California production call for treatment with insecticidal soap if more than 30% of the oldest trifoliates on 100 plants/ha are infested with aphids. It is expected that selective aphicides will continue to be components of aphid and virus management (e.g. Raworth and Clements, 1990), complementing host-plant resistance (Easterbrook *et al*., 1997) and biological control with natural enemies, which is being increasingly commercialized (Dassonville *et al*., 2013). *Chaetosiphon* spp. are very selective feeders, and a strawberry-free period between planting cycles greatly reduces the aphid population due to lack of an acceptable food source. With the increase in annual production of strawberries, combining a strawberry-free period with the use of virus-tested plants can often lead to fruit production without any aphid control needed for virus management (Martin and Tzanetakis, 2013).

Aphid IPM in Grape

Host-plant resistance has been used for over 120 years as the foundation of crop protection against *Daktulosphaira vitifoliae* (grape phylloxera) (Granett *et al*., 2001; Powell *et al*., 2013). However, a biotype has developed that can break this long-lasting resistance (Chapter 22, this volume). *Daktulosphaira vitifoliae* is by far the most economically important aphid pest of berry crops worldwide, with the potential to devastate *Vitis vinifera* vineyards by causing galls on roots. To protect vines from this pest, viticulturalists plant their desired cultivars grafted on to resistant rootstocks derived from *Vitis rupestris*, *Vitis vulpina* or *Vitis berlandieri*. Grapevines also support a complex of seven other aphid species (Blackman and Eastop, 2000), including *Aphis illinoisensis* (grapevine aphid), but populations of these foliar-feeding species are rarely large enough to require control.

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Executive Summary

In many berry crops, aphid transmission of viruses is the primary problem, and economic thresholds are often inappropriate. However, for containerized protected crops that are increasingly common, virus threats have declined and contamination of berries by aphids is more common. The exceptional quality standards demanded by consumers of fruit increasingly constrain berry growers' adoption of integrated pest management approaches. However, the withdrawal of available pesticides to protect the environment, pollinators and consumers is slowly forcing growers to adopt IPM as the main crop protection strategy, particularly in Europe.

Selective aphicides, such as the neonicotinoids and insect growth regulators, can control aphids, but their impact on virus transmission is less clear. Their registration for use in berry crops was expected to enable increased activity of biocontrol control agents, but invasion by spotted wing drosophila has made berry crop IPM more intensive in recent years. Additionally, the possible role of neonicotinoids in pollinator declines has promoted the uptake of more expensive and often less persistent biopesticides (UK).

There has been relatively little use of biocontrol agents in commercial production, apart from commercially available parasitoid wasps. However, the expansion of protected environments for berry production increases the need for inundative releases of natural enemies for aphid control, and so there is a growing availability of commercial biocontrol products.

Breeding for host-plant resistance has been the mainstay of control in several berry crops. The apparently durable resistance to aphids in raspberries and to phylloxera in grapes have both recently been broken, but there is also much greater use of marker-assisted breeding that will expedite the development of new cultivars incorporating multiple resistance genes.

The main cultural control practice is the removal and destruction of plants showing symptoms of virus disease.

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The use of semiochemicals is still at the experimental and field-testing stage, but looks promising (e.g. plant-based biopesticides with additional behaviour-modifying effects on pests and natural enemies).

Integrated management programmes that enable any synergism possible between different control methods are seen in the use of selective insecticides, the augmented release of biocontrol agents and the use of host-plant resistance. The further step of integrating the management of aphids with that of other insects, together with diseases and weeds, into unified programmes remains a future goal for most berry crops. For these high-value crops, the adoption of some IPM practices may be considered risky in the context of the pressures to deliver near-perfect fruit. The minor crop status of berry crops in most regions and societal pressure to reduce food residues and worker exposure mean that pesticide use is being increasingly restricted. In response, berry IPM programmes must aim to find effective sustainable alternatives with reduced chemical inputs that maintain fruit quality and protect beneficial insects, especially natural enemies and pollinators. This is leading to the expansion of IPM to integrated pest and pollinator management (Biddinger and Rajotte, 2015).

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32 IPM Case Studies: Deciduous Fruit Tree Aphids

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Introduction

Fruit tree aphids are here defined as those pest species that affect crop plants belonging to the Rosaceae subfamilies Pyroideae (mainly apple and pear trees) and Prunoideae (commonly known as stone-fruit trees). Comprehensive accounts of these aphids, including identification keys, and much updated literature records have recently been given by Blackman and Eastop (2000, 2015). Barbagallo *et al.* (1997) have provided some epidemiological notes and colour illustrations of the most damaging species.

Apple and Pear Aphids

Apple (*Malus domestica*) and pear (*Pyrus communis*) are the most economically important crops in the Pyroideae worldwide. Other cultivated plants belonging to the same group include: Japanese pear or 'Nashi' (*Pyrus pyrifolia*), quince (*Cydonia oblonga*), loquat (*Eriobotrya japonica*), medlar (*Mespilus germanica*), service tree (*Sorbus domestica*) and azarole (*Crataegus azarolus*). There are about 60 aphid species recorded worldwide as pests of these plants; the most economically damaging are some species infesting both apple and pear, as listed in Table 32.1.

Damage and virus transmission

Apple and pear aphids mostly cause direct damage through leaf deformation and shoot distortion, coupled with the effects of inoculated saliva and the draining of sap. Honeydew excretion causes further damage.

Eriosoma lanigerum (woolly apple aphid) is responsible for cankers on apple trunks and branches; infestation of roots and branches also causes the formation of nodules and tumours, a reduction of plant tissue weight and disturbance of the nutrient balance (Weber and Brown, 1988; Brown *et al.*, 1995).

Aphis pomi (green apple aphid) and occasionally *A. spiraecola* (green citrus aphid) attack the leaves throughout the season, while *Rhopalosiphum insertum* (apple–grass aphid) only infests the leaves in early spring.

Severe injury to both shoots and fruits can result from *Dysaphis plantaginea* (rosy apple aphid) on apple and from *Dysaphis pyri* (pear–bedstraw aphid) on pear; similar damage can be caused on pear by *Melanaphis pyraria* (pear–grass aphid).

Aphanostigma piri (pear phylloxera) and *Aphanostigma iaksuiense* (oriental pear phylloxera) can directly damage fruit, causing necrosis around the calyx. *Schizaphis piricola* (and a few other similar species, such as *Schizaphis pyri* and *Schizaphis rotundiventris* – see Blackman and Eastop, 2000) cause deformation of leaves and even defoliation, whereas dense populations of *Aphis gossypii* (cotton or melon aphid) lead to sooty mould development.

No virus transmission seems to be linked to aphids on apples, pears or other Pyroideae.

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Table 32.1. Aphid species damaging to deciduous fruit trees (Pyroideae).

Aphid	Life cycle	Host	Geographical distribution	Damage	Notes
Aphis pomi – Fig. 32.1a	Holocyclic, monoecious	Most Pyroideae	Northern hemisphere, particularly West Palaearctic	Young shoots in spring	Quite injurious pest
Aphis spiraecola	Holocyclic, heteroecious or anholocyclic	Polyphagous	Worldwide, mostly tropics and subtropics	Young shoots in spring	Minor pest Injurious in East Asia
Aphis gossypii	Mostly anholocyclic or rarely holocyclyc, heteroecious in East Asia	Polyphagous	Worldwide, mostly tropics and subtropics	Young shoots in spring	Minor pest
Melanaphis pyraria	Holocyclic, heteroecious	Pear (Poaceae as secondary host)	Southern Europe, Middle East	Young shoots in spring	Occasionally injurious
Anuraphis farfarae	Holocyclic, heteroecious	Pear (*Tussilago* [root collar] as secondary host)	Europe and central Asia	Pseudogalls on leaves	Negligible injury
Rhopalosiphum insertum	Holocyclic, heteroecious	Apple (Poaceae [roots] as secondary host)	Holarctic and Australia	Leaves in spring	Minor pest
Schizaphis piricola	Holocyclic, heteroecious	Pear (secondary host unknown)	East Asia	Pseudogalls on leaves	Minor pest
Dysaphis plantaginea – Fig. 32.1b	Holocyclic, heteroecious	Apple (*Plantago* spp. [roots] as secondary host)	Europe, Middle East, central Asia, introduced to parts of Africa and America	Leaf pseudogalls in spring, also flowers and young fruits	Most injurious species in Western Europe
Dysaphis devecta group – Fig. 32.1c	Holocyclic, monoecious (devecta) or heteroecious (other species)	Apple and other plants (heteroecious species)	Europe	Red pseudogalls on leaves	Usually minor pest
Dysaphis pyri	Holocyclic, heteroecious	Pear (*Galium* spp. as secondary host)	Palaearctic	Leaf pseudogalls; less injurious than *Dysaphis plantaginea*	Occasionally quite injurious pest
Dysaphis reaumuri	Holocyclic, heteroecious	Pear (*Galium* spp. as secondary host)	Southern Europe and central Asia	Leaf distortions	Occasionally on cultivated pear, while common on wild ones
Eriosoma lanigerum	Anholocyclic	Apple, rarely other Pyroideae	North America, introduced into Europe and now worldwide	Cankers on stems, branches and roots (collar parts)	Very injurious pest
Eriosoma lanuginosum	Holocyclic, heteroecious	European elm (galls) and pear (roots)	Europe and the Palaearctic	Poorly studied	Minor pest

Continued

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Table 32.1. Continued.

Aphid	Life cycle	Host	Geographical distribution	Damage	Notes
Eriosoma pyricola	Holocyclic, heteroecious	Elms (leaf gall) and pear (roots)	Southern Europe, Americas, Australasia	Poorly studied	Minor pest
Nippolachnus piri	Holocyclic, monoecious or anholocyclic	Pear and loquat	East Asia	Colonies on leaves	Minor pest
Pyrolachnus pyri	Holocyclic, heteroecious	Pear and other Pyroideae	Middle East and East Asia (China, Korea), including India	Colonies on branches	Minor pest
Aphanostigma piri – Fig. 32.1d	Holocyclic, monoecious or anholocyclic	Pear (mostly fruit and twigs)	South-west Europe, Middle East	2- to 3-year-old twigs, inner parts of calyx in summer	Localized as injurious pest
Aphanostigma iaksuiense	Holocyclic, monoecious or anholocyclic	Japanese pear (mostly fruit and twigs)	East Asia	2- to 3-year-old twigs, inner parts of calyx in summer	Localized as injurious pest

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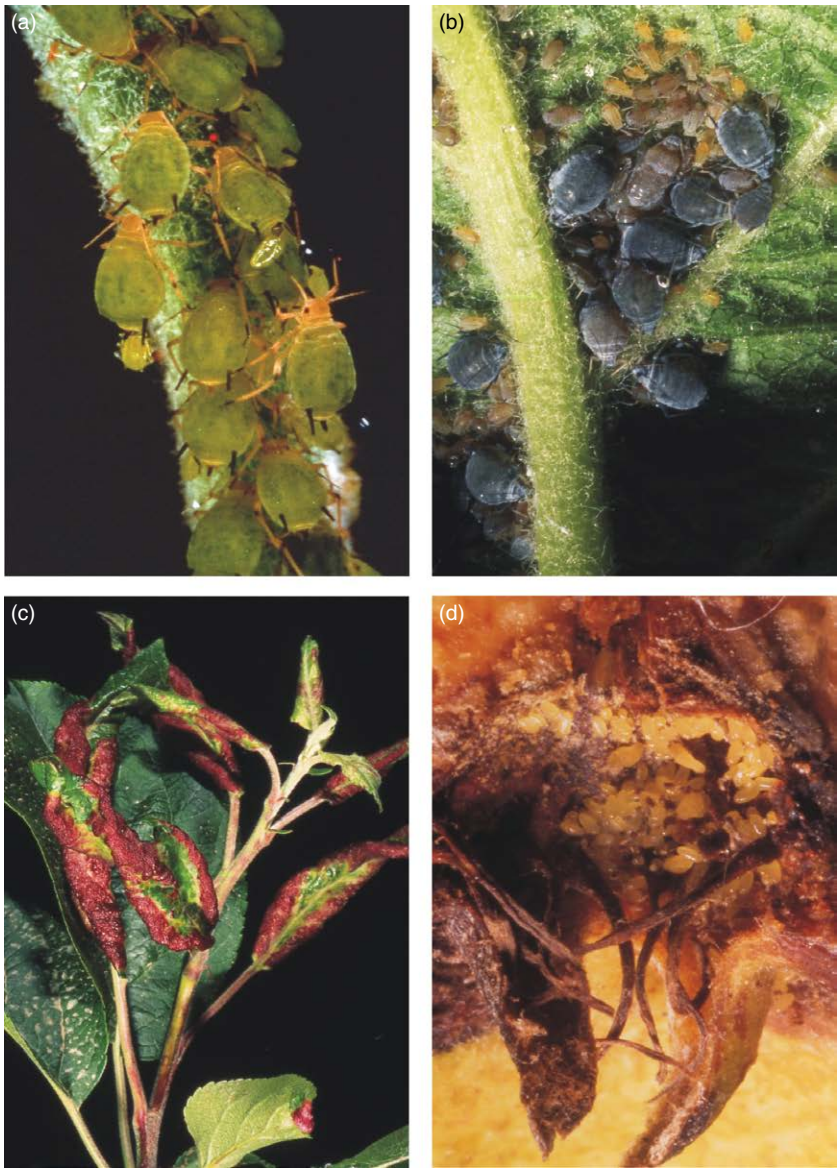

Fig. 32.1. Apple and pear aphids. (a) Colony of *Aphis pomi* on an apple shoot; (b) colony of *Dysaphis plantaginea* on an apple leaf; (c) pseudogalls of *Dysaphis anthrisci*, a member of the red-gall aphids, on apple; (d) a section through a pear fruit, showing a colony of *Aphanostigma piri* inside the calyx area. (From Barbagallo *et al*., 1997, courtesy of Bayer.)

Monitoring and economic thresholds

Visual counts are recommended for evaluating aphid density on apple and pear at the appropriate times (Pasqualini *et al*., 1981). Milaire *et al*. (1974) have suggested a simple methodology for different phenological periods, as well as economic thresholds for the main apple-infesting aphids in Western Europe.

Pre-flowering is the most critical phase, because early attacks of *D. plantaginea* during flowering can

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cause severe losses. The presence of *A. pomi* (or *A. spiraecola*) either on apple or pear can be tolerated at higher levels because the reproductive rate is lower and the aphid causes no direct injury to fruit; in summer, damage by this aphid is negligible.

Consequently, 1–2% of shoots infested is considered as a tolerance threshold for *D. plantaginea*, while attack by *A. pomi* can be tolerated up to 8–10% of shoots infested during the most critical period in spring. The same thresholds can be used on pear against *D. pyri* and *A. pomi* or *M. pyraria*, respectively. Although there are no data for pear phylloxera, we believe that 1–2% of fruit infested can be considered as a reasonable threshold.

Against *E. lanigerum* in Massachusetts (USA), standard inspection involves examination of five pruning cuts on one tree per 1.5 ha, with a provisional threshold for treatment of 50% infected pruning cuts (CABI, 2001). In Western Europe, however, the suggested threshold is 8–12 colonies/100 shoots (Milaire *et al*., 1974). Parasitization by *Aphelinus mali* (see later), which can keep *E. lanigerum* at a low level, can be promoted and preserved from destruction by avoiding or the judicious use of insecticides (see below).

Chemical and supervised control

Chemical control is applied frequently against *D. plantaginea* on apple, although it is usually not necessary against other aphids such as *A. pomi* and *R. insertum*. Fluvalinate is currently used against *D. plantaginea* in pre-flowering applications, but only when there is no risk of spider mite infestation. The more selective neonicotinoids, like imidacloprid, thiamethoxam, acetamiprid and clothianidin, have to be used post-flowering when pollinators are not present. Other effective aphicides are azadirachtin, pirimicarb, flonicamid and spirotetramat.

Eriosoma lanigerum is normally kept under biological control, but chemical measures are sometimes necessary. Post-flowering is the best time for such treatments because apple trees are at their maximum vegetative growth and natural antagonists have not yet become very active. Treatments using neonicotinoids and spirotetramat give good results. Against the same aphid, the use of resistant rootstocks (Malling–Merton series) is recommended whenever possible to limit underground infestations.

On pear, insecticide application is occasionally necessary against *D. pyri* and other shoot-infesting species, while locally the pear phylloxera, as well as *A. gossypii* and *A. spiraecola* on Japanese pear, may require spraying.

The main goal in applying aphicides on both apple and pear orchards should be to avoid their side effects on entomophagous and non-target pest species as much as possible. Alternation of chemicals with a different mode of action is important to prevent the development of resistance.

Biological control

Although several species of predators (mainly coccinellids, syrphids and chrysopids) are often found in or near aphid colonies, their late appearance means that chemical control usually cannot be avoided. Neither are parasitoids very effective, though *A. mali* usually keeps *E. lanigerum* under biological control. The efficiency of *A. mali* can easily be promoted whenever necessary by bringing apple shoots containing mummified aphid colonies from other orchards into the aphid-infested orchard; the use of broad-spectrum pesticides on that crop can then be avoided (Pasqualini *et al*., 1981; Mueller *et al*., 1992).

Stone-fruit Tree Aphids

Cultivated Prunoideae are affected by about 26 aphid species (Blackman and Eastop, 2000), only some of which are of economic importance for either the direct or indirect damage they cause. Peach (*Prunus persica*) and nectarine (*Prunus persica* var. *nucipersica*) host at least a dozen more or less harmful species, among which the well-known *Myzus persicae* (peach–potato aphid) is undoubtedly the most frequent and injurious. Spring colonies on the primary host usually derive from overwintering eggs; nevertheless, they can also arise from alatae arriving from anholocyclic populations overwintering on secondary host plants in warm climates or sheltered sites. On plum (*Prunus domestica*), the most injurious aphid pest is *Brachycaudus helichrysi* (leaf-curling plum aphid). Cherries (*Prunus avium* and *P. cerasus*) have just one serious aphid pest, *Myzus cerasi* (cherry blackfly). The above-mentioned and other aphids that are economically important on stone fruit, including apricot (*Prunus armeniaca*), Japanese apricot (*Prunus mume*) and almond (*Prunus dulcis*), are listed in Table 32.2.

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Table 32.2. Aphid species damaging to stone-fruit trees (Prunoideae).

Aphid	Life cycle	Host	Geographical distribution	Damage	Notes
Myzus persicae – Fig. 32.2c	Holocyclic, heteroecious on peach, or anholocyclic	Peach, also almond, plum, apricot, Japanese apricot and others (many different herbaceous and woody hosts)	Worldwide	Young shoots in spring	Most injurious species
Myzus amygdalinus	? Holocyclic	Almond	Central Asia	Young leaves	Minor pest
Myzus cerasi – Fig. 32.3b	Heteroecious	Cherry (*Galium* and *Veronica* as secondary hosts)	Worldwide	Serious leaf curling	Quite injurious pest
Myzus mumecola	Holocyclic, heteroecious	Plum, apricot and Japanese apricot	India and East Asia introduced in Southern Europe (Italy)[a]	Leaf curling	Occasionally injurious
Myzus siegesbeckiae	Holocyclic, heteroecious	Cherry, Japanese apricot, peach (Lamiaceae, i.e. *Plectranthus* and *Salvia*, as facultatively secondary hosts)	East Asia	Leaf curling	Occasionally injurious
Myzus varians – Fig. 32.3a	Holocyclic, heteroecious	Peach (*Clematis* as secondary host)	Native in East Asia, now widespread in Western Europe	Leaf curling	Quite injurious pest
Brachycaudus persicae – Fig. 32.2a	Anholocyclic or holocyclic, heteroecious	Peach, apricot, Japanese apricot, almond (Scrophulariaceae as secondary hosts)	West Palaearctic, Australasia and Americas	Dense colonies on twigs, buds, flowers and fruit	Overwinters on roots and collar area as virginoparae; a quite injurious pest
Brachycaudus schwartzi – Fig. 32.2b	Monoecious and usually holocyclic	Peach	West Palaearctic and parts of America	Deforms leaves	Sometimes overwinters as virginoparae; occasionally injurious
Brachycaudus amygdalinus	Holocyclic, heteroecious	Almond (*Polygonum aviculare* as secondary host)	Mediterranean and Middle East	Serious leaf curling	Occasionally injurious
Brachycaudus helichrysi	Holocyclic, heteroecious or anholocyclic where conditions allow	Plum, almond (many Asteraceae and other plants as secondary hosts)	Worldwide	Dense colonies on undersides of leaves, causing twisting	A serious pest of plum
Brachycaudus prunicola	Holocyclic, monoecious	Plum, also sloe (*Prunus spinosa*) and damson (*Prunus domestica* subsp. *insititia*)	Europe	Deforms leaves	Occasionally injurious

Continued

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Table 32.2. Continued.

Aphid	Life cycle	Host	Geographical distribution	Damage	Notes
Hyalopterus amygdali	Holocyclic, heteroecious	Almond (*Phragmites* and *Arundo* as secondary host)	West Palaearctic	Dense colonies on leaf undersides, but no deformation	Most injurious species in Western Europe
Hyalopterus persikonus – Fig. 32.2d	Holocyclic, heterocious	Peach (*Phragmites* and *Arundo* as secondary host)	West Palaearctic	Dense colonies on leaf undersides, but no deformation	Most injurious in Western Europe
Hyalopterus pruni	Holocyclic, heteroecious	Many *Prunus* (*Phragmites* and *Arundo* as secondary host)	Worldwide	Dense colonies on leaf undersides, but no deformation	Most injurious species in Western Europe
Rhopalosiphum rufiabdominale	Holocyclic, heteroecious	Peach, plum, Japanese apricot and cherry (Poaceae and other Monocotyledons as secondary hosts)	Worldwide	Dense colonies on young shoots	Occasionally injurious in East Asia
Phorodon humuli	Holocyclic, heteroecious	Plum (hop as secondary host)	West Palaearctic parts of America and New Zealand	Deformation of young shoots	Only occasionally damaging to plums
Pterochloroides persicae – Fig. 32.3c,d	Usually anholocyclic	Peach, plum, apricot, Japanese apricot, occasionally cherry and almond	Indian subcontinent to western Mediterranean	Heavy colonies on trunk and branches	Quite injurious

[a]Severe infestations on apricot have been recently recorded in Italy (Panini *et al*., 2017)

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Damage and virus transmission

Myzus persicae causes leaf twisting on infested buds; on nectarines it also affects fruit, causing typical pitting and discoloration. Symptoms are similar to those produced by *Brachycaudus schwartzi* (brown peach aphid), and sometimes these two species form mixed colonies. *Myzus varians*

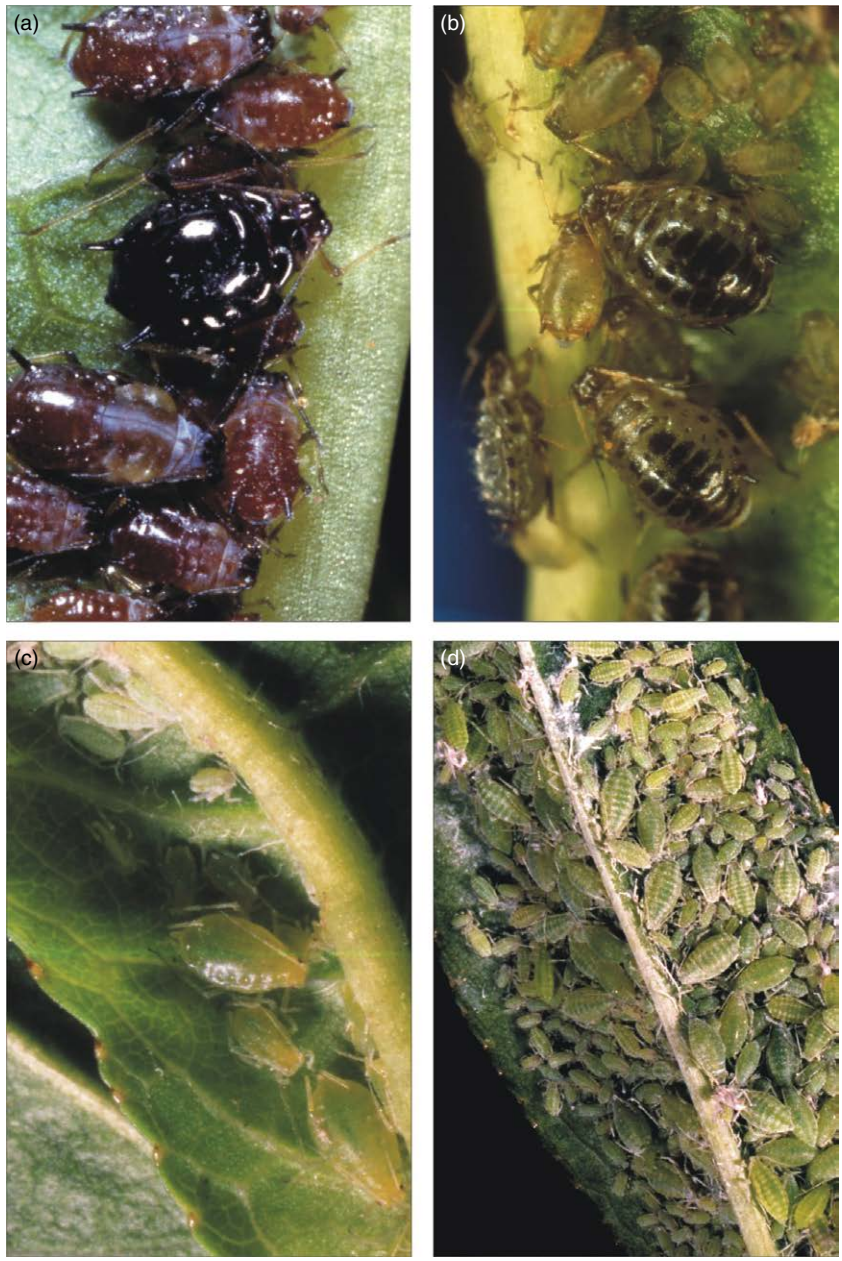

Fig. 32.2. Stone-fruit tree aphids. (a) Colony (one aptera and nymphs) of *Brachycaudus persicae* on peach; (b) colony of *Brachycaudus schwartzi* on peach (from Barbagallo *et al*., 1997, courtesy of Bayer); (c) colony of *Myzus persicae* on a peach leaf; (d) dense colony of *Hyalopterus persikonus* on a peach leaf.

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(cigar-rolling peach aphid) is economically less important, but causes leaf rolling.

Hyalopterus persikonus (mealy peach aphid) and *Hyalopterus pruni* (mealy plum aphid) produce copious honeydew. *Brachycaudus persicae* (black peach aphid) colonizes shoots and young fruit; during winter, it lives on the roots (on the collar area).

Brachycaudus helichrysi can cause severe deformations on leaves and the shedding of flowers and

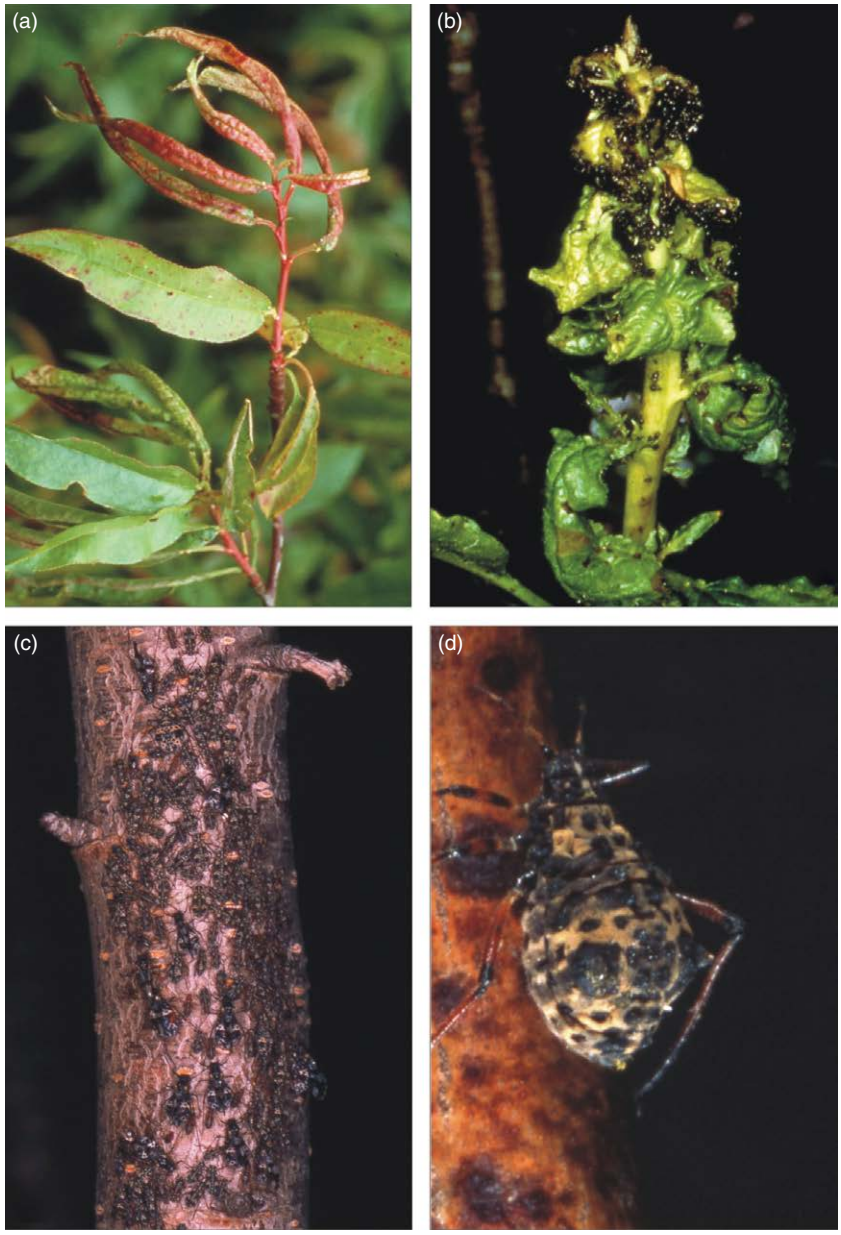

Fig. 32.3. Stone fruit tree aphids. (a) Typical damage of *Myzus varians* on peach leaves; (b) a dense colony of *Myzus cerasi* on a sweet cherry shoot (from Barbagallo *et al*., 1997, courtesy of Bayer); (c) colony of *Pterochloroides persicae* on an almond twig; (d) apterous viviparous female of *Pterochloroides persicae*.

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young fruit. *Myzus cerasi* causes severe curling and distortion of leaves.

Myzus persicae is considered as the most important virus vector on many plants. On stone fruit, it is an efficient vector of *Plum pox virus* causing 'Sharka'. Other vectors of the same virus disease are *Phorodon humuli* (damson–hop aphid), *B. helichrysi*, *H. pruni*, *M. varians* and some species that occasionally infest Prunoideae; these are *Brachycaudus cardui*, *A. spiraecola* and *Aphis craccivora* (cowpea aphid) (Wallis *et al.*, 2005).

Monitoring and economic thresholds

Control on peaches and nectarines must begin before the overwintering eggs hatch, therefore before flowering.

The pre-flowering threshold for *M. persicae* (as well as for *M. varians* and *B. schwartzi*) is estimated as 3% of buds infested. After flowering, the threshold stays at 3% for nectarines, but is raised on peach to 10% of shoots infested (Malavolta *et al.*, 1995). In summer, the effectiveness of natural enemies increases; at the same time, winged morphs develop and leave the tree. Monitoring during this period should evaluate both these population-reducing factors (i.e. natural enemies and emigration) in order to avoid unnecessary insecticide treatments. *Brachycaudus persicae* needs to be monitored at the end of winter when temperatures start to rise, because this species migrates from the roots to the shoots well before flowering. Late attacks are less harmful and easier to control, because the sensitivity of *B. persicae* to insecticides is then greater than it is earlier in the year. By contrast, with *Hyalopterus persikonus* on peach and *H. pruni* on plum, later attacks are more harmful than earlier ones and spraying with spot applications following visual monitoring is advised (Malavolta *et al.*, 1996).

The threshold used in Italy on plum trees for *B. helichrysi* and for *H. pruni* is 10% of shoots infested. In California, against the same aphids, an early or delayed dormancy spray is suggested if the aphid is a chronic problem, with thiamethoxam, imidacloprid or other suitable pesticides, followed if necessary by additional treatment(s) in spring/summer (UC IPM, 2009). For *M. cerasi* on cherries, a threshold of 3% shoots infested is recommended, and aphicide should be applied shortly after petal fall if this threshold is reached or exceeded (Malavolta *et al.*, 1995).

Chemical and supervised control

During spring and summer, several pesticides are currently applied against aphids. Pirimicarb is a selective aphicide, but resistance now often occurs. Neem oil from *Azadirachta indica* is used in 'organic' farming, and it has given good results against *M. persicae*. Synthetic pyrethroids are effective, but they are very toxic to beneficials; they also increase mite populations, so it is better to use them pre-flowering. Neonicotinoids show high efficiency, but because of their toxicity against bees and pollinators, they can be used only after flowering. Active ingredients like imidacloprid, thiamethoxam, spirotetramat and pymetrozine have shown high efficiency and selectivity.

Myzus persicae is a particularly frequent problem, both as regards damage and resistance to insecticides, which has several mechanisms (Chapter 19, this volume).

Biological control

Several parasitoids, predators and pathogens are known to affect stone fruit aphids, particularly *M. persicae* (for an updated list see CABI, 2016).

Unfortunately, natural enemies tend to appear too late in the season, when large aphid colonies have already developed, whereas damage by aphids is greatest well before then, in early spring. Therefore, the impact of natural enemies is usually low until late spring and summer, and this means that they are not able to prevent damage.

Acknowledgements

Many thanks are due to the editor (Bayer SpA, Milan) of the book *Aphids of the Principal Fruit-Bearing Crops* (Barbagallo *et al.*, 1997) for permission to reproduce Figs 32.1a–d, Fig. 32.2b and Fig. 32.3b from colour plates.

Executive Summary

Deciduous fruit trees are attacked by a very large number of aphid species, and economic thresholds and the appropriate timings of insecticides are well established for the majority of the most economically important species. Chemical control is often necessary, and choice of active ingredient is influenced by the insecticide-resistance status of the

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aphid population and with the aim of causing least damage to non-targets (particularly natural enemies). Countries also differ as to which effective compounds are still permitted (particularly among the organophosphates and carbamates); the more recent neonicotinoids are now often used. Winter oils and synthetic pyrethroids should be avoided. Timing may be affected by the need to avoid damage to pollinators.

Indigenous natural enemies are seen as a useful general restraint of inadequate strength and which appear late, but which should be preserved as far as possible. However, biological control of *E. lanigerum* by the parasitoid *A. mali* is often effective and can be manipulated by bringing prunings with aphid mummies into the orchard.

Other than the availability of rootstocks resistant to *E. lanigerum*, there is almost no use of host-plant resistance in such long-lived crops with long breeding programmes.

No cultural controls are practised, neither is there any use of semiochemicals for monitoring aphids or controlling their behaviour or that of their natural enemies.

There are no purposeful synergistic interactions between control methods, other than a general aim of avoiding damage to the beneficial fauna in determining the use of insecticides.

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33 IPM Case Studies: Tropical and Subtropical Fruit Trees

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Introduction

This chapter deals briefly with some applied aspects of the epidemiology, damage and control measures against pest aphid species affecting citrus trees and other widely grown tropical fruit tree crops.

Citrus Aphids

About 20 aphid species are recorded on citrus crops worldwide (Barbagallo and Patti, 1986; Blackman and Eastop, 2000, 2015), but only four or five strongly affect citrus trees by either direct or indirect damage (Table 33.1). For most of them, illustrations and/or identification keys are available (Barbagallo *et al*., 1997; Blackman and Eastop, 2000, 2015). The most widespread and harmful species are *Aphis spiraecola* (green citrus aphid), *Aphis gossypii* (cotton or melon aphid), *Aphis (Toxoptera) aurantii* (black citrus aphid) and *Aphis (Toxoptera) citricidus* (tropical citrus aphid).

Aphis spiraecola has a cosmopolitan distribution and appears to be mostly invasive and widespread in tropical and subtropical areas, while its presence in temperate climates is sometimes limited to sheltered or relatively warm habitats. In Japan, the aphid can occasionally lay overwintering eggs on citrus (Komazaki, 1991), and its populations in the warm temperate areas (the Mediterranean and comparable latitudes) show two main peaks of infestation, during spring and the early autumn months, synchronized with the flushing of the shoots.

Aphis gossypii is another species that very commonly infests citrus in most areas where the crop is grown. While the aphid is usually anholocyclic, holocyclic populations have been detected in a few of its distribution areas, including Japan, where winter eggs can be laid on citrus (Komazaki *et al*., 1979), as well as on several other unrelated plant species (Inaizumi, 1981). It is a highly polyphagous and genetically complex species (Komazaki and Toda, 2008). The most affected citrus are cultivars of orange (*Citrus sinensis*), mandarin orange, clementine and tangerine (all *Citrus reticulata*) and others, while lemon (*Citrus limon*) is infested very little.

Aphis (Toxopter) aurantii affects all citrus species and cultivars. While mostly polyphagous in the intertropical areas, citrus trees represent the main hosts of economic interest around the Mediterranean. It is considered to be strictly anholocyclic. Therefore, it overwinters solely as parthenogenetic morphs, usually in sheltered environments (e.g. greenhouses) in those temperate zones that have a rather cold winter.

Aphis (Toxoptera) citricidus is widespread all over the citrus-growing areas of the southern hemisphere, and is found as far north as 40° of latitude in Asia. Recently, it has spread quickly around the Caribbean and Florida (Halbert and Brown, 1996), and more recently it has also been detected in southern Europe in several northern localities of Portugal and Spain (Ilharco *et al*., 2005). Nevertheless, the aphid has not, as yet, been recorded around the inner Mediterranean basin, where it would pose a serious threat to citrus, since it is a highly efficient

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vector of *Citrus tristeza virus* (CTV). For a literature review on this aphid, see Michaud (1998).

All other citrus aphids listed in Table 33.1 are usually of secondary economic importance.

Damage and virus transmission

Direct damage varies with aphid species and the density of their populations, as well as with the species and age of the infested citrus groves. In addition to the sap and nutrient drain by aphid colonies, there are a variety of damage symptoms, such as the stunting of young shoots and the rolling and twisting of young leaves. The most harmful species is *A. spiraecola*, high-density colonies of which can lead to serious damage, especially to the growth of young orange and mandarin trees. Even at high population density, *Aphis gossypii* causes only minor deformations, while both *Aphis (Toxoptera)* species cause levels of damage intermediate between that of the two aforementioned species. There are other well-known damaging effects of aphid outbreaks, namely honeydew excretion followed by the development of sooty moulds, and problems with ants where aphids are myrmecophilous.

Indirect damage is due mostly to virus transmission. CTV, including both the 'stem pitting' and 'seedling yellows' strains, is a destructive disease and it has been known for many years that *A. (T.) citricidus* is the most efficient vector. A direct correlation between the spread of this aphid and the spread of CTV has been demonstrated across all citrus-growing areas. Other aphids infesting citrus (mainly *A. gossypii* and, to a lesser extent, *A. spiraecola* and *A. (T.) aurantii*) have also tested positively as vectors of CTV, indicating that transmission efficiency is correlated with different bioecological combinations of interacting factors such as virus strain, host plant and climatic conditions (Bar-Joseph *et al*., 1977; Roistacher *et al*., 1984; Davino *et al*., 1990; Komazaki, 1994; Halbert *et al*., 2004; Yokomi and DeBorde, 2005). *Aphis gossypii*, *Myzus persicae* (peach–potato aphid), *A. (T.) citricidus* and *Aphis craccivora* may also be involved in the transmission of *Citrus vein enation–woody gall virus* as well as *Citrus sudden death* and *Citrus yellow vein clearing disease* (Barbagallo and Massimino Cocuzza, 2014).

Monitoring and economic thresholds

Aphid populations on citrus can be evaluated directly in the field by inspection. A general sampling methodology has been suggested (Cavalloro and Prota, 1983), consisting of a weekly count on a convenient number of plants (usually between 5 and 10% of an orchard) during the period of exponential aphid population increase (i.e. mostly during the spring months and occasionally in early autumn in temperate climates such as the Mediterranean). Both aphid-infested and uninfested shoots are counted inside a frame of about 0.25 m^2 held up against the canopy on four sides of each of the randomly selected plants. The threshold is expressed as an overall percentage of shoots that are infested.

In relation to this sampling methodology, the suggested economic thresholds (at least for Mediterranean areas) for the application of chemical control measures against citrus aphids are: 25% of shoots infested by *A. (T.) aurantii* and *A. gossypii*, and 5 and 10% of shoots infested by *A. spiraecola* for clementine/mandarins and orange trees, respectively.

Chemical and supervised control

IPM methods can be suggested for controlling citrus aphid populations, and several factors should be considered before deciding to apply an insecticide. In addition to the threshold level of per cent of shoots infested, it is useful to look at the density (or size) of aphid colonies, the aphid species involved (since different species cause different levels of injury), the species and age of the host plants (younger orchards need a higher degree of protection than older ones) and, not least, the density of biocontrol agents in the aphid colonies (Barbagallo and Patti, 1986). It is important to consider that some cultural practices – such as irrigation, pruning and particularly nitrogen fertilization of the soil, and even more so as foliage sprays (as currently used by farmers during spring) – increase the flush of new growth, which promotes aphid populations both by accelerating their reproduction and increasing the time tender shoots are available to them.

Once the decision to apply a chemical spray against aphids has been taken, the selection of an appropriate pesticide is of paramount importance in citrus orchards in order to minimize negative side effects on non-target arthropods (particularly natural enemies). Commonly recommended at present are spirotetramat, acetamiprid, imidacloprid, thiamethoxam, flonicamid and a few others that have a similar range of biological activity. In general, more broad-spectrum pesticides including pyrethroids should be avoided because of their generally negative

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Table 33.1. Aphid species damaging to citrus trees.[a]

Aphid	Life cycle	Host	Geographical distribution	Damage	Notes
Aphis spiraecola (Fig. 33.1a,b)	Anholocyclic on citrus in warmer habitats; often holocyclic and heteroecious elsewhere	Polyphagous (citrus, Asteraceae, Rosaceae, etc.)	Cosmopolitan	Serious deformation of young shoots of orange, mandarin, clementine, grapefruit; negligible damage on lemon	Very injurious to citrus; vector of *Citrus tristeza virus* (CTV)
Aphis gossypii (Fig. 33.1c,d)	Usually anholocyclic; very rarely holocyclic and heteroecious in some areas	Highly polyphagous (citrus, Cucurbitaceae, Malvaceae, etc.)	Cosmopolitan	Infests young shoots (no deformation) of orange, mandarin, clementine and grapefruit	Commonly injurious on citrus; efficient vector of CTV
Aphis (Toxoptera) aurantii (Fig. 33.2a,b)	Anholocyclic everywhere	Polyphagous (citrus as main host)	Cosmopolitan	Infesting young shoots of all citrus species.	Commonly injurious on citrus; vector of CTV
Aphis (Toxoptera) citricidus (Fig. 33.2c)	Usually anholocyclic, very rarely holocyclic – monoecious in Japan	Mostly citrus and other plants	Southern hemisphere, up to 40°N in East Asia; also spread to Caribbean and Florida; recently introduced to Iberian peninsula	Infesting young shoots of all citrus species	Commonly injurious on citrus; highly efficient vector of CTV
Sinomegoura citricola	Anholocyclic	Polyphagous	Widespread from South-east Asia to Australia	Infests young shoots	Minor pest
Pseudomegoura magnoliae	Mainly anholocyclic	Rather polyphagous	East Asia	Infests young shoots	Minor pest
Aphis odinae (Fig. 33.2d)	Anholocyclic	Rather polyphagous	East Asia, sub-Saharan Africa	Infests young shoots	Minor pest
Myzus persicae	Holocyclic–heteroecious or anholocyclic	Highly polyphagous; occasionally on citrus	Cosmopolitan	Sometimes only single shoots	Occasional problem on citrus
Macrosiphum euphorbiae	Holocyclic–heteroecious or anholocyclic	Polyphagous; occasionally on citrus	Cosmopolitan	Sporadically on tender shoots	Minor pest
Aphis fabae	Holocyclic–heteroecious or anholocyclic	Polyphagous; occasionally on citrus	Cosmopolitan	Sporadically on tender shoots	Minor pest
Aphis craccivora	Mostly anholocyclic	Polyphagous; occasionally on citrus	Cosmopolitan	Sporadically on tender shoots	Minor pest

[a]*Note*: The literature also contains a few records of other species (e.g. *Brachycaudus cardui*, *Brachycaudus helichrysi* and *Pterochloroides persicae*) which it is unlikely were really living on citrus.

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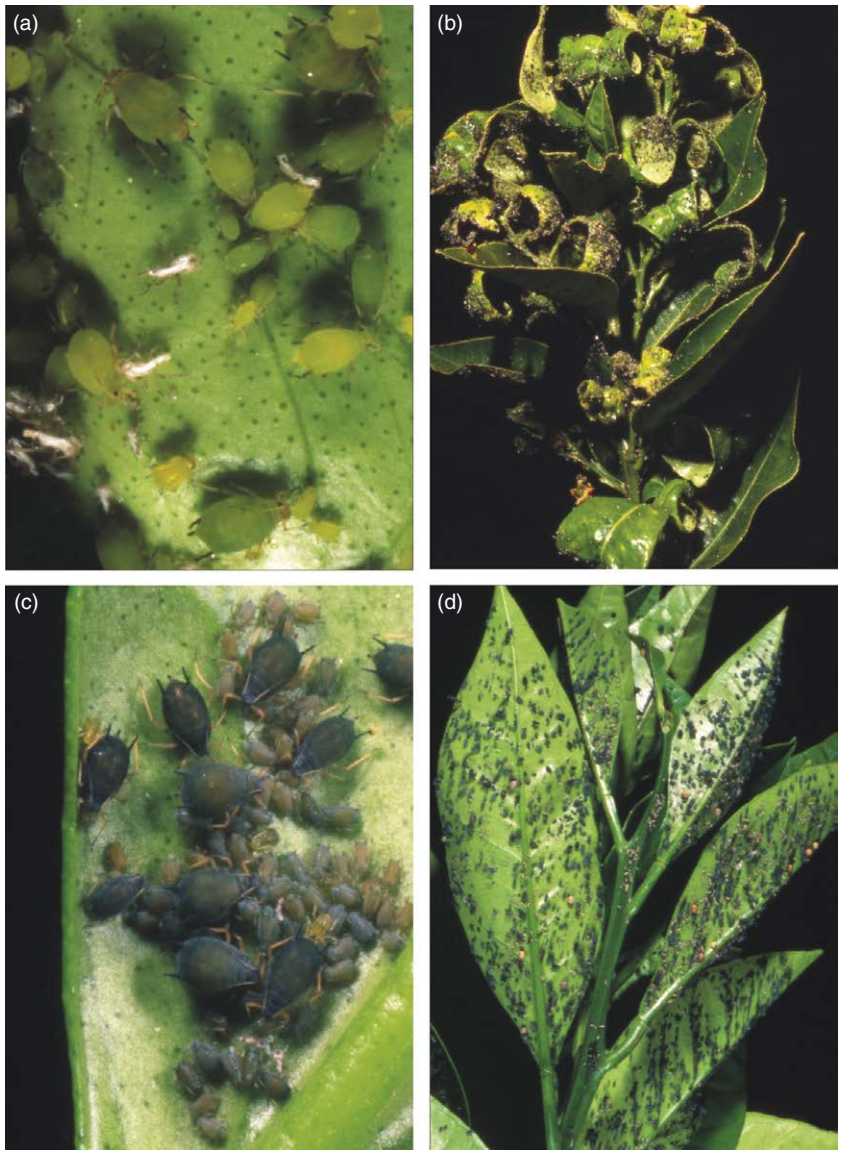

Fig. 33.1. Tropical and subtropical fruit tree aphids. (a) Colony of *Aphis spiraecola* (apterae and nymphs) on a clementine leaf; (b) strong deformations following a severe attack of *A. spiraecola* on the shoot apex of clementine; (c) colony of *Aphis gossypii* on an orange leaf; (d) colonies of *A. gossypii* on an orange shoot: despite the severe attack, leaves usually remain undeformed. (Colour original from Barbagallo *et al*., 1997, courtesy of Bayer.)

side effects in increasing mite populations and in killing beneficial arthropods.

Insecticide resistance has been shown in several aphid species on citrus. *Aphis gossypii* is undoubtedly the aphid that seems most adept at showing resistance to different pesticides, including some selective aphicides such as pirimicarb. Komazaki *et al.* (2011) have detected resistance in strains collected from different crops, including citrus in Japan, and a change in the acetylcholinesterase gene has been identified in pirimicarb-resistant strains (Andrews *et al*., 2004; Toda *et al*., 2004). In Korea, Song *et al.* (1995) also

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Fig. 33.2. Tropical and subtropical fruit tree aphids. (a) Small colony (aptera with nymphs) of *Aphis (Toxoptera) aurantii* on lemon (colour original from Barbagallo *et al*., 1997, courtesy of Bayer); (b) alate viviparous female of *A. (T). aurantii* (from Barbagallo *et al*., 1997, courtesy of Bayer); (c) colony of *Aphis (Toxoptera) citricidus* on a grapefruit leaf (from Alcântara Santos and Barbagallo, 1989; photograph by S. Barbagallo); (d) colony of *Aphis odinae* on a tender cashew leaf (from Barbagallo and Alcântara Santos, 1989; photograph by S. Barbagallo).

found resistance to pirimicarb in *A. spiraecola*. In any case, this latter species – independently of any resistance – is quite difficult to control effectively, because the heavy deformation of infested citrus shoots protects the colonies of this aphid from being reached directly by sprays.

Biological control

Predators and parasitoids can reduce citrus aphid populations significantly under some ecological conditions. Among predators, several species of coccinellids, syrphids and chrysopids are the most

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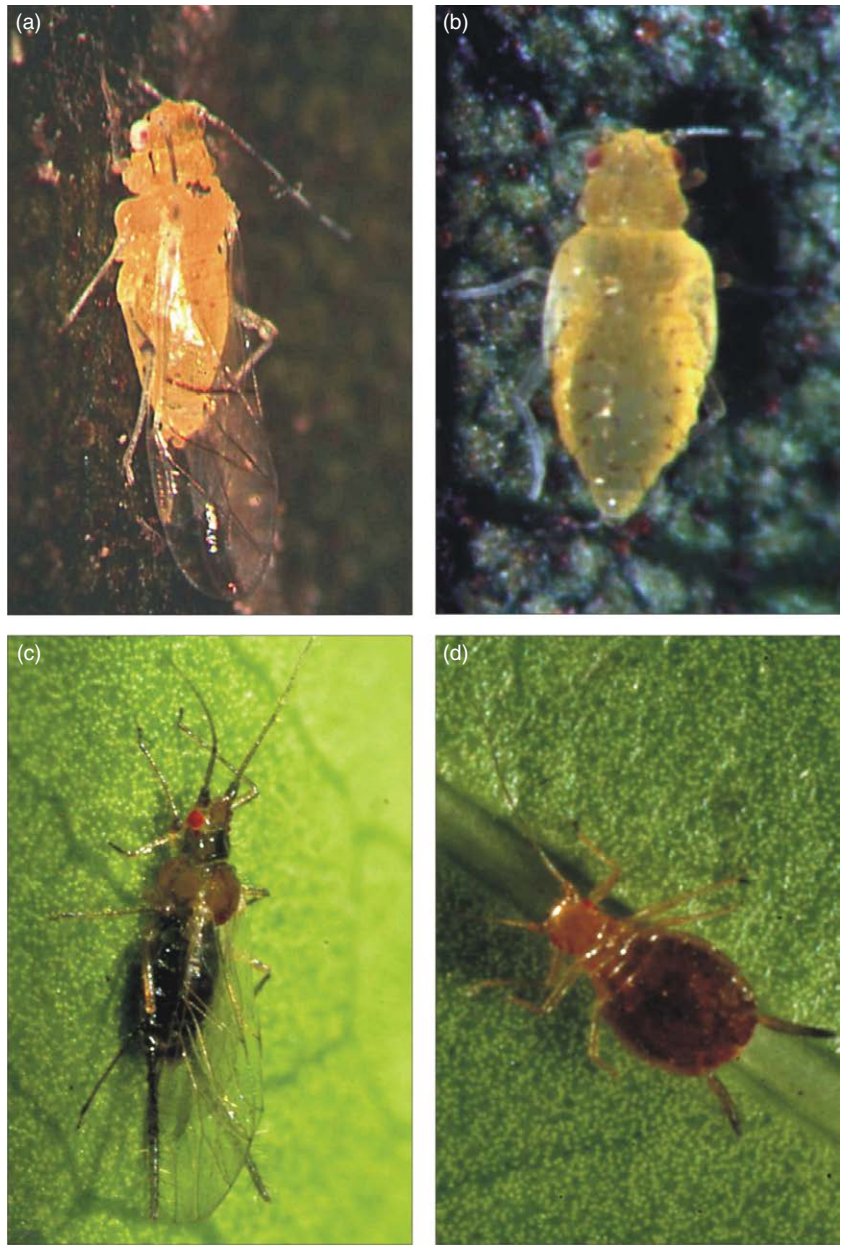

Fig. 33.3. Tropical and subtropical fruit tree aphids. (a) Alate viviparous female of *Monelliopsis pecanis* (from Barbagallo and Suma, 1999; photograph by S. Barbagallo); (b) fourth-instar nymph of *M. pecanis* (from Barbagallo and Suma, 1999; photograph by S. Barbagallo); (c) alate viviparous female of *Greenidea ficicola* (from Barbagallo *et al*., 2005; courtesy of *Informatore Fitopatologico*); (d) apterous viviparous female of *G. ficicola* (from Barbagallo *et al*., 2005; courtesy of *Informatore Fitopatologico*).

efficient groups. Some species of parasitoids in the Aphidiinae – such as *Lysiphlebus testaceipes*, *Lysiphlebus fabarum* and *Lysiphlebus confusus* – can reach levels of parasitism as high as 90–100% on *A. (T.) aurantii* and *A. gossypii* in the Mediterranean countries (Tremblay *et al*., 1980; Starý

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et al., 1988; Meliá, 1993). Unfortunately these parasitoids seem unable to parasitize *A. spiraecola*, against which the aphelinid wasp *Aphelinus spiraecolae* has proved promising in Florida (Tang and Yokomi, 1996). Natural biological control of citrus aphids is therefore usually more effective against *A. gossypii* and *A. (T.) aurantii* than against *A. spiraecola*. The efficiency of biological control agents of *A. (T.) citricidus* is variable (Michaud, 1998). Some natural enemies of this species are known from some areas (De Huiza and Ortiz, 1981; Nickel and Klingauf, 1985; Takanashi, 1990; Komazaki, 1994), whereas none are known from other large regions such as sub-Saharan Africa (Remaudière *et al*., 1985). In Japan, *Lysiphlebia japonica* can parasitize up to 70% of *A. (T.) citricidus* late in the season. Predators and fungal diseases (Rondón *et al*., 1983) are apparently commonly found infecting this aphid, but are not very effective.

On the whole, natural enemies only have an impact on citrus aphid populations late in the season; as a consequence, farmers often cannot avoid using chemical control.

Tropical Fruit Tree Aphids

Several cultivated tropical fruit trees can be affected by aphid pests. This section focuses on the main species infesting the following crops, which have been selected as being grown fairly extensively in tropical countries (Paull and Duarte, 2011, 2012): avocado (*Persea americana*), mango (*Mangifera indica*), guava (*Psidium guajava*), custard-apple (*Annona cherimola*) and other congeneric species (i.e. soursop, sugar-apple, atemoya, bullock's heart), banana (*Musa* × *paradisiaca*), cashew nut (*Anacardium occidentale*) and pecan (*Carya illinoensis*), though the latter is also cultivated outside the tropics.

Blackman and Eastop (2000) updated and keyed all aphids recorded on these plants, while Martin (1983) gave a general illustrated identification key for common aphid pests in the tropics. A variable number of four to nine aphid species is recorded for each of the named cultivated plants (Table 33.2); most are polyphagous. The commonest are well-known representatives of the genus *Aphis* (*A. gossypii*, *A. spiraecola*, *A. craccivora* (cowpea aphid), *A.(T.) aurantii*, *A. (T.) citricidus* and *Aphis odinae*). Most of these have already been mentioned as citrus pests. These aphids, as well as a few other polyphagous species (i.e. *M. persicae*, *Macrosiphum euphorbiae* (the potato aphid) and occasionally *Sinomegoura citricola*) are reportedly common on a variety of tropical fruit crops (i.e. avocado, cashew nut, litchi (*Litchi chinensis*), macadamia nut (*Macadamia integrifolia*), mango, passion fruit (*Passiflora edulis*)). These aphids are permanently anholocyclic in the tropics, and their seasonal outbreaks are linked mainly to the periods of strongest growth of their host plants.

In addition, there are several oligophagous or, more rarely, monophagous aphids injurious to some of the above-named crops. Among these species are *Pentalonia nigronervosa* (banana aphid) and a few *Rhopalosiphum* species infesting banana, some *Greenidea* species recorded on several host plants (e.g. *Annona* species, guava, mango, litchi) and a group of species linked mainly to pecan, as shown in Table 33.2.

Damage and virus transmission

Direct damage varies within the different crops and is correlated with aphid population density. Thus, *P. nigronervosa* can form quite high infestations on banana, and so can other aphids (*Monellia caryella* and *Monelliopsis pecanis* – the yellow pecan aphids) on pecan. *Aphis gossypii* is relatively common on several other fruit crops. Most aphid species affecting tropical crops develop colonies on young shoots and leaves, but occasionally also on flowers and young fruit. *Pentalonia nigronervosa* infesting banana develops myrmecophilous colonies on the inner leaf sheaths and folded apical leaves, including flower bracts. *Longistigma caryae* is a bark feeder, developing large colonies on branches of pecan, while *Phylloxera* species develop leaf galls on the same host plant. Sap drain and saliva injection lead to loss of productivity and general debilitation of affected plants. The development of sooty mould and ant attendance on colonies of myrmecophilous aphids are additional problems and inconveniences for growers. Virus transmission by aphids, however, is the most important source of losses for several tropical crops. Non-persistent viruses can even be transmitted by the probes of vagrant alatae on receptive hosts, i.e. by aphid species that usually do not develop colonies on those plants. The widespread *Banana mosaic virus* (a variant strain of *Cucumber mosaic virus*) is transmitted non-persistently by several aphid species, including *A. gossypii*, *M. persicae* and *Rhopalosiphum* spp. (Hughes and Eastop, 1991). *Pentalonia nigronervosa* infesting banana

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Table 33.2. Aphid species damaging to tropical fruit trees.[a]

Aphid	Life cycle	Host (main tropical fruit)	Geographical distribution	Damage	Notes
Aphis spiraecola (Fig. 33.1a,b)	Anholocyclic in the intertropical zone	Avocado, custard-apple, cashew, papaya, guava, mango, etc.	Widespread in the intertropical zone	Infests young shoots and leaves	Commonly recorded as a pest
Aphis gossypii (Fig. 33.1c,d)	Anholocyclic in the intertropical zone	Avocado, custard-apple, cashew, papaya, guava, mango, etc.	Widespread in the intertropical zone	Infests young shoots and leaves	Most common species affecting guava and other crops
Aphis craccivora	Anholocyclic in the intertropical zone	Papaya, guava, litchi, avocado, etc.	Widespread in the intertropical zone	Infests young shoots and leaves	Occasionally injurious
Aphis (Toxoptera) aurantii (Fig. 33.2a,b)	Anholocyclic everywhere	Cashew, mango, guava, litchi, avocado, etc.	Widespread in the intertropical zone	Infests young shoots and leaves	Commonly recorded
Aphis (Toxoptera) citricidus (Fig. 33.2c)	Anholocyclic in the intertropical zone	Cashew, mango, guava, litchi, avocado, etc.	Widespread in the intertropical zone	Infests young shoots and leaves	Commonly recorded
Aphis odinae (Fig. 33.2d)	Anholocyclic in the intertropical zone	Mango, cashew, etc.	East Asia, sub-Saharan Africa	Infests young shoots and leaves	Occasionally injurious
Myzus persicae	Anholocyclic in the intertropical zone	Avocado, guava, papaya, passion fruit, etc.	Cosmopolitan	Infests young shoots and leaves	Commonly recorded
Sinomegoura citricola	Anholocyclic in the intertropical zone	Mango and avocado	South-east Asia, Australia	Infests young shoots and leaves	Minor pest
Pentalonia nigronervosa	Anholocyclic everywhere	Banana and other Musaceae	Throughout the intertropical zone; occasionally in Europe and North America (in greenhouses)	Infests leaf sheaths and folded leaves	Efficient vector of *Banana bunchy top virus*
Rhopalosiphum rufiabdominale	Anholocyclic or holocyclic heteroecious	Occasionally on banana	Nearly worldwide	Occasionally infests roots	Minor pest. There are a few other species of the same genus infesting banana and vectoring *Banana mosaic virus*
Greenidea mangiferae	Anholocyclic	Mango	Recorded from Taiwan	Infests young shoots	Minor pest

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Greenidea psidii	Anholocyclic	Guava and several other Myrtaceae	Widespread from India to East Asia	Infests young shoots	Occasionally injurious
Greenidea ficicola (Fig. 33.3c,d)	Anholocyclic	Guava, litchi and other Myrtaceae and Moraceae	Mediterranean, South-east Asia, Africa, Australia, North America	Infests young shoots	Minor pest
Taiwanaphis kalipadi	Anholocyclic	Sugar-apple	India (West Bengal)	Infests young shoots	Minor pest
Monelliopsis pecanis (Fig. 33.3a,b)	Holocyclic monoecious	Pecan, Juglans	North and Central America, Mediterranean, South Africa	Infests leaves	Commonly injurious
Monellia caryella	Holocyclic monoecious	Pecan	North America; Israel and Spain (introduced)	Infests leaves	Commonly injurious
Longistigma caryae	Anholocyclic or holocyclic monoecious	Pecan	North America	Infest twigs and barks	Commonly injurious
Melanocallis caryaefoliae	Holocyclic monoecious	Pecan	North America	Infests leaves	Commonly injurious
Phylloxera spp. (group of five species)[a]	Holocyclic (mostly monoecious, except one species)	Pecan	North America (one species introduced in south-eastern Europe: Georgia)	Galls on leaflets, or sometimes on twigs and nuts	Commonly injurious

[a]*Note*: For details see Blackman and Eastop (2000, 2015).

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is responsible for semi-persistent transmission (Hu *et al*., 1996) of the more severe *Banana bunchy top virus* in several regions (Africa, East Asia, India, Pacific regions, Australia). *Papaya ringspot virus* is another destructive disease transmitted by polyphagous aphids (mainly *A. gossypii* and *M. persicae*, but also *A. spiraecola* and *M. euphorbiae*); it is widespread in eastern Asia, the Caribbean, Hawaii and South America (Gonsalves, 1998; Valdes-Estrada *et al*., 2005). The same aphids, particularly the first two species, are also vectors of various virus diseases of passion fruit (*Passion fruit woodiness virus*, *Passion fruit mottle virus*, *Sri Lanka passion fruit mottle virus*) in Asia and Australasia (Chang and Lin, 1992; Parry *et al*., 2004).

Monitoring and economic thresholds

Although the monitoring of aphid populations can be carried out easily by direct inspection of the plants, very little is known about damage thresholds for aphids in most of the tropical crops referred to here. In areas of high humidity in southeast USA (Alabama, Georgia), a variable threshold for pecan of 10–20 aphids in the 'yellow aphid' complex (*M. pecanis* and *M. caryella*) per leaf in June, and an average of 3 individuals of *Melanocallis caryaefoliae* (black pecan aphid) per leaf later in the season are suggested (Harris, 1983). Against the 'yellow aphid' complex in California, thresholds of an average of more than 20 aphids/leaf (from June to mid-August) or more than 10 aphids/leaf (after mid-August to autumn) have been recommended (Sibbett and van Steenwyk, 2000).

Supervised chemical control

Chemical control, if it is necessary, should ideally follow the methodology of supervised control as suggested for citrus orchards (i.e. based on economic thresholds and therefore on the economic benefits of treatment). However, for most situations, such thresholds have not yet been determined. As for citrus orchards (see earlier), it is necessary to make the correct choice of pesticides, with emphasis on some selectivity, in order to reduce undesirable side effects, particularly on entomophagous and other non-target organisms in the crop system. This means that the more broad-spectrum insecticides, still applied (because they are usually cheaper) against aphids on these crops (especially pecan and banana), should be replaced by specific aphicides as suggested for citrus, whenever applicable for each crop.

Biological control

In tropical climates, biological control plays an important role in limiting the population increase of aphids. Several species of predators and parasitoids have been recorded, but their efficiency is not well known (see, for example, Remaudière *et al*., 1985, for a general overview on the efficiency of Aphidiinae in tropical Africa; also Verghese and Tandon, 1987).

Some parasitoid wasps, like *L. testaceipes*, play an important role in the natural biological control of different aphid pests (i.e. *A. gossypii* infesting several tropical fruit tree crops, *P. nigronervosa* on banana) in several countries. On pecan against the 'yellow aphids' complex, the two parasitoids *Aphelinus perpallidus* and *Trioxys pallidus*, in combination with predators, can make a useful contribution to limiting aphid population growth in the USA and Israel (Watterson and Stone, 1982; Monsour, 1988).

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Executive Summary

The extensive research effort that has been devoted to citrus means that economic thresholds and monitoring protocols, which may involve assessing other criteria such as host-plant age and abundance of natural enemies, have been proposed for most of the injurious aphid species on this crop; in contrast, thresholds are far less developed for tropical fruit trees and largely still remain to be worked out.

For both citrus and tropical fruit, the choice of a selective insecticide such as pirimicarb is desirable to preserve natural enemies that, although they may appear too late to prevent the first increase of aphid numbers in the spring, often provide good control later in the season. In this respect, the modern neonicotinoids appear more suitable than the older residual insecticides.

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Currently, any biological control relies on the indigenous entomophagous populations (especially parasitoids); there is no release of natural enemies in the Mediterranean region.

No use is made of host-plant resistance.

Cultural control is involved in citrus IPM in the sense that farmers should avoid practices such as irrigation and nitrogen fertilization that predispose crops for rapid aphid increase.

Semiochemicals do not form part of aphid IPM in citrus or tropical fruit tree crops.

Interactions between control measures only involve care in the use of insecticides to avoid damage to biological control.

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