# TROPICAL ROOT AND TUBER CROPS

2nd Edition

## CASSAVA, SWEET POTATO, YAMS AND AROIDS

Vincent Lebot

CROP PRODUCTION SCIENCE IN HORTICULTURE

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**Vincent Lebot**

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# Acronyms and Abbreviations

| | |
|---|---|
| A | amylose |
| ABA | abscisic acid |
| ABS | accelerated breeding scheme |
| ACMBFV | African cassava mosaic Burkina Faso virus |
| ACMV | African cassava mosaic virus |
| AFLP | amplified fragment length polymorphism |
| a.i. | active ingredient |
| ATP | adenosine triphosphate |
| AYT | advanced yield trial |
| BA | 6-Benzyladenine |
| Bt | *Bacillus thuringensis* |
| CBB | cassava bacterial blight |
| CBDV | *Colocasia bobone* disease virus |
| CBSD | cassava brown streak disease |
| CCMV | cassava common mosaic virus |
| CET | clonal evaluation trial |
| CFSD | cassava frogskin disease |
| CG | cyanogenic glucosides |
| CGA | chlorogenic acid |
| CGIAR | Consultative Group on International Agricultural Research |
| CGR | crop growth rate |
| ChYNMV | Chinese yam necrotic mosaic virus |
| CIAT | Centro Internacional de Agricultura Tropical |
| CIP | Centro Internacional de la Papa, Peru (International Potato Center) |
| CIPC | isopropyl-N-(3-chlorophenyl) carbamate |

| | |
|---|---|
| CIRAD | Centre de Coopération Internationale en Recherche Agronomique pour le Développement |
| CIS | constant immersion system |
| CMD | cassava mosaic disease |
| CMMGV | cassava mosaic Madagascar virus |
| cpDNA | chloroplast DNA |
| CMV | cucumber mosaic virus |
| CRRD | cocoyam root rot disease |
| CsALV | cassava American latent virus |
| CsCAMV | cassava Caribbean mosaic virus |
| CsCMV | cassava common mosaic virus |
| CsFSaV | cassava frogskin associated virus |
| CsNAV | cassava new alphaflexivirus |
| CsPLV | cassava polero-like virus |
| CsSLV | cassava symptomless virus |
| CsVX | cassava virus |
| CTCRI | Central Tuber Crops Research Institute |
| CsVMV | cassava vein mosaic virus |
| DaBV | *Dioscorea alata* bacilliform virus |
| DAP | days after planting |
| DAV | *Dioscorea alata* virus (syn. yam mild mosaic virus) |
| DbBV | *Dioscorea bulbifera* bacilliform virus |
| DdV | *Dioscorea dumetorum* virus |
| DDV | *Dioscorea dumetorum* potyvirus |
| DEV | *Dioscorea esculenta* virus |
| DLV | *Dioscorea latent* virus |
| DM | dry matter |
| DmoV | *Dioscorea* mottle virus |
| DMSO | dimethyl sulfoxide |
| DsMV | dasheen mosaic virus |
| DNA | deoxyribonucleic acid |
| DTV | *Dioscorea trifida* virus |
| EACMAV | East African cassava mosaic Malawi virus |
| EACMCV | East African cassava mosaic Cameroon virus |
| EACMKV | East African cassava mosaic Kenya virus |
| EACMV | East African cassava mosaic virus |
| EACMZV | East African cassava mosaic Zanzibar virus |
| ELISA | enzyme-linked immunosorbent assay |
| EPIC | erosion productivity impact calculator |
| ET | evapotranspiration |
| FAO | Food and Agriculture Organization |
| FC | field collected |
| FEC | friable embryogenic callus |
| FFS | farmer field school |
| FISH | fluorescence *in situ* hybridization |
| $GA_3$ | gibberellic acid |
| GBS | genotyping by sequencing |

| | |
|---|---|
| GBSS | granule-bound glucosyl transferase |
| GCA | general combining ability |
| GEBV | genomic estimated breeding values |
| GMO | genetically modified organism |
| GS | genomic selection |
| GUS | β-glucuronidase |
| G × E | genotype × environment |
| HCN | hydrogen cyanide |
| HFC | high flavonoid content |
| HPLC | high performance liquid chromatography |
| HP-TLC | high performance thin layer chromatography |
| IAA | indole-3-acetic acid |
| IBS | internal brown spot |
| IBSV | internal brown spot virus |
| ICMV | Indian cassava mosaic virus |
| IITA | International Institute for Tropical Agriculture |
| IN | India |
| INEA | International Network for Edible Aroids |
| INRA | Institut National de la Recherche Agronomique |
| IPGRI | International Plant Genetic Resources Institute |
| IPM | integrated pest management |
| IPPC | isopropylphenylcarbamate |
| IRAP | inter-retrotransposon amplified polymorphism |
| ISEM | immunosorbent electron microscopy |
| JYMV | Japanese yam mosaic virus |
| KM | Konamizuki |
| LA | leaf area |
| LAI | leaf area index |
| LED | light emitting diode |
| LSU | Louisiana State University |
| LTR | long terminal repeat |
| MAS | marker-assisted selection |
| MDH | malate dehydrogenase |
| MLO | mycoplasma-like organism |
| MS | Murashige and Skoog |
| NAA | naphthaleneacetic acid |
| NAR | net assimilatory rate |
| NARI | National Agricultural Research Institute |
| NGS | next generation sequencing |
| NIRS | near infra-red spectroscopy |
| NPK | nitrogen, phosphorus and potassium |
| NRCRI | National Root Crop Research Institute |
| OFSP | orange-flesh sweet potatoes |
| OP | open pollinated |
| PCNB | pentachloronitrobenzene |
| PCR | polymerase chain reaction |
| PEG | polyethylene glycol |

| | |
|---|---|
| PNC | primary nodal complex |
| PNG | Papua New Guinea |
| PPB | participatory plant breeding |
| PPD | postharvest physiological deterioration |
| PPO | polyphenol oxidase |
| PT | pathogen tested |
| PYT | preliminary yield trial |
| QTL | quantitative trait loci |
| RH | relative humidity |
| RAPD | random amplified polymorphic DNA |
| Rf | reproduction factor |
| RFLP | restriction fragment length polymorphism |
| RNA | ribonucleic acid |
| RS | reducing sugar |
| RT | regional trial |
| RTISP | retrotransposon insertion polymorphism |
| RUE | radiation use efficiency |
| S | starch |
| SACMV | South African mosaic virus |
| SAH | semi-autotrophic hydroponics |
| SCA | specific combining ability |
| SED | super-elongation disease |
| SLCMV | Sri Lankan cassava mosaic virus |
| SLS | static liquid system |
| SNK | Student–Newman–Keul |
| SNP | single nucleotide polymorphism |
| SPC | Secretariat of the Pacific Community |
| SPCFV | sweet potato chlorotic fleck virus |
| SPCSV | sweet potato chlorotic stunt virus |
| SPE | standard pan evaporation |
| SPFMV | sweet potato feathery mottle virus |
| SPMMV | sweet potato mild mottle virus |
| SPMV | sweet potato mild virus |
| SPSMD | sweet potato severe mosaic disease |
| SPV2 | sweet potato virus 2 |
| SPVD | sweet potato virus disease |
| SPW | sweet potato weevil |
| SPYN | South Pacific Yam Network |
| SRAP | sequence related amplified polymorphism |
| SRT | single row trial |
| SSF | simultaneous saccharification and fermentation |
| SSH | suppression subtractive hybridization |
| SSR | simple sequence repeat |
| T-medium | tuberization medium |
| TA | total anthocyanin |
| TaBV | taro bacilliform virus |
| TaBCHV | taro bacilliform CH virus |
| TAN | tropical ataxic neuropathy |

| | |
|---|---|
| TANSAO | Taro Network for South-east Asia and Oceania |
| TaRV | taro reovirus |
| TaVCV | taro vein chlorosis virus |
| TBC | total beta carotene |
| TCC | total carotenoid content |
| TCNB | tetrachloronitrobenzene |
| TCS | true cassava seeds |
| T-DNA | transfer DNA |
| TIA | trypsin inhibitor activity |
| TIS | temporary immersion system |
| TLB | taro leaf blight |
| TP | total phenol |
| UHT | ultra-high temperature |
| USDA | US Department of Agriculture |
| UYT | uniform yield trial |
| VGI | vegetative growth index |
| VU | Vanuatu |
| WAP | weeks after planting |
| WP | wettable powder |
| WUE | water use efficiency |
| W*x* | waxy locus |
| YMMV | yam mild mosaic virus (syn. *Dioscorea alata* virus) |
| YMV | yam mosaic virus |

# Preface

Vegeculture – tropical food production based on vegetatively propagated energy crops – emerged well before agriculture based on cereals and grains. The tropical root and tuber crops (cassava, sweet potato, yams and aroids) are among the oldest on earth and archaeological evidence indicates that man used them for subsistence more than 20,000 years ago. In many areas, especially in the wet tropics, they were the only staples and fed extensive populations before the introduction of cereals. Today, they represent the second most important set of food crops in developing countries, closely following the cereals. They are produced with low inputs but are an important source of income and employment in marginal areas, especially for women. Consumed mostly by the poorest, they contribute greatly to food security and are held in high esteem culturally. They are also cash crops and are used for animal feed or as raw material for industrial processing.

Sometimes considered as plants of the past, they are, on the contrary, crops of the future since they allow local production of carbohydrates, which can substitute expensively imported cereals with high carbon footprint. With world population projected to increase from the present 7.7 bn to 9.8 bn by 2050, it may be argued that the demand for carbohydrates will soon exceed the production potential of areas devoted to the cultivation of cereals. This is especially critical in the wet tropics, where the majority of the world population lives. In circumstances of global climatic change, such a scenario may render increased production of tropical root and tuber crops imperative. This may come about all the sooner if some countries decide to retain their harvests of cereals for their population needs and stop exporting. As a group, the tropical root and tuber crops are efficient plants and if marginal land is to be exploited to support burgeoning populations, their potential, clearly untapped, will need to be developed. Although these species belong to different botanical families, they are grouped together because they are vegetatively propagated, bulky and perishable (Table I). Despite these constraints, they have proven surprisingly transferable and are now cultivated throughout the world. In many places, they are grown together within the same plots, in home gardens or in mixed

**Table I.** Characteristics of the tropical root and tuber crops. Source: author's own

| Characteristics | Cassava | Sweet potato | Yams | Aroids |
|---|---|---|---|---|
| World production 2017 (million t)* | 272 | 113 | 73 | 10 |
| World cultivated area 2017 (million ha) | 26.3 | 9.2 | 8.5 | 2.1 |
| World average yield 2017 (fresh t/ha) | 11.1 | 12.2 | 8.6 | 5.9 |
| Yield potential (fresh t/ha) | 90 | 120 | 110 | 110 |
| Planting material (propagule) | Stems | Vine cuttings | Tubers | Corms, suckers |
| Growth period (months) | 8–36 | 3–6 | 8–36 | 6–16 |
| Optimal rainfall (mm) | 1,000–2,000 | 750–1,500 | 1,200–2,000 | 2,000–3,000 |
| Optimal temperature (°C) | 25–30 | 20–25 | 30 | 20–35 |
| Drought resistant | Yes | Yes | Yes | No |
| Waterlogged tolerant | No | No | No | Yes |
| Shade tolerant | No | No | No | Yes |
| Fertility and organic matter requirements | Low | Low | High | High |
| Seasonality of crop cycle | No | Yes | Yes | No |
| In-ground storage life | Long | Moderate | Moderate | Long |
| Postharvest storage life | Very short | Short | Long | Moderate |
| Leaves used for human consumption | Yes | Yes | No | Yes |
| Leaves used for animal feed | Yes | Yes | No | Yes |
| Dry matter (% fresh weight, FW)* | 30–40 | 20–35 | 20–40 | 20–30 |
| Starch (% FW) | 27–37 | 18–28 | 20–25 | 15–25 |
| Starch grain size (diameter in microns) | 5–50 | 2–40 | 1–70 | 1–6 |
| Amylose (% starch) | 15–30 | 8–32 | 10–30 | 3–45 |
| Gelatinization temperature (°C) | 49–73 | 58–65 | 69–88 | 68–75 |
| Total sugars (% FW) | 0.5–2.5 | 1.5–5.0 | 0.5–2.0 | 2.0–3.0 |
| Proteins (% FW) | 0.5–2.0 | 1.0–3.0 | 2.0–4.0 | 1.5–3.0 |
| Fibres (% FW) | 1.0 | 1.0 | 0.6 | 0.5–3.0 |
| Vitamin A (mg/100 g/FW) | 17 | 900 | 117 | 0–42 |
| Vitamin C (mg/100 g/FW) | 50 | 35 | 25 | 10 |
| Minerals (% FW) | 0.5–1.5 | 1.0 | 0.5–1.0 | 0.5–1.5 |
| Energy (KJ/100 g/FW) | 600 | 500 | 440 | 400 |
| Anti-nutritional compounds | Cyanogens | Trypsin inhibitors | Alkaloids, tannins | Oxalate crystals |

*After FAO (2017).

cropping systems, complementing each other throughout the year to produce a steady supply of energy.

However, compared to other crops of equivalent economic importance, the tropical root and tuber crops are seriously under-researched. Considered in most developing countries as of lesser priority, well below traditional export commodities inherited from the colonial era, these food crops do not receive from governments the attention they deserve. More widely, western ethnocentric prejudices have induced an even more striking neglect of their essential food security role.

They share common biological traits. All are perennial species in the wild, but cultivars are annual and need to be replanted to produce desirable underground storage organs. The flowering ability of cultivars is erratic; they have variable ploidy levels but are predominantly allogamous and highly heterozygous. Unlike most crops, they are not grown for their fruits or seeds and their reproductive biology is often unknown to farmers. As the major traits under selection are not assessed visually, the domestication process is somewhat peculiar compared to other crops. The focus is not on the aerial morphotype but rather on the chemotype of underground organs. Wild forms accumulate secondary metabolites as a natural defence against predators, and domestication entails reducing these anti-nutritional compounds, while increasing those of value in human consumption.

The origin of these species is a puzzling enigma. Cultivated varieties were collected by botanists as early as the voyages of the first European explorers, and these were used to describe the botanical species. Taxonomists argue that the cultivated species are now unknown in the wild state, which encourages much speculation regarding their wild progenitors. The scientific community has engaged in controversial debate to pinpoint their direct ancestors and the exact geographic location of their domestication. Evidence is now accumulating, with the contribution of molecular markers and of archaeological studies, to reveal that domestication probably occurred on several occasions over a vast geographical area and in different periods of history. In fact, the process of domestication is still being used by farmers who capture attractive, volunteer, genotypes appearing spontaneously in their cropping cycles. If they do not use true botanical seeds, they somehow benefit from the results of sexual recombination by cloning spontaneous hybrids. Their varieties do exchange genes and gene flows occur between wild and cultivated forms, sometimes between cultivated and feral plants escaped from cultivation and surviving in the wild via vegetative propagation.

As for most vegetatively propagated species, breeding is based on selection of numerous hybrids evaluated for a few traits of agronomic interest. Parents selected for their individual value are intercrossed and visual appraisal is used to discard undesirable genotypes. This phenotypic recurrent selection is conducted on research stations, even though it is well known that genotype × environment interactions are significant. Moreover, the distribution of selected

clones is constrained by their low multiplication rate, the large number of smallholders, their geographical isolation, the absence of a 'seed' industry and strict international quarantine regulations. Participatory plant breeding, although considered as illusory for decades, now appears increasingly attractive.

The understanding of the developmental physiology of these crops, an essential prerequisite for improving their performance, is poorly documented to say the least. Unlike cereals and pulses, they are big plants that are not grown easily in greenhouse pots. It is, therefore, difficult to secure the controlled conditions necessary for reliable physiological studies. However, they are amazing converters of solar energy. Their canopies transfer the photosynthates very efficiently to their undergrounds organs, where sugars are converted into starch with low nutrients needs. In fact, when only roots and tubers are taken out of the plots, it appears that soil mineral depletion is low compared to cereals. Their yield potential is very high (Table 1) and it expected that, with increasing costs of mineral fertilizers and elevated $CO_2$ in the atmosphere, the particular physiology of these plants may represent an asset to feed the forthcoming human population growth.

Because of their biological constraints, when cultivation intensifies these species often appear vulnerable to build-up of pest and pathogen populations. Their clonal nature accelerates the spread of diseases. Virus infections of planting material greatly enhance disease dispersal. In many cases, farmers cannot rely on an outside source of healthy planting material and have to manage the health status of their propagating stocks themselves. Seed systems are especially complex and represent a major bottleneck. There is, however, an array of practical solutions for early generation seed and quality control, and these deserve attention to secure their rapid adoption by the private sector. As these crops are mostly cultivated by smallholders, pesticides are rarely used. Ironically, recently developed pest and disease integrated management systems tend to recommend techniques very similar to ancient ones, in which different varieties or intercrops are mixed together, thereby creating obstacles to pathogen expansion within sustainable agroforestry systems. In such conditions, vegeculture appears to be a promising approach for the future, especially as soil disturbance is often limited to the loci of planting.

The lack of technical information is likely to constrain the development of processing these crops for the feeding of urban dwellers. Their underground organs are not of uniform shape, making mechanical peeling difficult. Flesh colour and texture vary, and the paucity of data on their starches hinders wider utilization. Among the numerous research priorities are their nutritional properties. Their greater future might come not only from their historical substitution for cereals but also from new uses, or as sources of new forms of starch (gluten free) or for as yet undefined processed products based on secondary metabolites (e.g. antioxidants). These compounds are increasingly needed by food industries, and the tropical root and tuber crops have the potential for high yields of them, compared to other crop species.

In most countries, increases in production and area cultivated are following a fast population growth and it is expected that these trends will accelerate to satisfy future needs. The most important root crop by far is cassava, which is both a subsistence crop essential for food security and an industrial crop processed into a wide diversity of products. The phenomenal development encountered by cassava in the last 10 years is a clear indication of the untapped potential for the sweet potato, yams and aroids, but increased research investment will be necessary.

The first edition of this book was written in 2008. During the last decade there has been a remarkable expansion of investment and interest in tropical root and tuber crops, and an impressive volume of research has been produced to assist growers. For this second edition, I have attempted to retrieve and to summarize this remarkable scientific production but, because of the inevitable constraints of space, I am not able to report all these fascinating achievements. The powerful new tools used by the omics have generated new data; these, however may be difficult to absorb by the various development programmes, often with very limited means, which are conducted in developing countries. I have, therefore, decided to focus on the applied research results that are readily accessible and transferable to scientists, technicians and producers, rather than trying to decipher the potential future impact of blue skies research. The aim of this book is to summarize the information available on the origin, taxonomy, breeding, physiology, agronomy, pathology and processing of cassava, sweet potato, yams and aroids. Each of these crops deserves a book to itself, and it has been a rather cumbersome task to reduce the wealth of information available to a single volume. In so doing, I may well have overlooked some important data in my efforts to extract the most significant. This book is for my colleagues who are researchers in the developing countries. It attempts to explain that some problem-solving approaches used for one species may often be applicable to another and that none of these crops, therefore, should be neglected. This book is also for farmers, students and all stakeholders in developing countries, to persuade them that imported food dependency is not inevitable. Local crops and local foods for local markets can be promoted while developing agro-processing industries to satisfy local needs. Finally, this book is for those who, working in prestigious international institutions, consider that the tropical root and tuber crops are a mere folk heritage of the past which cannot adapt to modern globalization when, in fact, they represent a rational local solution for development.

I wish to express my deepest gratitude to the numerous farmers who have taken the time to explain to me the amazing performance of their plants. Special thanks are due to Alfreda Mabonlala for all of the illustrations. The contribution of CIRAD, my home institution, is gratefully acknowledged.

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# Section I

# Cassava

Cassava (*Manihot esculenta* Crantz, *Euphorbiaceae*, Dicotyledons) is the sixth most important crop after wheat, rice, maize, potato and barley and is a primary staple for more than one billion people in the world, mostly in the poorest tropical countries. The term cassava is most likely derived from the Arawak word for bread, *casavi* or *cazabi*, and the term manioc from the Tupi word *maniot*, which French explorers converted to manioc. Cassava plays an essential food security role because its matured edible roots can be left in the ground for up to 3–4 years. The crop represents a household food bank that can be drawn on when adverse climatic conditions limit the availability of other foods. Cassava is also an industrial crop with a dynamic market and diversified new products. Cassava's potential to adapt to climatic changes and the variety of foods that are made from the roots and the nutritious leaves are reasons why cassava cultivation is expanding worldwide.

# 1

# Origin and History

## DOMESTICATION

The exact place and circumstances of the origin of cassava are mysterious and have been debated profusely. Until the end of the 19th century, all authors agreed that all *Manihot* species originated in South America. They observed that Brazil was the most likely area of origin because, confirming de Candolle and Vavilov's theories on the geographical origin of cultivated plant species, this country was host to the greatest intraspecific variability. This is particularly true in northern Brazil. The Brazilian hypothesis is based on archaeological evidence from the Upper Madeira river (state of Mato Grosso) showing that cassava was already used between 6500–5500 BC (Walting *et al.*, 2018). There is also archaeological evidence indicating that the Mayas cultivated cassava in Ceren, El Salvador (Sheets *et al.*, 2011).

Other historical and archaeological data point to two other potential centres of origin. One could be in Central America (Mexico, Guatemala and Honduras) and is supported by evidence from Sierra de Tamaulipas in the north-east of Mexico, dated 200 to 900 BC, and on starch grains found in the Tehucan Valley, state of Pueblo, Mexico. The other centre could be located in the dry coastal savannahs of Venezuela and Peru, where there are some graphical representations of roots dated to around 2000 BC. Traditional ovens used to cook *casabe* pancakes made of cassava have been dated to around 1200 BC in Malambo, northern Colombia, and in other archaeological remains found on the site of Rancho Peludo (Maracaïbo Lake in Venezuela) and dated to 2700 BC (Isendahl, 2011).

Manioc use is difficult to document archaeologically because its organic remains are poorly preserved. It is sometimes argued that sweet varieties of manioc, which do not need special preparation, were domesticated first. Present distribution of sweet and bitter cultivars shows that sweet types are predominant in the east of South America, and especially in the Amazon, while bitter types are more frequent in the west and in Central America and

Mexico. In fact, sweet types are cultivated mostly where cassava is consumed as a vegetable, and bitter types are cultivated where cassava is processed, but the situation is not clear-cut.

The occurrence of morphologically related species in South and Central America indicates a large number of species in Mexico and on the Pacific coast of Central America, as well as in north-western South America. It is believed that there are four separate areas of origin for *Manihot* species: Guatemala and Mexico; the coastal savannahs of north-western South America; eastern Bolivia and north-western Argentina; and eastern Brazil (Chacón *et al.*, 2008). Numerous interspecific hybrids between several *Manihot* species have been reported in Brazil. Cassava is now known to include cultivated and wild forms, and three subspecies have been recognized (Table 1.1).

Spontaneous wild forms of cassava are growing in the central Brazilian state of Goiás, and Allem (1994) believes that this latter region is the centre of domestication. Others, however, argue that cassava and its potential ancestor (*M. esculenta* ssp. *flabellifolia*) were probably domesticated in the seasonal forests of the Guyanas and Venezuela or in central Brazil (Piperno and Pearsall, 1998) but genetic evidence identifies southwestern Amazonia as the area of origin (Olsen and Schaal, 1999; Léotard *et al.*, 2009).

Molecular phylogenetic approaches have been used to understand the relationships of *Manihot* species in an attempt to elucidate the origin of the cultivated *M. esculenta*. Deoxyribonucleic acid (DNA) sequences, including chloroplast DNA and nuclear regions such as the internal transcribed spacer region of ribosomal DNA, were used to construct a phylogeny. The overall sequence similarity between species within the genus is striking. *Manihot* is thought to be a fairly recently composed genus, based on morphological similarities and the lack of chromosome differentiation. However, two distinct groups are clearly revealed, one representing South American species and the other representing Central American ones (Bertram, 1993; Hillis *et al.*, 1996).

**Table 1.1.** Subspecies of cassava and *Manihot* closest related species.

| Subspecies and related species | Geographical origin |
|---|---|
| *Manihot esculenta* ssp. *esculenta* | Brazil, cultivated |
| *M. esculenta* ssp. *flabellifolia* | Brazil, wild forms |
| *M. esculenta* ssp. *peruviana* | Brazil, Peru, wild forms |
| *M. carthaginensis* | Countries bordering the Caribbean |
| *M. aesculifolia* | Mexico, Central America |
| *M. aesculifolia* | Brazil, Paraguay, Uruguay, Argentina |
| *M. flabellifolia* | Brazil, Paraguay, Uruguay, Argentina |
| *M. leptophylla* | Brazil |
| *M. pruinosa* | Brazil, states of Mato Grosso and Goiás |
| *M. tristis* ssp. *saxicola* | Guiana, Surinam, Venezuela |

Source: adapted from Allem (2002).

Molecular sequencing also revealed close similarity between cassava (*M. esculenta*) and *M. esculenta* ssp. *flabellifolia*. This close genetic relationship has been confirmed with different markers, including amplified fragment length polymorphisms (AFLPs) (Roa *et al.*, 1997) and microsatellites (Olsen and Schaal, 1999, 2001). Analyses of single nucleotide polymorphisms (SNPs) and simple sequence repeat (SSR) variation in more than 200 individuals collected from wild populations of two closely related *Manihot* species reveal that, for all the genes examined, SNPs and SSR alleles are shared between domesticated cassava and a specific geographical subset of wild *Manihot* populations. These findings indicate that: (i) cassava was probably domesticated from a single wild *Manihot* species, *M. esculenta* ssp. *flabellifolia*, rather than from multiple hybridizing species; and (ii) the crop most likely originated in the southern Amazon basin, in the Brazilian states of Rondónia and Mato Grosso (Olsen, 2004).

Microsatellite markers also reveal the occurrence of morphological hybrids between *M. esculenta* and an unidentified wild relative in French Guiana, in the northern part of the Amazon basin (Duputié *et al.*, 2007). The use of DNA sequences demonstrates that *M. esculenta* landraces do not form a monophyletic group and suggests the possibility of multiple introgression of genes from related wild species (Chacón *et al.*, 2008). However, when DNA sequences are used to analyse six wild *Manihot* species and landraces of *M. esculenta*, the analyses suggest that cassava was domesticated only once in the southwestern Amazonian rim (Léotard *et al.*, 2009).

Molecular data confirm previous field observations indicating that species boundaries are not clearly delimited and that *Manihot* species are interfertile (Rogers and Appan, 1973). These molecular data, combined with morphological data, strongly suggest that *M. esculenta* ssp. *flabellifolia* is the wild ancestor of cassava (Allem, 1994, 2002; Olsen and Schaal, 1999). As this subspecies occurs in the transition zone between the southern humid Amazon forest and the dry Cerrado of Brazil and Peru, it is logical to assume that cassava was domesticated somewhere in this vast geographical zone. This region is also thought to be the area of domestication of groundnut, chilli pepper and jack bean (Piperno and Pearsall, 1998; Walting *et al.*, 2018). One of the assumptions was that cassava was domesticated directly from the wild and, because the crop was vegetatively propagated, traditional cultivars preserved similar botanical morphologies as the living ancestor.

Archaeological studies of plant remains indicate that an increase in seed size is correlated with intensive cultivation and domestication of seed crop plants. For cassava, the hypothesis is that starch granules of domesticated types should be significantly larger than those of wild, or less intensively cultivated, species. This hypothesis was demonstrated as valid when a comparative study analysed modern starch granules from cassava roots collected in the Upper Rio Negro region of Venezuela and the north coast of Peru, and archaeological data. One conclusion of this work is that two clear lines of evidence suggest that the coastal and lowland regional varieties of cassava

differ from one another. The pattern of starch granule formation is different in the Peruvian and Panamanian cassava, and the morphology is also distinct. The distinct types are 8,000 years old in the lowlands of Panama and at least 3,000 years old in Peru. These may be representatives of different taxa (Piperno and Holst, 1998).

The first diagnostic phytoliths from the underground storage organs of cassava have demonstrated their usefulness in identifying prehistoric root processing with a study of stone artefacts from a Valdivia household (2800–2400 BC, calibrated) at Real Alto, Ecuador. Heat altered (gelatinized) and unaltered starches from cassava were also found on these stone tools. In combination, these phytoliths and starch residues provide evidence that both raw and cooked cassava were processed in Ecuador's early agricultural economy (Chandler-Ezell *et al.*, 2006). Cassava could have been domesticated more than once over time and in distant sites across the Brazilian states of Rondónia, Mato Grosso and Goiás (Allem, 2002). Some parts of Peru, Ecuador and Bolivia, however, cannot be excluded (Fig. 1.1).

**Fig. 1.1.** Putative areas of origin and initial domestication of cassava (according to Allem, 1994; Olsen and Schaal, 1999; Walting *et al.*, 2018).

Cassava domestication is an ongoing process which has been comprehensively described. Farmers allow seedlings that appear in their fields to grow. Seedlings can result from cross-pollination between different varieties and different related species. Patterns of genetic diversity reveal that the incorporation of these volunteer seedlings is frequent and leads to an increase in a farmer's variety portfolio (Elias *et al.*, 2001). These seedlings contribute new genotypes but many are inbred, whereas multiplied clones are highly heterozygous since vigour, plant size and seedling heterozygosity are correlated, as in most plant species. In Guyana, Amerindian farmers traditionally select heterozygous seedlings. When they weed the fields, they kill small volunteers but retain large ones (Pujol *et al.*, 2005).

Domesticated cassava evolved from a fire-adapted and fire-following ancestor: *M. esculenta* ssp. *flabellifolia*. Cassava was therefore pre-adapted to slash-and-burn agriculture, which allowed the spread of this species into habitats wetter than those colonized by its wild ancestors (Ellis *et al.*, 1982). However, cassava stops all photosynthetic functions, closing its stomata, when atmospheric humidity decreases, even when there is still water in the soil (El-Sharkawy and Cock, 1987). Some argue that this behaviour, typical of forest plants, may indicate an origin in the humid Amazon, where the relative humidity is rarely less than 70% (Allem, 2002). Phylogenetic analysis of *Manihot* species indicates that a taxonomic revision of this genus is necessary (Chacón *et al.*, 2008). The debate is far from ended.

## DISCOVERY OF THE CROP BY WESTERN EXPLORERS

Cassava was first introduced into Africa by Portuguese traders around 1550. The Portuguese learnt from the Tupinamba Indians of eastern Brazil how to process cassava into *farinha*. This flour was used as a provision for ships travelling between Africa and Brazil. It was first cultivated in Africa for the sole purpose of provisioning slave ships until 1600. Cassava was cultivated in Benin, São Tomé and Príncipe, and on the Congo coast near the delta (Cabinda). During the 17th century, its cultivation progressed slowly in Angola, Zaire and along the Guinea Gulf. Cassava became an important food in Nigeria as early as 1700, but it seems that its cultivation and consumption in Africa only became significant in the late 1800s. It is argued that this development might have been the result of the introduction, by freed slaves, of processing and preparation techniques developed originally in Brazil (Jones, 1969).

The diffusion of cassava into the interior is poorly documented and only reported by European explorers who penetrated central Africa in the 19th century. Early dissemination of cassava to inland areas, at least in pre-colonial Congo, was carried out solely by Africans. When Europeans entered the interior, beginning with Stanley in 1877, the crop was already established.

It is assumed that it initially expanded throughout the Bantu territories through traditional trade. Its spread was probably slow. Linguistic studies based on the similarities of local names indicate several routes. One extended from Angola to Mozambique, while another went from Zaire to Zimbabwe. The spread of cassava towards the north-east along the Congo might have been faster. It has been suggested that cassava filled an important niche in tropical forest agriculture where few crops were properly adapted, most of the endemic African crop species (millet, fonio, niébé, voandzou, African rice, sorghum, yams) being domesticated in the savannahs or nearby. Many of the people of the Congo Basin were already accustomed to plantains, which required similar cultivation and processing techniques. Reports from 19th-century French explorers in central Africa support the hypothesis of diffusion along the Oubangui River. Cassava was introduced in francophone Africa along the coast of Cameroon and Gabon and, in this case also, it spread along fluvial trade routes. It became the principal food crop in the Estuaire (south of Libreville) in 1865 and further inland, in Franceville, in 1875. Unlike in central Africa, the diffusion of cassava in West Africa was slow and most of the spread occurred in the 19th and 20th centuries (Carter *et al.*, 1992).

Just as in South America, in central African forest areas where cassava is an important staple, mostly bitter types are cultivated, while in coastal areas where cassava is complementary to other foods, sweet types are cultivated. The biological characteristics of the plant, its ability to survive after cultivation and the viability of its cuttings have contributed greatly to its spread. In the Indian Ocean, the French navy introduced cassava into the Réunion and Mauritius Islands in 1738 and 1739, respectively. From there, the French introduced it into Madagascar, where it was cultivated on the central high plateaux of Imerina in 1875. The consumption of cassava leaves was probably an African invention, but they are highly appreciated in Madagascar.

Western explorers introduced it to Sri Lanka in 1786 and Calcutta in 1794. From the Indian Ocean islands, it was introduced to East Africa via Zanzibar in 1799 and reached Lake Victoria in 1862. Stanley recorded it in Uganda in 1878 (Carter *et al.*, 1992). In India, the Portuguese settlers introduced cassava to Goa during the 16th century, and from there to the coast of Kerala. Spanish traders introduced cassava in the Philippines, directly from Mexico, in the 17th century. From there it went to Indonesia during the 18th century. Cassava was brought to Penang from Jakarta and the first recorded commercial planting in Malaysia was in Malacca state around 1851. Just as in Africa, it seems that its cultivation really expanded in South-east Asia during the 19th century. In the Pacific, cassava was introduced by the French to New Caledonia from Réunion Island and then to the New Hebrides (now Vanuatu) (Fig. 1.2). Cassava reached Queensland, Australia, at the beginning of the 20th century.

**Fig. 1.2.** Cassava has been distributed and adopted around the world because of its outstanding agronomic performances. Here, the root of a sweet type variety cultivated on the island of Tanna, Vanuatu (South Pacific) (photo: A. Champagne).

## PRESENT GEOGRAPHICAL DISTRIBUTION

Cassava is now cultivated in all the tropical countries of the world, including some isolated and remote islands of the Pacific. The great adaptability of cassava to marginal areas and its flexible growth cycle facilitate expansion worldwide, especially where there is high population pressure. When land is scarce, food requirements per unit of cultivated area rise and farmers shift to crops such as cassava with its higher output of energy per hectare. A few countries, however, account for the majority of world production: Nigeria, Congo, Ghana, Thailand, Indonesia and Brazil (Table 1.2) (FAO, 2017).

Africa produces more cassava than the rest of the world. Total production in Africa increased from c.35 million t in 1965 to 80 million t in 1995 and to 178 million t in 2017 at an annual growth rate of 2.9%, which is roughly the same as the population growth rate. The increases in production during the past two decades were due largely to increases in cultivated area rather

**Table 1.2.** Major cassava-producing countries in the world in 2017.

| Region | Country | Production (thousand t) | Area (thousand ha) | Average yield (t/ha) |
|---|---|---|---|---|
| Africa | Nigeria | 59,485 | 6,792 | 8.8 |
| | Congo (ex Zaire) | 31,596 | 3,878 | 8.1 |
| | Ghana | 18,470 | 965 | 19.1 |
| | Angola | 11,748 | 1,011 | 11.6 |
| | Mozambique | 8,773 | 1,070 | 8.2 |
| | Cameroon | 5,798 | 398 | 14.6 |
| | Côte d'Ivoire | 5,367 | 874 | 6.1 |
| | Tanzania | 5,014 | 896 | 5.6 |
| Asia | Thailand | 30,973 | 1,343 | 23.1 |
| | Indonesia | 19,046 | 779 | 24.4 |
| | Cambodia | 10,580 | 392 | 27.0 |
| | Vietnam | 10,268 | 532 | 19.3 |
| | China | 4,847 | 293 | 16.5 |
| | India | 4,171 | 199 | 21.0 |
| | Philippines | 2,808 | 235 | 11.9 |
| | Laos | 2,277 | 70 | 32.5 |
| America | Brazil | 18,876 | 1,315 | 14.4 |
| | Paraguay | 3,167 | 182 | 17.4 |
| | Colombia | 2,187 | 218 | 10.0 |
| | Peru | 1,196 | 98 | 12.2 |
| | Cuba | 686 | 84 | 8.2 |
| | Haiti | 498 | 111 | 4.5 |
| | Venezuela | 250 | 20 | 12.5 |
| | Bolivia | 202 | 29 | 7.0 |
| | Argentina | 193 | 19 | 10.2 |
| | Ecuador | 102 | 17 | 6.0 |

Source: adapted from FAO (2017).

than in yield. The crop frequently replaces fallow, or is planted just before fallow. Cassava also replaces more demanding root crops, such as yams, in humid zones. Cassava leaves, rich in protein, are a preferred vegetable in many African countries.

Nigeria is now the largest producer in the world. The constant increase in consumption and output of cassava in this country during the past two decades can be attributed to a combination of factors. The low per capita income and rapid population growth make cassava both a staple and a food security crop; but also, a ban imposed on cereal imports between 1987 and 1990 stimulated production. Multiple uses increase consumption, the roots being consumed in fresh and boiled form, in toasted granules (*gari*), chips, flour (*lafun*) and as unsteamed paste (*fufu*). Urbanization and rising incomes are also strengthening the demand for cassava (Hershey, 2017). Nigeria is host country to the

International Institute of Tropical Agriculture (IITA), which has been conducting long-term research programmes on cassava for more than five decades. Nigerian farmers have the opportunity to be early beneficiaries of the technical packages developed by IITA, and improved varieties and cultivation techniques are quickly and widely adopted. Mostly, cassava is consumed locally, so the crop does not play an important role as a foreign exchange earner but, with Asian countries having difficulties in satisfying growing international demand, African countries may have opportunities in the European Union market. Already, Ghana is exporting significant volumes of cassava chips.

Cassava is grown today in all the tropical and subtropical countries of Asia. The major producing countries are Thailand, Indonesia, Cambodia, Vietnam, India (Kerala and Tamil Nadu states), China (Guangdong and Guanxi provinces located along the Vietnamese boarder), the Philippines and Laos. The soils used for cassava are usually of low fertility, as the best soils are reserved for rice. Most of Thailand's production occurs on the north-eastern and central plains. In Indonesia, the most important cassava-producing areas are Java, south Sumatra and Kalimantan. Cassava is becoming an important crop in the Pacific Islands, one of the most intensive users of root crops in the world, but other traditional root crops predominate.

Latin America currently represents less than one-fifth of the global cassava output. Brazil alone accounts for about 70% of the region's output. Some of the world's most advanced cassava cropping systems are found in Brazil's subtropical regions, which are mostly producing starch for food and industrial uses. In Colombia, almost half of the production comes from the seasonally dry Atlantic coast region and the other half from the Andean valleys of the eastern range and from the central part of the country. Cassava traditionally is planted by smallholders, but large-scale commercial plantings are being established in response to demand by processors. Colombia is host to the Centro Internacional de Agricultura Tropical (CIAT), which is the world's leading international research institute on cassava, and local farmers are the direct beneficiaries of the Institute's results. In Cuba, cassava is found on large state-owned farms using high-input cropping systems, while in Haiti it is cultivated mostly by smallholders with very limited means.

# 2

# Taxonomy and Botany

## CLASSIFICATION

The genus *Manihot* belongs to the Dicotyledon family, *Euphorbiaceae*. The *Euphorbiaceae* comprises no fewer than 300 genera and 8000 species. Almost all of them are tropical species and produce latex. *M. glaziovii*, for example, was once cultivated in Brazil and Nigeria for rubber production. The genus *Manihot* has been classified under the *Manihotae* tribe and comprises 98 tropical species, all from the New World, among which the only commercially cultivated one is *M. esculenta* Crantz (Allem, 1994).

*Manihot* species range in habit from herbs to shrubs, small trees and even climbing vines. All species have normal or tuberizing roots rich in starch and can produce toxic cyanogenic glucosides (CG). Their skin can range from smooth to rough and peeling. Lenticels and the central vascular strand are clearly visible. Their stems are very variable and can reach 30 cm in diameter, with extremely short or long internodes. Stem skin colour varies from very light grey to brown, yellowish or reddish. Internal tissues are always tender. Leaves are alternate, sessile or with a well-developed petiole. The lamina is highly variable. They are spirally arranged on the stem and have petioles 5–30 cm long, usually longer than the blades. The blades are deeply divided with 5–7, occasionally 3–9 lobes, obovate, lanceolate, pointed and with entire margins. The young leaves vary in colour from yellowish green to deep purple.

The inflorescences of the *Manihot* species are monoecious and, in extremely rare cases, dioecious, grouped in racemes or panicles. These are generally composed of one to a few female flowers, attached at their base to long pedicels and numerous male flowers with shorter pedicels. Pistillate flowers open before staminate flowers of the same inflorescence. Pollination is by insects. All *Manihot* species out-cross and this leads to extremely heterozygous gene pools. The fruits are capsules and can be elliptic, conical, smooth or with small wings along their length. The seeds of all *Manihot* species present a caruncle, which usually plays a role in water exchange, enhancing germination in dry areas. The cotyledons are flat and large.

## MORPHOLOGICAL DESCRIPTION OF *M. ESCULENTA* CRANTZ

Cassava flowers are borne on terminal panicles, with the axis of the panicle being continuous with that of the branch (Fig. 2.1). Each panicle bears male and female flowers. The first ones are numerous and located near the tip of

**Fig. 2.1.** Inflorescences, male and female flowers and fruits of cassava.

the inflorescence. The female ones occur at the base of the axis, on the lower part of the inflorescence, and are fewer in number than the male flowers. Each flower, male or female, has five united sepals and there are no petals. The male flowers have ten stamens grouped in two whorls of five each. The anthers are small and there is a nectar-bearing gland within the flower. The female flower has an ovary, mounted on a ten-lobed glandular disc, with three locules and six ridges (3–4 mm), each containing a single ovule. The stigma has three lobes, joining together to form a single style. The female flowers of *M. esculenta* always open first and the male flowers of the same inflorescence open 1 week or 10 days later (protogyny). However, male and female flowers on different branches of the same plant can open at the same time and self-pollination can occur (Fig. 2.2). Cassava is cross-pollinated by insects. The fruit is a trilocular capsule, 1–5 cm in diameter, with six prominent ridges. Each locule contains a single carunculate seed (Fig. 2.3).

When cassava grows from seed, the plant develops a taproot, which becomes fibrous and tuberous. When grown from cuttings, adventitious roots develop from the base of the cuttings into a fibrous root system. Only a few fibrous roots become tuberous and most of the others continue their function of nutrient absorption. The cassava root is circular in cross section and is thicker

**Fig. 2.2.** The male flowers are numerous and are located in the upper part of the inflorescence. The female flowers are larger but are fewer in number and are at the base of the axis, on the lower part of the inflorescence (photo: V. Lebot).

**Fig. 2.3.** Cassava fruits are capsules. They turn brown when mature, are dehiscent and explode to release the seeds (photo: V. Lebot).

at its proximal end. The distal portion tapers slowly towards the end and, beyond the tuberous section, the root extends as a normal root. The tuberous root is connected to the base of the plant by a woody section called the neck. The internal section of a starchy root is composed of three parts:

**1**. The bark (also called periderm), representing the outermost layer, is an assemblage of dead cork cells which seal the surface of the root. The periderm represents 0.5%–2.0% of the total weight of the root and can be removed easily by simple scratching. As the root develops, new cambium forms and produces cork and restores the integrity of the protective layer.
**2.** Just beneath the periderm is the peel layer (also called phelloderm, cortex or secondary skin), which is only 1–2 mm thick and is usually white, pinkish or brownish. It can represent between 8% and 15% of the total weight of the root and is removed easily from the central cylinder by pulling.
**3**. The central portion representing the bulk of the root is the parenchyma. The flesh consists mostly of parenchymatous cells with large amounts of stored starch and is the edible portion. Extremely thin vascular bundles ramify through the flesh. There are no eyes or buds on the cassava root surface and it cannot be used as a means of vegetative propagation (Fig. 2.4).

A single cutting can produce one to three stems, the number of stems depending on the number of nodes and the type of planting of the cutting. Planted flat cuttings produce more stems. The mature stem is woody and the nodes present protuberant leaf scars. The main stems divide di- or trichotomously, producing secondary branches. Branching is the consequence of the transformation of the apex into a flowering bud. Two to three branches can be produced by the apical meristems. Cassava plants therefore branch depending on their flowering and some varieties can produce up to ten successive ramifications while others have none. Branching is variable: some cultivars branch near the base, others are erect and branch above 2 m of height.

Older leaves are shed and are replaced by those formed by terminal buds, producing a hemispheric appearance of the canopy. Cassava leaves are lobed with palmated veins. The number of lobes ranges from 3 to 9, occasionally 11. Leaves located near the inflorescence are usually reduced in size and number of lobes. The leaves are alternate. Mature leaves are usually glabrous. The upper leaf surface is covered with a shiny and waxy epidermis. Most stomata are found on the lower surface of the leaves (hypostomatous leaves) but some cultivars also have some stomata on the upper surface (amphistomatous leaves), although this was found in only 2% of 1500 cultivars (El-Sharkawy and Cock, 1987). Cassava photosynthesis follows a $C_3$ pathway adapted to a tropical environment requiring high temperature and high solar radiation (Angelov *et al.*, 1993).

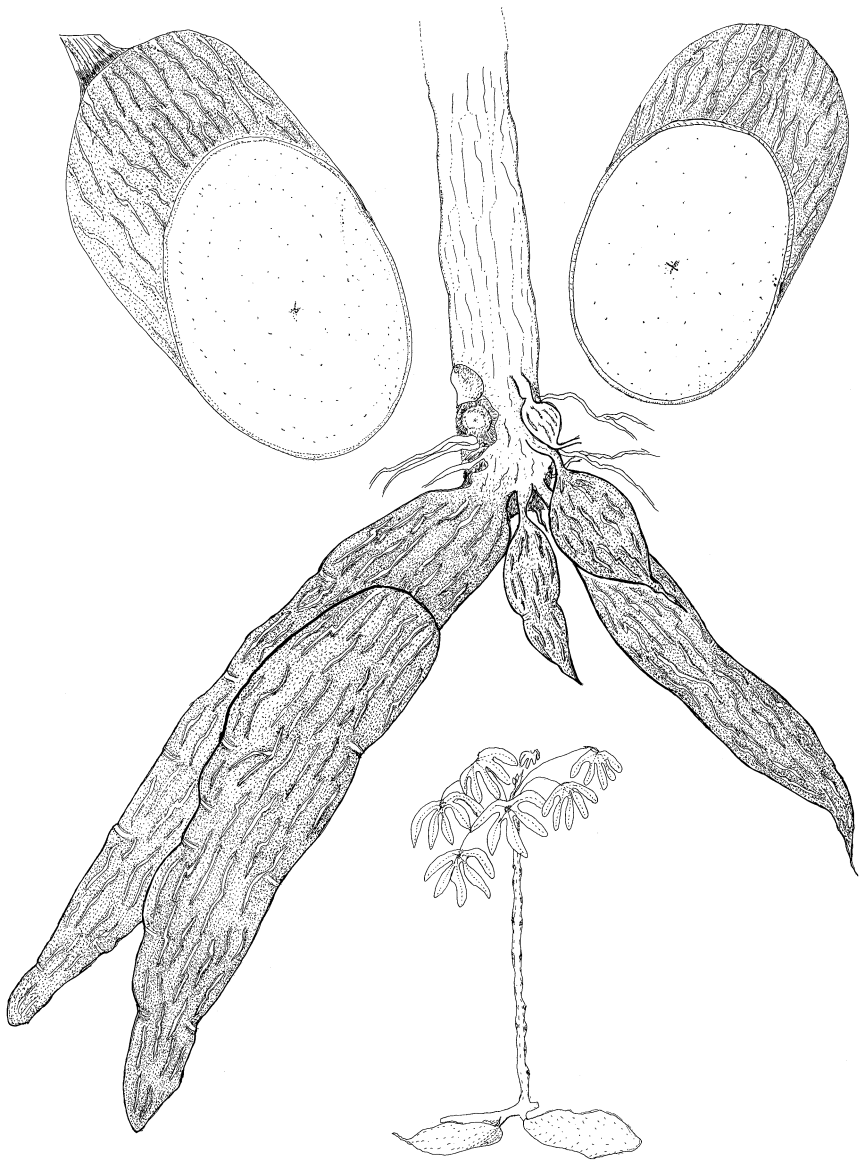

**Fig. 2.4.** Transverse section of the cassava root.

The morphological characteristics of cassava are highly variable (Fig. 2.5). Given the large number of cassava varieties (morphotypes) cultivated in a large diversity of environments, it is difficult to describe precisely the extent of the continuum of variation found in farmers' fields. There are numerous morphological descriptors that can be used for cultivar characterization (Fukuda *et al.*,

2010). The following are the basic descriptors to be considered when identifying a cultivar:

- Apical leaf colour and pubescence.
- Central lobe shape.
- Petiole colour.
- Stem cortex and external colours.
- Root peduncle presence.
- Root flesh, cortex and external colours.
- Root epidermis texture.
- Flowering.

The cassava plant can release cyanide in quantities that are toxic to humans. Cyanide occurs as two related cyanogenic glucosides (CGs), linamarin and lotaustralin, but linamarin alone accounts for 93% of the total. Both the roots and the leaves contain CGs. These two CGs liberate hydrogen cyanide (HCN) on hydrolysis. At high concentrations, cyanide can cause death. The lethal dose of HCN for humans, when taken by mouth, ranges between 0.5 and 3.5 mg/kg body weight. Cyanogenesis occurs when the plant tissue is damaged and the linamarin present in the vacuole is brought into contact with linamarase, an endogenous enzyme in the walls of the cassava plant cells producing acetone cyanohydrin. All these compounds, acetone cyanohydrin, CGs and HCN, are commonly referred to as cyanogens. The cyanogen content is expressed in mg/kg, ppm (parts per million) or mg HCN/kg (Dufour, 2007). All cassava varieties contain CGs in varying concentrations. The total cyanogen content of the roots varies from less than 20 mg to more than 4000 mg/kg dry matter (DM). The factors responsible for this variation are not yet clearly understood (McMahon *et al.*, 1995), but the genotype plays a determining role. Cultivars are classified as sweet (less than 100 mg total cyanogens/kg peeled fresh roots) and bitter (more than 100 mg cyanogens). It has been suggested that bitter taste is correlated with the cyanogen content, and genotypes rich in CGs are easily identified by farmers (Chiwona *et al.*, 2004).

Cyanogenic glucoside accumulation varies with genotypes, growing conditions, age and part of the plant. CGs are probably higher in the leaves and skin of the roots because they act as a repellent to predators. Some Tukanoan farmers in the north-west Amazon tend to favour the bitter types over the sweet types, although no statistically significant correlation seems to exist between the root yield and the total cyanogen content. In this area there is, however, a tendency for bitter types to produce higher yields because farmers preferentially plant them on more fertile soils and give them better care. The fact that cyanogenic plants release HCN when attacked by pests suggests a defence mechanism that could contribute to explaining why pests apparently attack bitter cultivars less than sweet cultivars (Wilson and Dufour, 2002). However, in a disease-free environment, farmers also select landraces resulting from spontaneous seedlings, which are sweet type. The analysis of

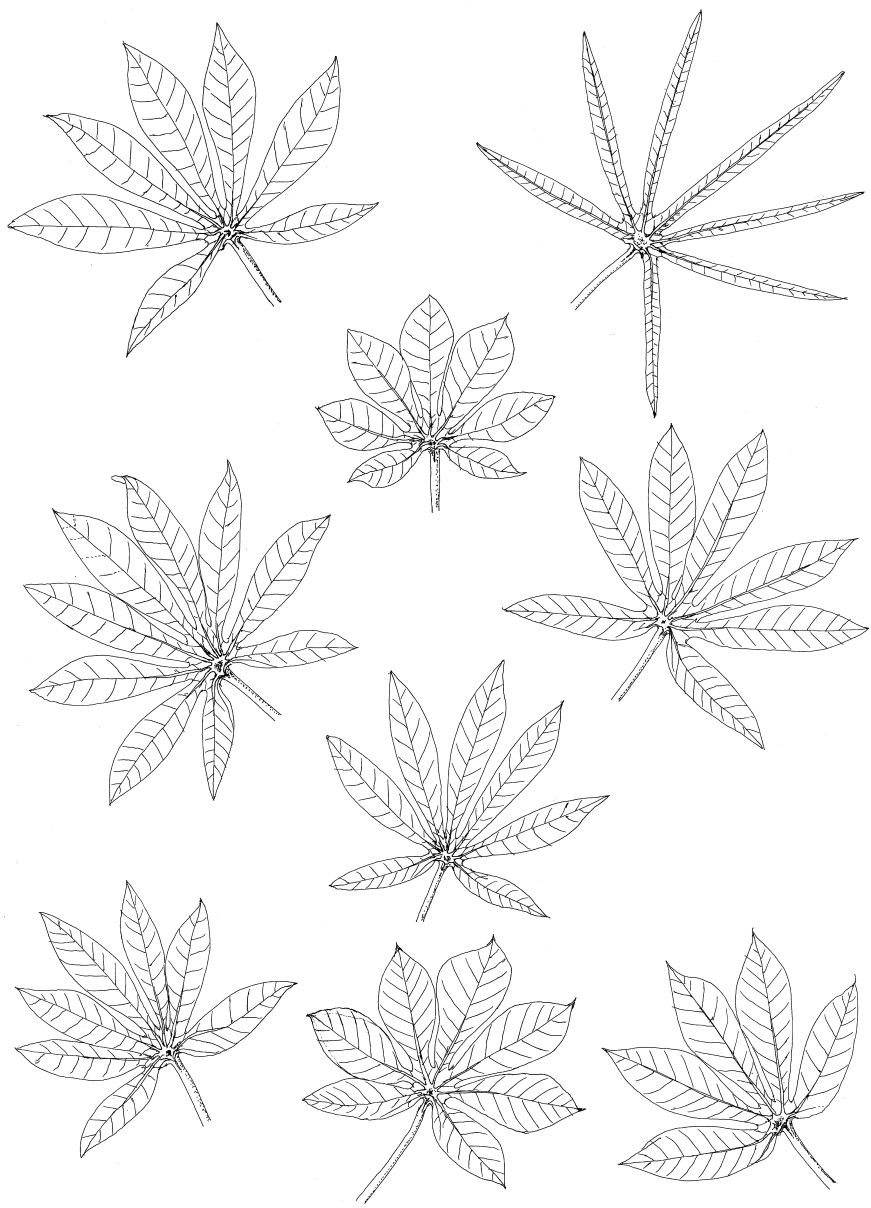

**Fig. 2.5.** Leaf shapes of different cassava landraces presenting variation in lamina length and width.

147 sweet type landraces revealed a total sugar content varying from 2.5 to 10.6 g (fresh weight). Interestingly, all landraces presented extremely low linamarin content (not detected with high performance thin layer chromatography, HP-TLC). It is hypothesized that when farmers select new landraces,

they eliminate genotypes that are bitter and suspected to be toxic (Lebot *et al.*, 2015a; Lebot and Kaoh, 2017).

## RELATED SPECIES

The taxonomy of *Manihot* has long been obscure because of some overlap in morphology between species, the plasticity of some morphological traits and the lack of highly discriminating characters. The classification developed by Rogers and Appan (1973) is now accepted. It is based on multivariate analysis of 44 morphophysiological traits and classifies the 98 species in 19 different sections, varying from trees in the *Arboreae* section (i.e. *M. glaziovii*) to small shrubs in the *Stipularis* section. The cultivated species, *M. esculenta*, is placed in the *Manihot* section of the genus. This section contains low-growing shrubs adapted to savannahs and grasslands. Deoxyribonucleic acid (DNA) sequencing, however, reveals a need for taxonomic revision (Chacón *et al.*, 2008).

The majority of *Manihot* species are colonizers of well-drained limestone soils. They rarely become the dominant species in their habitat and are rather sporadic in their spatial distribution. There are two centres of diversity for the genus *Manihot*: the first is located in Brazil and hosts at least 80 different species. The other is located in Central America and hosts approximately 17 *Manihot* species. In Brazil, microcentres of diversity have also been defined where large numbers of species are concentrated in fairly small areas of approximately 2000 km$^2$. These microcentres result from frequent hybridizations between species and a highly heterogenic habitat that contributes to the isolation of fragmented gene pools. The region of greatest specific diversity is the Central Plateau of Brazil with 58 species. The majority of these species are found in dry regions, only a few being in the rainforest. Some, such as *M. pohlii*, *M. zehntneri* and *M. grahamii*, are weedy and able to colonize recently disturbed habitats rapidly. Tree-like species such as *M. glaziovii* are found mostly in north-eastern Brazil, whereas shrub-like species are found in the drier central Brazil (Schaal *et al.*, 2006).

There are numerous reports of natural hybridization among *Manihot* species, between wild species and between these and cassava. Interspecific hybrids of cassava with *M. glaziovii*, *M. pseudoglaziovii*, *M. aesculifolia*, *M. pilosa*, *M. dichotoma*, *M. pohlii*, *M. neusana* and *M. anomala* were obtained successfully through controlled crosses, although their frequency was rather low (Nassar, 1989).

## CYTOLOGY

All wild *Manihot* species examined cytologically have a chromosome number of $2n = 36$. Despite this fairly high chromosome number, all species behave

like diploids at meiosis. Cassava generally is considered based on regular meiosis as a normal diploid with $2n = 36$ chromosomes (Allem, 1994) but natural triploids also occur, are selected by farmers and cultivated for their attractive features (Sardos *et al.*, 2009). There are occasionally some meiotic irregularities such as delayed separation and non-orientation of bivalents, restitution nuclei, monads and polyads. Cassava has also been reported as an allopolyploid, in fact a segmental allo-tetraploid, with a basic chromosome number of $x = 9$, suggesting that it could be derived from crosses between two closely related parental taxa. Studies conducted with isozymes, co-dominant markers, support this hypothesis and show a disomic inheritance at 12 loci (Magoon *et al.*, 1969; Umanah and Hartmann, 1973 but this has not been confirmed yet with more powerful DNA markers.

Apparently, mitosis frequencies in root tips are higher between 07:30 and 08:30. Root tips are pretreated with 8-hydroxyquinoline for 1 h or with 0.2% colchicine for 10 min and fixed in 1:3 acetic acid:alcohol. Squashes are done in acetocarmine. Information on mitosis is, however, rather weak. On the other hand, meiosis has been well studied. There are remarkable differences between varieties for chromosome behaviour during meiosis, which could be the result of an allopolyploid origin of cassava. For meiosis studies, pollen stainability and cytological behaviour, flower buds of appropriate stages are fixed in a mixture of three parts ethyl alcohol to one part proprionic acid for 2–3 days, after which they are transferred to 70% alcohol. Metaphase is extremely brief and occurs between 09:00 and 10:00 (Sreekumari *et al.*, 2000).

Anthesis occurs 2 weeks after meiosis. The pollen grains are stained in 2% propionocarmine, the deeply stained pollen being considered viable (Hahn *et al.*, 1990). When flower buds are 1.6 mm in diameter, pollen grains are between 20–25 μm and reach 30 μm when the buds are 1.8 mm in diameter, which is when tetrad mucilage is disappearing. When mature, pollen grains can reach up to 190 μm in diameter. Grains with a diameter above 130 μm germinate easily and represent approximately 60% of the pollen grains.

# 3

# Breeding and Genetics

The International Institute for Tropical Agriculture (IITA) in Ibadan, Nigeria, and Centro Internacional de Agricultura Tropical (CIAT) in Cali, Colombia, began successful breeding programmes in the 1970s. National research institutes in Brazil, Cuba, China, Ghana, Kenya, India, Indonesia, Mozambique, Tanzania, Thailand, the Philippines, Uganda and Vietnam have also conducted scientific research on cassava breeding.

## OBJECTIVES AND SELECTION CRITERIA

Objectives vary from one country to another and depend on the final use of the crop, whether for industrial needs or human consumption and subsistence. For industry, yield improvement (starch and dry matter, DM) per unit of area and time is the main objective, while the situation is more complex for the subsistence crop, where chemotype and yield stability are very important.

There is some consensus on the ideotype (Ceballos *et al.*, 2015), namely:

- Only one stem per cutting, with little or no branching.
- High ratio roots/stems.
- Leaf area index (LAI) between 3 and 3.5.
- Large single leaf area.
- Short internodes and total height of the plant less than 2 m.
- Leaves of long life.
- Approximately eight tuberous roots.
- Short, compact roots, easy to harvest and to peel.
- Quality traits (starch, protein, carotene, low cyanogenic glucosides).
- Reduced postharvest deterioration.

The necessity of combining all these major traits is still debated and, for example, some hybrids with profuse branching have produced very high yields. There are, of course, many other traits that improved cultivars should have. Some important traits are difficult to evaluate in field conditions. It is accepted

that a deeper root system provides access to more soil water for the crop during drought but this characteristic is difficult to phenotype. Breeding for improved root system characteristics is complex and simple methods to evaluate root systems have yet to be developed (Okogbenin *et al.*, 2013). Yield stability is associated with tolerance or resistance to local pests and diseases. In Africa, cassava mosaic disease (CMD) and cassava brown streak disease (CBSD) are the major constraints. In India, a disease similar to CMD is also a constraint in Kerala and the southern region. Bacterial blight (induced by *Xanthomonas axonopodis* pv. *manihotis*) is present in Asia, Africa and Latin America and is also a major constraint.

## SEXUAL REPRODUCTION AND STERILITY

An erect plant architecture is better suited to mechanical planting and intensive cultivation but is also a key adaptative trait in response to climatic change (Ceballos *et al.*, 2017). Erect, non-branching types are preferred by farmers and the elite cultivars in most regions are often those that flower poorly, or not at all. Consequently, it is often difficult to cross them with others. Some clones can flower as early as 6 weeks after planting (WAP), while others will do so only after at least 10 months of growth. Cassava flowers do best at moderate temperatures, approximately 24°C. Generally, the first inflorescences which appear with the first ramifications tend to abort and only the ones following the subsequent ramifications are functional. Female flowers are open 10–14 days before the male ones on the same branch. The opening of the last female flowers might coincide with the opening of the first male flowers located on the same inflorescence, or with those of other inflorescences located on the same plant. Self-pollination can occur because male and female flowers on different branches or on different plants of the same clone can be open at the same time. During the day, female flowers remain open for 5–6 h before the male flowers open around noon. All flowers are closed during the second half of the afternoon. Anther dehiscence starts approximately 2 h after the opening of the flower and is complete after 1 h.

Pollen longevity is approximately of 1 week and the grains are disseminated by wind and insects. Abundant nectar produced 3 days before the flowers open, and the sticky nature of the pollen and stigmas, contribute to efficient insect pollination. Bees are especially fond of cassava flowers and visit them actively. The natural pollination rate is quite high. It has been demonstrated that plants located 30 m away from the father plant can be pollinated naturally (Kawano *et al.*, 1978). In practice, it is recommended therefore that genotypes are isolated by a distance of at least 50 m to avoid unwanted accidental pollination of mother plants.

Male sterility is frequent among cultivars. Pollen sterility is often observed and is thought to be the result of meiosis perturbations. Clones that are male

sterile can have a normal formation of tetrads but, in some cases, monads and triads are also encountered. This suggests the formation of a nucleus after the first or second meiosis division, the absence of division or the irregular formation of the cell wall. Male sterility could be attributed either to the allopolyploid origin of the species *M. esculenta*, which leads to meiosis abnormalities, or to particular genes. The problem needs further investigation to find out how breeders might take advantage of this phenomenon.

## CROSSING TECHNIQUES AND TRUE SEED PRODUCTION

Propagation from seeds occurs spontaneously in farmers' fields and farmers have, consciously or not, also contributed to the genetic improvement of the crop and the generation of useful diversity. Landraces are clones of hybrids (Ceballos *et al.*, 2015).

For controlled hand pollination between two parents, the pollen can be collected in bags and preserved for a few days in a dehydrated atmosphere with silica gel. Stigma receptivity lasts approximately 24 h. The day following the opening of the female flower, the stigma turns brown, dries and falls off. Apparently, the time between pollination and fertilization is 8–19 h. Stigma receptivity is quite brief and necessitates, when hand pollinating, repeating the operation every day to make sure that pollen is applied very soon after the opening of the flowers. For the production of full-sib progenies, all male and female flowers that are already open on a single inflorescence are eliminated. The inflorescence is then protected in a bag, ensuring good ventilation (not in plastic). Anthers that have been collected on the male parent are applied to the stigmas. Capsules mature in 10–14 weeks and seeds are harvested when the capsules are brown and start to open (Fig. 3.1).

**Fig. 3.1.** Cassava seeds present a caruncle, which usually plays a role in water exchange, enhancing germination in dry areas. They can be stored for up to 2 years at temperatures between 20 and 30°C (photo: V. Lebot).

Another system is to plant a set of varieties in a specially designed crossing block and to eliminate all the male flowers from the plants used as female parents. Muslin bags are then placed with netting bags to catch the seeds as the capsules dehisce explosively. Polycross field designs using a random distribution of selected genotypes replicated several times are common and allow the production of cross-bred seeds, although this does not prevent occasional self-pollination. The fertility of some genotypes can be very low, but an average of one seed per capsule is commonly obtained, with a maximum of three. Studies conducted in India have shown that the number of capsules per plant can range from 16 to 168 for a male sterile cultivar ('Ambakadan') (Rajendran *et al.*, 2000).

In the humid ecological zone of Nigeria, a comparative study was conducted to assess the hybrid seed production efficiency after natural and artificial pollinations conducted on ten different genotypes. The time to 50% flowering and the number of pistillate and staminate flowers showed significant variation among parents. More staminate than pistillate flowers were produced in all ten genotypes, with a mean ratio of 8:1 (staminate:pistillate) per genotype. The hybrid seed production was also found to be significantly different in the ten genotypes after natural and artificial pollination, and natural pollination was found to be three times more effective than artificial pollination for the rate of seed set. It was concluded that, in Nigeria, optimum seed production was obtained using male sterile females combined with male fecund parents, properly arranged in the field to promote cross-pollinations by wind or insects (Ogburia and Okele, 2001).

Cassava being highly heterozygous, its sexual progenies are heterogeneous with wide morphological variation among them. This type of plant–plant variation is not acceptable to commercial growers owing to the strong preference of farmers for a particular variety but, in cases where the plant is grown for subsistence, plant variation is not a serious problem and true cassava seeds (TCS) give some advantages. The propagation rate is increased more than 15-fold and TCS are much more compact than cuttings (1.5 kg of TCS can cover 1 ha). TCS also have a longer viability than cuttings and can be stored easily and viruses are not seed transmitted. Finally, TCS can contribute to the rapid spread of the crop in distant areas because they are not bulky and are therefore easy to distribute. In some rare cases, seed production can be over 30% of the number of flowers pollinated, but for some genotypes, it is close to nil (Rajendran *et al.*, 2000).

In moist tropical climates, germination rates are very low after 6 months of storage. If the atmosphere is sufficiently dry, however, it is possible to store cassava seeds for up to 2 years at temperatures between 20 and 30°C. Seed germination occurs between 10 and 20 days after sowing. Germination percentage declines with the storage duration. Different treatments have been used to improve the germination percentage: scarification, immersing the seeds in water at different temperatures and treatment

with sulfuric acid at different concentrations and for varying lengths of time. All have negative or no effects.

High temperatures stimulate germination. Dry heat treatments (at 60°C or more) over a period of days or weeks improve germination. Under moisture conditions favourable for germination, maximum germination occurs when the mean temperature is around 33°C (Ellis *et al.*, 1982; Pujol *et al.*, 2005). Light appears to have a negative effect, decreasing the probability of germination or slowing it down. If sown directly in soil, germination rates are between 30% and 50%. But, when trays are fully covered by dark cloth and kept for 2 weeks, a germination percentage of over 50% is easily obtained. In the field, good germination can be obtained by spreading a uniform, thick layer of soil on the seeds.

When sown directly *in situ*, survival of the seedlings ranges between 30% and 50%. If the seedlings are managed in a nursery and transplanted to the field, the establishment rate varies from 70% to 90%. Seedlings produce fibrous taproots and their removal while transplanting enhances tuber development. In India, studies conducted on popular cultivar ('Ambakadan') progenies indicated that seedlings had a CG and DM content comparable to the parents, and some of the hybrids were found to have a better DM content than the parents (Rajendran *et al.*, 2000). Tuber yield of first clones (C1) is significantly superior to that of the seedlings. It is difficult to predict the yields of future clones by evaluating the performance of plants resulting from true botanical seeds.

Farmers select their own cultivars from seedlings. In Ghana, a study showed that most communities had grown cassava for more than 100 years and had acquired and abandoned landraces (Manu *et al.*, 2005). Farmers do not understand the role of pollination in setting seed, do not purposely plant seeds and ignore or weed out cassava seedlings. However, some use stem cuttings from self-sown seedlings, often when planting material from their crops is scarce, and some purposely grow cuttings from a few such seedlings. Many seedlings are both reported and seen in newly planted crops, suggesting that some may be used accidentally as planting material, especially those seedlings that are perceptually indistinct from the planted crop, resulting in polyclonal landraces.

In Costa Rica, the role of the agricultural practices of Chibchan Amerindians in the maintenance of high levels of diversity has been demonstrated using isozyme markers. Low weeding, typical in traditional home gardens, contributes to the survival of seedlings and their subsequent capture in vegetative propagation (Zaldivar *et al.*, 2004). A similar situation is observed in French Guyana (Elias *et al.*, 2001) and Gabon (Delêtre *et al.*, 2011).

Finally, in Vanuatu, South Pacific, it appears that the incorporation of volunteer plants, the products of sexual recombination, occurs commonly enough to have affected genotypic diversity greatly. The use of simple sequence repeats (SSRs) revealed a large excess of heterozygotes at almost all loci, indicating that human selection, perhaps also bolstered by natural selection, has favoured heterozygous genotypes. SSR data confirm that mechanisms linked

to clonal propagation, mutations, genotype × environment interactions and sexual recombinations have promoted diversification. It is, however, difficult to weigh the respective contributions of these processes (Sardos *et al.*, 2008).

## SELECTION METHODS AND PROGRAMMES

Programmes start with the collection, characterization and evaluation of germplasm, followed by crossing the selected accessions (Bradshaw, 2010). The difference in agronomic performance between artificially produced hybrids and local traditional cultivars is not striking since, in many places, cassava breeding is still a fairly recent practice. Crosses are conducted between parents, local or introduced, which have been chosen on their performance, with little selection of genotypes based on their general combining ability, as is the rule for seed-producing crops. Crosses can be done manually by controlled pollinations to produce full-sib progenies, or in polycross plots where natural open pollination is used to produce half-sib progenies and, when bulked together, populations for recurrent phenotypic selection.

Field layout designs aimed at maximizing the frequency of crosses and at approaching theoretical panmixis have been elaborated. It is of utmost importance that sufficient knowledge on the flowering characteristics of the genotypes is available, since synchronization of flowering is a major constraint with such designs. It is, however, possible to delay planting of early-flowering genotypes to increase the chances of synchronized flowering with late flowering genotypes. Male sterile accessions can be used as female parents in polycross plots.

Once seedlings are obtained, they must be propagated clonally and the material multiplied through successive clonal generations before accurate assessment of their performance can be conducted. Except for a very few deleterious traits, such as their susceptibility to local disease, it is necessary to assess the performance in the first clonal cycle (C1), in C2 and so on (Fig. 3.2). This is a time-consuming process because only a limited number of cuttings can be taken from each stem. Cuttings from the midsections perform better than those from the top or bottom of the stems. Table 3.1. describes a typical selection cycle for cassava that is fairly conventional for a vegetatively propagated crop.

Success in cassava breeding programmes depends on:

- The choice of parents. Good genotypes do not always give good progeny.
- The size of progeny and the need to screen large numbers.
- The selection scheme. Selection during the second cycle of clonal evaluation (single row trial, SRT) is the most crucial, eliminating 95% of the genotypes.

Depending on the technical and financial means, there is some variation between existing programmes, but the rationale is the same. Heavy selection

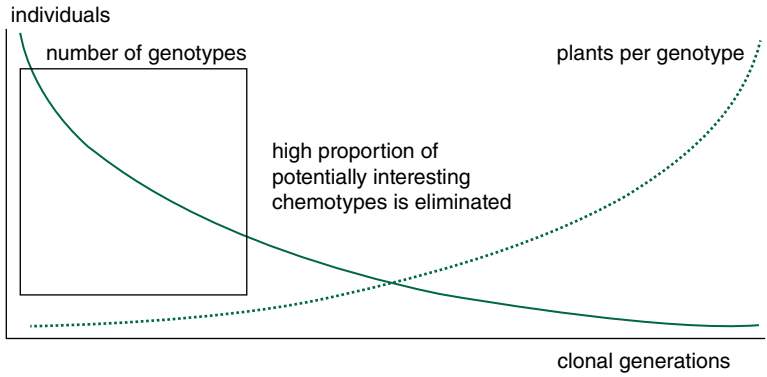


**Fig. 3.2.** The selection of new genotypes focuses mostly on agronomic traits, while potentially interesting chemotypes can be eliminated (Source: Lebot *et al.*, 2005).

**Table 3.1.** Selection cycle in cassava.

| Year | Activity | Number of genotypes | Plants per genotype |
|---|---|---|---|
| 1 | Crosses between parents | Up to 100,000 | |
| 2 | F1: evaluation of seedlings, strong selection for local diseases, single row trial (SRT) | 17,500–100,000 | 1 |
| 3 | Clonal evaluation trial (CET) | 2,000–3,000 | 6–12 |
| 4 | Preliminary yield trial (PYT) | 100–300 | 20–80 |
| 5 | Advanced yield trial (AYT) | 20–100 | 100–500 |
| 6 | Regional trials (RT) | 5–30 | 500–5,000 |

Source: adapted from Ceballos *et al.* (2004).

pressure is applied at the seedling stage for resistance to disease. At IITA, Nigeria, approximately 100,000 seedlings are visually screened for their resistance to CMD and bacterial blight and only 3000 are selected; while at CIAT, Colombia, 50,000 seedlings are screened (Ceballos *et al.*, 2004). In the clonal evaluation trial (CET), where 2000–3000 clones are evaluated, selection relies on high-heritability traits such as harvest index (ratio of storage mass to total plant biomass) (Kawano, 2003). Plant architecture is also under heavy scrutiny at this stage, plants that do not branch until they reach about 1 m being favoured. This selection process is visual, without any data recording in order to minimize costs and maximize the number of genotypes assessed (Fig. 3.3).

When the preliminary yield trial (PYT), advanced yield trial (AYT) and, especially, the regional trial (RT) stages are reached, breeders are more interested in yield stability across different locations. Cooking quality (or 'poundability' for *fufu* at IITA) also begins in these trials. In the case of CIAT, the first selection (based on fresh root yield and DM content) takes place at the single row trial

**Fig. 3.3.** Clones of selected hybrids resulting from a polycross block being field propagated in their second clonal generation (C2) for proper evaluation of their agronomic performances (photo: V. Lebot).

and is then followed by PYTs, AYTs and uniform yield trials (Ceballos *et al.*, 2017). The use of local checks, a local variety well known to farmers, allows comparison at each selection stage and permits an assessment of the progresses being made. The selected clones are then released as new varieties. A new selection cycle can begin in which the new selected varieties are used as parents. Unfortunately, chemotypes with very attractive properties can be eliminated at an early stage because of the high selection pressure on other traits (Fig. 3.2). New techniques such as near infra-red spectroscopy (NIRS) have been used for high throughput screening of accessions for high starch content (Champagne *et al.*, 2009; Lebot *et al.*, 2009), carotenoids (Belalcazar *et al.*, 2016) and waxy starch detection using iodine solution (Morante *et al.*, 2016).

A fairly common difficulty in breeding programmes is to satisfy the requirements of both industry and the fresh market. An industrial variety, for example, must have a high DM yield potential (t/ha) with a high DM content (% of fresh weight). In Thailand, selected varieties should have roots with very white flesh and the starch gels should be very clear in colour, with high viscosity (Kittipadakul *et al.*, 2017). For the bioethanol industry, accessions with small starch granules, reducing the cost of starch hydrolysis, are favoured. For human fresh consumption, flesh colour, low cyanogenic potential and good

cooking quality are important traits. High carotene cassava varieties are preferable for the poultry industry and also for areas where fresh yellow-fleshed roots are popular for human consumption (Africa and Melanesia). For the feed industry, high-protein accessions have been identified (Ceballos *et al.*, 2006a, b). The selection process is equivalent to phenotypic recurrent selection. Great numbers have to be screened to achieve some progress. The process is based on the capture of additive effects and is particularly efficient for traits with high heritability when there is a broad genetic base, such as in South America. In Asia, the genetic variability is much narrower. It is, however, estimated that since the early 1980s, CIAT has introduced half a million $F_1$ hybrid seeds from the Colombia breeding programmes, to broaden the genetic base, and this has speeded up progress significantly (Howeler *et al.*, 2006). In Thailand, for example, approximately 372,000 genotypes obtained from more than 4100 crosses were screened by CIAT, but only three genotypes were selected and released as new varieties. They have contributed greatly to increasing cassava production in Thailand and South-east Asia. The total hectarage of CIAT-related improved cultivars in Asia is more than 1 million ha (Kawano *et al.*, 1998; Kawano, 2003).

Conventional breeding programmes of cassava conducted since the 1970s across Asia have developed adapted varieties based on five common objectives: high yield capacity under low inputs, high root DM content, ease of harvest, resilience (tolerance to pests and diseases and low soil fertility) and lower cyanide content. The number of officially released varieties has constantly increased and the continuous adoption of new varieties will contribute to further increase the yields in Asia. In India, the first improved variety was released in 1971 and, since then, new varieties have been released regularly and have contributed to a remarkable increase in yield (Aye, 2017).

The Thai variety KU 50, released by Kasetsart University (Thailand) in 1992 is now grown under different names on 900,000 ha in Thailand, Vietnam, Indonesia and Cambodia and is probably the most widely grown variety in the world. The Thai programme has been very successful, but it has been suggested that its genetic base is somewhat narrow, and this could be one of the reasons why there has not been much genetic gain in yield since the release of KU 50. Several recommendations have been formulated to secure future progress such as continuous import of new germplasm, accurate field evaluation of germplasm, avoid inbreeding depression in selected lines, determine the combining ability of parents, and introgress novel traits important for the industry (high nutrients and starch contents, high starch viscosity) (Kittipadakul *et al.*, 2017).

Successful breeding has also been achieved in Colombia, Brazil, India and Nigeria. Many improvement programmes in Africa have received IITA materials in tissue culture and true seed form. When tested in local environmental conditions, some of them outperformed local varieties and were released to farmers. In Nigeria, over 100 improved varieties have been released by the

National Programme and various projects; new hybrids have also been released in Sierra Leone and Ghana; and the situation is comparable in Eastern and Austral Africa where improved varieties are regularly released. In Malawi, the local breeding programme has shown that resistance to CBSD and storage root bulking are predominantly controlled by additive gene action. This demonstrates that phenotypic recurrent selection after hybridization of elite clones would be effective for the development of cassava varieties resistant to CBSD as well as storage root bulking (Chipeta *et al.*, 2018). There are some parts of Africa, however, that are not impacted yet by breeding efforts and where farmers are encountering great difficulties in coping with CMD (Chikoti *et al.*, 2016). In some countries, it is obvious that breeding programme objectives targeting the end-users' preferences could enhance the adoption of new varieties (Nduwumuremyi *et al.*, 2016).

The HarvestPlus Programme has successfully developed elite yellow-fleshed varieties of cassava with higher carotenoid content (Moura *et al.*, 2015) and more than 50 elite provitamin A varieties are now being distributed in Africa with a good rate of adoption by farmers and processors. In Nigeria, it is observed that yellow *fufu* and *gari* have recorded a fast-growing preference among consumers. It has been suggested, however, that a negative correlation exists between total DM content and total carotenoid content (TCC) and therefore more breeding work is necessary for continuous improvement of these varieties (Ngenga *et al.*, 2014). The objective is to reach 15 µg of TCC and more than 30% of DM content while preserving root mealiness to improve cooking quality (Parkes and Aina, 2017). In CIAT, Colombia, significant gains have been obtained through recurrent selection for TCC as well as for total beta carotene (TBC). It has been observed that simultaneous gains for TCC, TBC and DM content are feasible (Ceballos *et al.*, 2013).

However, the selection process has a few important constraints: breeding cycles are very long, no data are taken at the early stages to allow estimates of the general combining ability of the parents and it takes several steps until multi-location trials are established. A new scheme has been proposed for the CIAT programme based on a more accurate clonal evaluation and the use of a selection index (Ceballos *et al.*, 2006c; Ceballos *et al.*, 2017). In Brazil, it has been recommended to obtain a greater number of clones per family so that the efficiency in the selection of superior genotypes is maximized in early CETs. Most the genetic variation is thought to be dissipated within families, so families with higher numbers of clones are more likely to generate superior clones evaluated at the final stage of the breeding programme (Freitas *et al.*, 2018).

In Colombia, mutation breeding using gamma rays on seeds has been attempted to select new phenotypes absent in local germplasm. Variability was found in the granule characteristics and properties of the mutants' paste between years, suggesting significant influence of genotype × environment interactions. There were also differences in paste properties associated with

the level of irradiation. Promising mutants were identified with postharvest physiological deterioration tolerance, but there is a need for further research (Tofiño *et al.*, 2011).

## HERITABILITY OF MAJOR TRAITS

Very little is known about the heritability of qualitative traits. It has been shown that thin lobes of the leaves are a dominant trait compared to wide lobes and that the brown colour of the root skin is dominant over white. It has also been observed that the size of the leaf is most likely a monogenic trait and that the red colour of the lamina is dominant over the green, indicating that anthocyanin pigmentation is probably a dominant trait on all parts of the plant (Kawano *et al.*, 1978). High leaf retention (long leaf life) is a major trait which is not negatively correlated with others and should, therefore, be fairly easy to improve (Lenis *et al.*, 2006).

The screening of about 2500 genotypes for their nutritional (cyanogenic potential, carotene, mineral and sugar content) and agronomic (DM content, colour intensity and postharvest deterioration) traits reveals tremendous variation. Carotene content in the roots ranges from 0.102 to 1.040 mg/100 g fresh tissue and is correlated positively with colour intensity and cyanogenic potential. Average levels of Fe and Zn are 17.1 and 7.5 mg/kg, respectively. Many clones derived from Meso-America show high protein levels in the roots, probably as a result of introgression with wild species. The observed values for carotene, protein and mineral content suggest that there is potential for improving the nutritive value of cassava (Chavez *et al.*, 2005). Significant gains have been achieved to increase root carotene content; the quantification protocols for the carotenoids have been improved as well, and are now reliable and accurate (Sánchez *et al.*, 2014). There is variation in starch quality in relation to its amylose percentage, with a mean around 15% (Iglesias *et al.*, 1997). Breeding efforts are ongoing to develop varieties with amylose-free starch and useful information has been produced on the relationship between this trait and DM content (Karlström *et al.*, 2016).

It is useful to estimate the combining ability of the parents before crossing them, but there are some practical difficulties when undertaking such studies with cassava. These are due mostly to high heterozygosity and to the fact that morphological variation often masks real genetic variation. Frequently, the coefficients of variation obtained for a particular trait are so high that it is difficult to assess the performance of a clone (Ceballos *et al.*, 2006c).

CIAT has conducted diallel studies in three contrasting agroecological zones (acid soil savannahs, sub-humid environment and mid-altitude valleys). These studies allow a first assessment of: (i) the general combining ability (GCA), which corresponds to the average performance of parents in crosses; and (ii) the deviation of individual crosses from the average performance of

parents. They also allow the estimation of epistasis; in other words, the extent of the interaction between non-homologous genes. It is observed that genetic variability is concentrated in the within-family component and is significant for fresh root yield, fresh foliage yield, harvest index, root DM content and plant type scores. Estimates of dominance variance are considerably larger than those of additive variance for fresh root and foliage yields and it is therefore assumed that epistasis plays an important role in fresh root and foliage production (Pérez *et al.*, 2005a, b; Ceballos *et al.*, 2017).

In the sub-humid environment, there are significant genetic effects for reaction to thrips, fresh root and foliage yields, harvest index, DM content and root DM yield. Significant epistatic effects are also observed for all variables, except harvest index. Dominance variance is significant and additive variance is significant only for reaction to thrips. Dominance probably plays an important role in complex traits such as root yield. It appears that not only are additive effects useful for determining the performance of progeny, but also that there is a large component of dominance effect. Heterosis is significant for traits such as fresh root yield. It is concluded that significant epistasis would justify the production of inbred parental lines to fix favourable allele combinations in the production of hybrids (Cach *et al.*, 2005).

It is thought that cassava improvement could benefit greatly from the introduction of inbreeding into the selection process. The production of homozygous lines through tissue culture techniques for the purpose of capturing hybrid vigour could offer promising perspectives. Increased homozygosity could result in a decrease of the genetic load and double haploids are expected to produce better hybrids. In India, inbred lines have also been produced, with evident inbreeding depression in most morphological traits. Selected inbred progenies have been crossed with high-yielding released cultivars and a few hybrids appear significantly better in yield than the released cultivars (Ceballos *et al.*, 2006c). It appears that inbreeding depression ranges from low levels for DM content (5% depression) to high levels for fresh root yield (more than 50% depression). Inbreeding causes a drastic reduction in vigour during the first cycles of selection but tolerance to inbreeding can be built up. The development of an efficient protocol for the production of double haploids could speed up the time necessary to reach sufficient levels of homozygosity. Inbreeding is also helpful for detecting useful genes and one of these is the waxy locus (*Wx*), which encodes the starch granule-bound glucosyl transferase (GBSS). The 'waxy' starch lacks amylose, and starch composed exclusively of amylopectin is advantageous for commercial applications. A clone resulting from the screening of self populations has been shown to present a naturally occurring mutation on the *Wx* locus and the strategy is now to transfer this mutation to other genotypes (Ceballos *et al.*, 2008).

Experiments were conducted in Brazil to evaluate the effects of inbreeding depression in five self-pollinated varieties and it was observed that inbreeding can lead to the selection of individuals with superior agronomic performances

(De Freitas *et al.*, 2016). In CIAT, the production of inbred progenitors began in the mid-2000s but the successive self-pollinations encouraged the use of early-flowering varieties which are not suitable because of their low branching (Ceballos *et al.*, 2017).

## GENOTYPE × ENVIRONMENT INTERACTIONS

Cassava is subject to remarkable genotype × environment interactions. In most of the countries where it is cultivated, natural pollinations between local cultivars have produced landraces well adapted to local conditions, and have been selected by farmers. However, observations made in Benin, West Africa – where 37 cassava genotypes, including advanced breeding lines, were tested for their reaction to bacterial blight in three distinct ecological zones – show significant interactions. Among the 37 genotypes tested, several genotypes could be recommended to farmers in specific ecozones, but only one was relatively stable in disease resistance and in high yield across the three ecozones (Zinsou *et al.*, 2005). In Uganda, 13 provitamin A clones were evaluated in six environments to assess genotype × environment interactions. There was significant variation among genotypes. TCC was found to be negatively correlated with DM content, which is an important trait for farmers (Esuma *et al.*, 2016).

Studies conducted by CIAT in Colombia with different clones cultivated in contrasting environments have shown that fresh root yield is subject to strong genotype × environment interaction. General and specific combining ability effects, and their interaction with the environment, are significant for most traits (Calle *et al.*, 2005; Jaramillo *et al.*, 2005). There is an important interaction between the genotype and the temperature for yield. When four different cultivars are evaluated under three different temperatures (20, 24 and 28°C), higher yields are obtained, varying with the cultivar and temperature used (Irikura *et al.*, 1979). This indicates that the incidence of natural and local selection is highly significant on cultivar adaptation.

In Africa, breeding resistant genotypes is the best strategy to cope with CMD and cassava bacterial blight (CBB). In order to assess the performances of 21 $F_1$ progenies in two different locations in Ghana, these were evaluated for CMD and CBB resistance and agro-morphological traits. The results revealed that the environmental effect was significant for all traits and it is therefore recommended to evaluate new hybrids in different sites in order to have a fair assessment of their resistance to these diseases (Parkes *et al.*, 2013).

Genotype × environment interactions, combined with farmers' particular tastes in subsistence agriculture and the lengthy process of bulking and distributing an improved variety to smallholders, favour the development of geographically decentralized cassava breeding. Several experiences of participatory plant breeding have already been conducted successfully in Brazil (Gonçalvez

and Saad, 2001). In Asia, participatory activities have been successful (Howeler and Tan, 2001; Howeler, 2006). Cassava programmes in Africa are also considering farmer participatory selection. In Vanuatu, South Pacific, farmers are demanding varieties with high root quality traits. The wide distribution of new hybrids shows that farmers are very critical but adopt new genotypes when they satisfy their criteria (Lebot *et al.*, 2015; Lebot and Kaoh, 2017a). In Ghana, the approach ensures that disease resistance and yield are coupled with qualities important to farmers and communities (Manu-Aduening *et al.*, 2014). Using this approach, breeders involve farmers directly in their work to identify their preferences, which may involve taste, good cooking ability, early maturity, good storage in the ground, more roots per plant, pest and disease resistance and leaves suitable as a good vegetable (Nduwumuremyi *et al.*, 2016).

## USE OF RELATED SPECIES

Wild *Manihot* species have been used to introduce desirable genes into cassava, particularly for resistance to diseases such as mosaic virus and bacterial blight and to pests such as green spider mite and mealy bugs. They have also been used to increase protein content and decrease cyanide content. Interspecific progenies are highly variable, but a wide range of species appear to be useful. These include:

- *M. anomala* (compact roots, adapted to shade and the wet tropics, normal meiosis, viable pollen).
- *M. caerulescens* (drought resistant, tolerant to toxic soils and adapted to low temperatures).
- *M. catingae*, *M. dichotoma*, *M. glaziovii* (resistance to mosaic virus).
- *M. oligantha* subsp. *nesteli* (numerous roots, well adapted to drought, low CG content, 7% of protein content in the roots, normal meiosis with 18 bivalents).
- *M. pseudoglaziovii* (tolerant to drought).
- *M. stipularis* (drought resistance, adapted to low temperature, dwarf trait).
- *M. tripartita* (compact roots, whitish flesh, high protein content).
- *M. tristis* subsp. *saxicola* (high protein content).

The interspecific hybrid of *M. oligantha* with cassava had a protein content up to 4% in the peeled roots (double that of common cassava), combined with a relatively low hydrogen cyanide (90 mg/kg HCN) content. Facultative apomixis exists in *M. dichotoma* and *M. glaziovii*; apomixis corresponds to the formation of seeds without fertilization. It is, however, present at very low levels (1%–2%) and apparently depends on meiotic irregularities (Nassar and Dorea, 1982).

Adaptation to marginal stressful environments could be achieved by crossing wild species such as *M. rubricaulis* and *M. grahami* with *M. esculenta*.

The first two species have amphistomatous leaves, a notably elevated activity in leaf extracts of the $C_4$ photosynthetic enzyme PEP carboxylase, very high leaf net photosynthetic rates and relatively low photorespiration. As most cassava cultivars have hypostomatous leaves, with a high stomatal density only on the lower surface of the leaf, it might be possible to transfer, via crosses, the efficient $C_4$ photosynthetic pathway and the amphistomatous leaves to *M. esculenta* (El-Sharkawy, 2004).

The most frequently used species is *M. glaziovii*, which has been shown to hybridize naturally with *M. esculenta*, although pollination rates are low. Resistance to mosaic virus and bacterial blight, as well as low cyanide content, have been transferred successfully from *M. glaziovii* to locally adapted *M. esculenta* varieties in Africa (Hahn *et al.*, 1980). The deoxyribonucleic acid (DNA) sequencing of a global collection of *Manihot* accessions including wild *M. glaziovii* and 208 African cassava varieties, revealed interspecific introgression, both through conventional breeding programmes and through natural introgression. In Africa, specific *M. glaziovii* haplotypes are widespread among preferred cassava varieties, indicating that genes from wild species can contribute positively to cassava performance (Bredeson *et al.*, 2016).

The wild relative, *M. esculenta* ssp. *flabellifolia*, has been used as a source of high protein content to improve commercial cultivars, and the storage protein ranged from 2.8% to 12.2% in $F_1$ hybrids (Akinbo *et al.*, 2012).

## POLYPLOIDY BREEDING

Polyploids are morphologically distinct with their leaves generally broader, thicker and of a darker green. These leaf characteristics are distinct, even at the seedling stage. The stomata are generally larger in size and are fewer per unit of area on the lamina (Fig. 3.4). Finally, the pollen grains of the tetraploids are uniformly large, while some pollen grains of triploids are large and others small. In Brazil, the cultivar most tolerant to drought is a natural triploid ('Manebeba Branca'). Spontaneous polyploids exhibit greater genetic variability and are also more vigorous than autotetraploids induced by colchicine treatment (Fig. 3.5). In Vanuatu, farmers have selected triploid landraces ('Biskit', 'Mariongo Red') and these are high yielding with good-quality roots (high DM and starch contents) (Sardos *et al.*, 2009). Unfortunately, their conservation in the ground after 10 months of growth impacts root quality.

Triploidy, as an effective tool in cassava improvement, and especially for the production of high-starch varieties for industrial use, was first realized in Kerala, India. Artificial autotetraploids with $2n = 4x = 72$ chromosomes were obtained through somatic doubling using colchicine (Abraham *et al.*, 1964) and a selected triploid called 'Sree Harsha' was released in 1998 by the Central Tuber Crops Research Institute, India (CTCRI) (Sreekumari *et al.*, 1999).The triploids produced in India are found to be more vigorous than tetraploids,

**Fig. 3.4.** Cassava triploid leaves (up) are larger and wider than diploids (bottom left and right) (photo: V. Lebot).

**Fig. 3.5.** Differences in root growth vigour between triploid (left) and diploid (right) cuttings (photo V. Lebot).

having stout stems and high leaf retention capacity. They also have an erect plant type with a mean number of 8.8 roots per plant. DM content is mostly above 45% compared to 29%–35% in diploids and 30%–36% in tetraploids. The starch content is also higher in triploids (Sreekumari *et al.*, 2000). These triploids can satisfy the needs of the industry, but more work is required to find out if they can also satisfy the fresh 'table' market, where consumers are hard to please.

Spontaneous tetraploids, triploids and 2*n* pollen (unreduced gametes) were also obtained in IITA from the diploid interspecific crosses and from open-pollinated interspecific hybrids. These involved female diploid plants of *M. esculenta* crossed with male parents of *M. pruinosa* or *M. glaziovii* (Hahn *et al.*, 1990).

## USE OF MOLECULAR MARKERS

Isozymes have been used successfully to study the genetic variation of cassava in West and central Africa (Lefèvre and Charrier, 1993), in Brazil (Resende *et al.*, 2000) and Costa Rica (Zaldivar *et al.*, 2004). In all four cases, enzyme systems, which are co-dominant markers, reveal sufficient polymorphism to study the genetic diversity of the crop.

SSRs (or microsatellites) and amplified fragment length polymorphism (AFLPs) have been used in combination with isozymes to develop a core collection (Chavarriaga-Aguirre *et al.*, 1999). The picture produced by the three different markers is consistent. The application of these markers and the variability of chloroplast and nuclear ribosomal DNA are also useful to clarify the taxonomy of wild *Manihot* species (Fregene *et al.*, 2003; Roa *et al.*, 1997).

A molecular map has been developed using these various markers and it was thought that molecular marker-assisted selection (MAS) could be used for key agronomic traits following the identification of quantitative traits loci (QTL). The map was constructed from the segregation of RFLP (restriction fragment length polymorphism), SSR, RAPD (random amplified polymorphic DNA) and isozyme markers in a cross between two elite lines, one from IITA and the other from CIAT. Results revealed a few randomly distributed duplicated loci (< 5% of the total number of markers) that corresponded to what was observed in normal diploids (Fregene *et al.*, 1997, 2001). Together, the male- and female-derived maps today have more than 300 markers and this is estimated to cover approximately 80% of the cassava genome (Jorge *et al.*, 2000; Fregene *et al.*, 2003). Other maps (using different progenies) looking at different QTL with different markers have since been produced, including the development of high-density genetic linkage maps. However, despite these significant financial efforts, the practical use of these molecular maps in cassava breeding programmes is extremely limited. There are technical reasons for this, including the fact that molecular markers used in most QTL studies are not reproducible and not convenient to use for high throughput genotyping (Rabbi, 2017).

The identification of a large number of single-nucleotide polymorphism (SNP) variants via next generation sequencing (NGS) is now allowing more accuracy. It is hoped that the reduction in DNA sequencing costs will accelerate this process (Soto *et al.*, 2015). A consensus linkage map has already been produced and is assembling more than 90% of the predicted protein-coding genes (Becerra Lopez-Lavalle, 2017). It is now hoped that molecular markers will be used to:

- Increase the selection efficiency for root DM content, disease and pest resistance and harvest index during the seedling trial in order to improve early selection at the SRT.
- Improve the choice of parents.

The broadening of the genetic base in Africa has been done by introducing South American seeds and *in vitro* cultured genotypes, where the dominant *CMD2* gene for CMD resistance was introgressed through MAS. Marker-assisted introgression of CMD resistance seems to produce interesting results, which could improve the potential value of South American genotypes for Africa (Okogbenin *et al.*, 2007).

MAS could represent an attractive approach for traits expensive or difficult to evaluate in the field, such as postharvest physiological deterioration or resistance to whiteflies or green mites (Becerra Lopez-Lavalle, 2017). Substantial genomic resources, such as linkage maps, annotated reference cassava genome, catalogues of genetic variants and identification of genomic regions linked to major traits, have been produced (Rabbi, 2017). The practical use of QTL in cassava breeding is, however, limited (Ceballos *et al.*, 2015). The major constraint lies with the approach itself: MAS requires DNA extraction to process hundreds of individuals and, in developing countries, breeders do not have the financial means or human resources to implement such activities. Conventional breeding programmes have so far produced a remarkable return on investment compared to these new, attractive but expensive technologies.

It is now expected that genomic selection will soon deliver new statistical models that will be used to predict interesting individuals for further selection. In brief, a training population is developed with a full set of phenotypic and genotypic data (SNPs). The markers are then used to select individuals in a larger validating population that is only assessed with markers. The key issue with this approach is that SNPs should be closely linked to the phenotype. If G × E interactions are not important, the genomic selection (GS) model could be used in two different countries. However, when G × E interactions are not important, heritability is high and there is no real need to breed for high-heritability traits. So, it is very likely that new models will have to be developed for different countries and this will, of course, introduce extra costs in developing new models for each situation. It is not sure yet if the return on investment will be significant enough to compensate for such development costs and if, in practice, GS will be attractive enough to be adopted by cassava breeders.

## TRANSGENIC TECHNOLOGIES

The use of transgenic technologies to incorporate desired traits into the most popular cassava cultivars is interesting because they allow rapid gene transfer from one cultivar to another, or from a wild species to a cultivar, bypassing problems related to heterozygosity and inbreeding. Cassava somatic embryos can be produced and whole plants can be recovered from immature leaf lobe explants (Szabados *et al.*, 1987). These embryos are used as the target for transgene insertion. The first transgenic cassava was made in 1995 at Wageningen University in the Netherlands, where amylose-free cassava genotype was produced using

antisense technology to silence the *GBSS-I* gene (Taylor *et al.*, 2004b). The key for successful transformation is the regular production of friable embryogenic callus (FEC) for use in *Agrobacterium*-mediated transformation experiments. Various protocols have been developed and improved to produce high quality FEC. The different transformation systems rely on the production of embryonic tissues from *in vitro* leaf lobe explants (Fig. 3.6).

There is a desire to develop very low or even acyanogenic cassava on the assumption that a decreased cyanogenic content in the most popular cultivars would reduce the danger of consumers' exposure to cyanide. The industrial processing of large quantities of cassava often generates toxic effluents. Overcoming such problems would improve cassava's economic potential (Anderson *et al.*, 2000; Siritunga *et al.*, 2004).

A programme for transgenic control of the stem borer (*Chilomina clarkei*) and the hornworm (*Erinnyis ello*) has been developed by CIAT. Transgenes have been integrated into the most popular cultivars in Colombia but the results are not convincing yet. It is also considered that transgenic cassava plants could play an important role in combating CMD in Africa by introducing new sources of resistance in the germplasm (Sangaré *et al.*, 1999; Zhang *et al.*, 2017). Transgenic varieties could be useful for intensive cropping systems but property

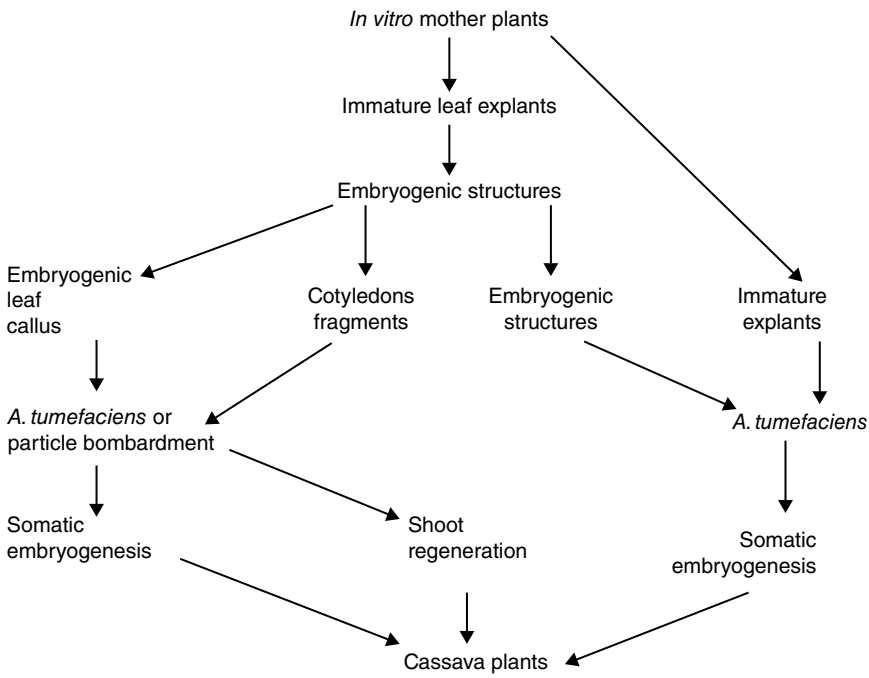


**Fig. 3.6.** Schematic representation of the four systems currently used to transform cassava plants genetically with *Agrobacterium tumefaciens* (Source: Taylor *et al.*, 2004b).

rights issues have prevented the development of transgenic cassava plants with the 5-enolpyruvylshikimate-3-phosphate (EPSP)-synthase gene, which confers resistance to glyphosate, a widely used herbicide. Finally, it appears possible to manipulate the protein content of the cassava root through genetic transformation, but this also presents other constraints (Zhang *et al.*, 2017).

The complete chloroplast genome sequence has been produced. This genome is composed of approximately 164,450 base pairs and includes about 128 genes; 49% of the gene code for proteins. The *atpF* intron (non-coding region), which was thought to be conserved in all land plants, is apparently absent in the cassava chloroplast genome. The intron loss is, however, a characteristic of most species belonging to the cassava family. The availability of the cassava chloroplast genome may accelerate the development of pathogen- and herbicide-resistant and drought-tolerant cassava varieties through plastid transformation (Daniell *et al.*, 2008).

Several experiments have been successful in achieving stable genetic transformation of cassava for micronutrient biofortification, such as zinc, iron, carotenoids and vitamin B6. Also, starch modification for industrial applications has been achieved, especially as the waxy trait can be engineered without impacting the expression of other traits. However, there are no commercially planted transgenic varieties yet, although several field experiments have already been established. The new cultivar should be non-allergenic and should not affect adversely root yield, cooking and storage quality of the final food products (Zhang *et al.*, 2017).

It has been shown that cassava varieties can cross-pollinate naturally with wild relatives; therefore, in South America, transgenes can move easily from a genetically modified variety to other *Manihot* species. However, the risk assessment has also been conducted for gene flow from cassava genetically engineered to the wild, now naturalized *M. glaziovii* in Africa. It was concluded that gene flow will occur but that it is not likely that this will reduce the diversity. It was found difficult to predict the impact of the virus resistance in the naturalized population of *M. glaziovii*, and it is assumed that an increase in its abundance should be manageable and will not lead to an environmental threat (Hokanson *et al.*, 2016). Transgenes should not represent a problem to the release of transgenic cassava varieties in Africa.

## GERMPLASM CONSERVATION

It is estimated that about 27,000 landraces of cassava exist but not all are preserved in gene banks (Abberton *et al.*, 2017). There are approximately 70 cassava germplasm collections in the world, but only 12 countries have tissue culture laboratories for *in vitro* conservation, and about 20,000 accessions of cassava and its wild relatives are now preserved in *ex situ* germplasm collections in CIAT, IITA and in national programmes. Various conservation techniques

are available: field gene bank, seed storage, *in vitro* reduced growth storage and cryopreservation of shoot tips and pollen. Many countries combine tissue culture and *in vitro* conservation with other activities such as pathogen cleaning, rapid multiplication and international exchange.

Large cassava collections are often difficult to use by breeders. CIAT has successfully used different sets of molecular markers to develop a core collection (to assemble the maximum allelic diversity in a reduced number of accessions) (Chavarriaga-Aguirre *et al.*, 1999). The IITA collection maintains 2544 accessions originating from 28 countries in a field gene bank. A core collection based on 40 descriptors has been developed to ease the management of these precious resources. Different strategies were used to capture the maximum diversity and the core is now composed of 428 accessions with no redundancies (Bhattacharjee *et al.*, 2012).

Field genebanks are by far the most common conservation approach and provide readily accessible plant material for characterization and evaluation by breeders. However, they require large fields to maintain large collections and are exposed to pests and diseases. Cassava seeds (Fig. 3.1) store best in cool and dry conditions. Once dried, they can be sealed in aluminium foil envelopes and stored at −20°C for long-term conservation. Seeds for breeding programmes can be stored in paper bags at 5°C in a cold room with less than 30% humidity.

*In vitro* conservation techniques are being applied routinely (Ng *et al.*, 1999). Clones are conserved in constant temperatures of 23–25°C day and night, with 12 h light (at 1000–1500 lux), on a slightly modified Murashige and Skoog (MS) culture medium. Three to five tubes per accession are maintained. Using disease and virus indexing, germplasm accessions can be multiplied safely and exchanged internationally (Frison and Feliu, 1991). *In vitro* conservation is the most practical way to maintaining germplasm in a small space protected from pests and diseases, and it gives the possibility of high throughput propagation. It also allows the development of other more complex techniques, such as somatic embryogenesis, protoplast fusion and cryopreservation. The shoot tip is the most suitable material for the cryopreservation of clones and is the most amenable to tissue culture. Current protocols involve slow cooling with cryoprotectants and dehydration before direct immersion of cassava shoot tips in liquid nitrogen. IITA has developed various cryogenic techniques for the long-term conservation of germplasm and cryopreservation via droplet vitrification has shown high efficiency (Dumet *et al.*, 2013).

The use of SNP allows a more accurate assessment of the genetic diversity in germplasm collections and in farmers' fields compared to previous DNA markers. It can be used to track released improved varieties to see their rate of adoption (Rabbi *et al.*, 2015). On-farm conservation methodology has yet to be developed, but should be encouraged to complement conventional *ex situ* approaches, especially as it presents the advantage of allowing genotype adaptation in response to climate change (Abberton *et al.*, 2017). In Uganda, farmers use traditional knowledge to select and preserve their germplasm.

Their preferences focus on culinary attributes, storability in the ground, early maturity and cooking quality, and these influence their decisions to retain or abandon some landraces or introduced varieties. By planting varieties in multiple plots, replanting immediately after harvesting, sharing with others in the community and planting disease-free materials, farmers ensure that they preserve their preferred genotypes (Nakabonge *et al.*, 2018).

*In situ* conservation of wild relatives is also an interesting approach as DNA sequencing has revealed that interspecific hybridization has played an important role in the evolution of cassava (Bredeson *et al.*, 2016).

# 4

# Developmental Physiology

## GROWTH CYCLE

Cassava is a perennial shrub that can grow for years, alternating periods of vegetative growth and periods of storage in the roots, with eventually some periods of dormancy (if temperatures are low). The storage roots are developing simultaneously with the aerial parts of the plant. There is a continuous and competing development of both, with no clearly separated physiological phases. But, for descriptive purposes, it is convenient to differentiate five distinct phases during plant growth with duration depending on varietal differences, environmental conditions and cultivation techniques.

### Phase 1. Sprouting

Sprouting occurs 5–15 days after planting (DAP) the stem cutting. Five DAP, the first adventitious roots develop from the cut surface of the stem cutting and also from the buds, which are situated under the soil surface. After 10 DAP, the first sprouting occurs. One or more axillary buds form a bud, a palmate leaf blade, subtended by a long petiole and an internode. Sprouting is influenced by the position of the stake: when the stem cutting has been planted vertically, there is a strong apical dominance, whereas when it has been placed almost horizontally, several buds can sprout but the fastest ones start next to the base. Vertically planted cuttings usually give rise to single stem plants and horizontally planted cuttings produce several stems, with those sprouting from the base being the more vigorous.

### Phase 2. Leaf and root system development

The beginning of leaf development and the formation of the root system occurs between 20 and 90 DAP. Shoot and root growth rely on the reserves of the

cuttings until 30 DAP. The leaves start to expand 30 DAP and the photosynthetic process begins to contribute to the plant growth. Fibrous roots replace the first adventitious roots and start to grow at 25 cm/month or more, penetrating the soil to a depth of 40–50 cm. Few of these fibrous roots will later become starchy roots.

### Phase 3. Canopy establishment

The development of the stems and the establishment of the full leaf canopy occur between 90 and 180 DAP, and this period corresponds to the maximum growth rates for leaves and stems. It is also during this phase that the architecture of the plant and its branching habit are established. After 120 DAP, the leaves are able to intercept most of the light falling on the canopy, when the maximum size of the canopy with the maximum dry matter (DM) partition of the leaves and stems are obtained. It is during this period that the most active vegetative growth of the plant occurs. Stem elongation can reach 4 cm/day and the rate of production of new leaves varies from 20 to 40 leaves per month. The leaf lifespan varies from 50 to 140 days but is much shorter during this phase than during phase 4, the root development phase. If branching occurs, then there is also a significant decrease in the individual leaf area. This phase can be considered to end when the total leaf area index (LAI) reaches a maximum, between 3 and 6 months, and then decreases (Alves, 2002).

### Phase 4. High carbohydrate translocation

The translocation of carbohydrates to the roots occurs between 180 and 300 DAP. During this period, the photoassimilate partition from the leaves to the roots is accelerated and storage in the roots is faster. It is also during this period that the highest rates of DM accumulation occur in the roots. In the meantime, leaf senescence increases, more leaves fall and the stems become lignified.

### Phase 5. End of vegetative growth

Between 300 and 360 DAP, the leaf production is reduced and shoot vegetative growth has finished. Translocation of starch to the roots continues and maximum DM in the roots is reached. This phase is more pronounced in geographical regions with a significant variation in rainfall and temperature. Cassava roots do not have endogenous dormancy, they have no function in vegetative propagation and they do not present bud primordia from which growth could start again. Cassava can be considered as a perennial species cultivated as an annual crop. Once the plant has completed its growth cycle, usually 1 year

after planting, a new phase of vegetative growth can start again with phases of DM accumulation in the roots. The cassava plant is rarely harvested later than 2 years from planting because old plants tend to produce lignified roots and are susceptible to lodging and rot (Fig. 4.1).

When the plant starts from a true botanical seed, there is no phase 1 and the young plant develops a taproot and numerous superficial roots. The rapid vegetative growth is followed by the storage of DM in the roots but the yield is poor. There is a positive correlation between leaf area, or the leaf area duration, and the yield of the roots. The leaf area per plant depends directly on the total number of apices, the number of leaves formed per apex, and the leaf size and life. Plants produced from seeds develop less leaf area than those produced from stem cuttings.

New leaves are produced continuously at a rate of approximately one leaf per day when the plant is young and only one leaf per week when the plant is mature. There are considerable differences between genotypes, as well as interactions with environmental conditions. Under normal conditions, the cassava leaf reaches its full size approximately 10–12 days after its emergence. Total leaf life, from its emergence to fall, depends on the cultivar, levels of shade, water and temperature and can range from 40 to more than 200 days, usually between 60 and 120 days (Alves, 2002). Again, there is considerable variation in leaf size between cultivars and between diploid and triploid cultivars, and this size depends on the age of the cassava plant. Usually, the leaves produced between

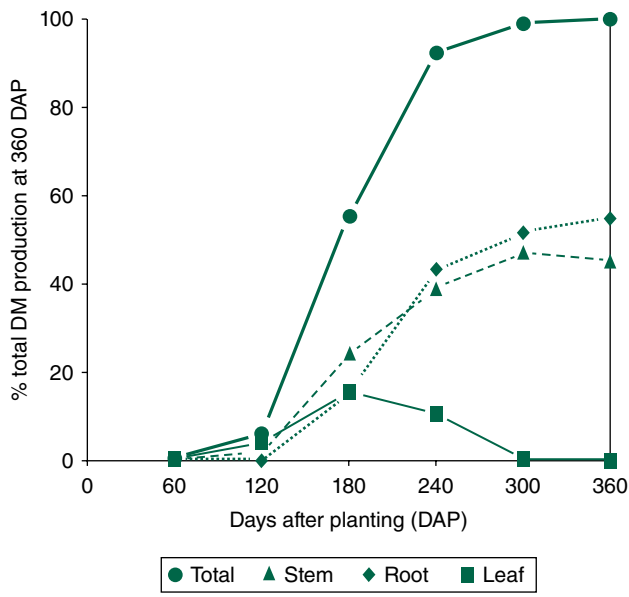


**Fig. 4.1.** Partitioning of dry matter (DM) during the initial development of cassava (source: Alves, 2002).

3 and 4 months after planting are the largest, but the branching pattern also influences the leaf size. Large leaves are produced when the number of apices is low and, conversely, branching types tend to produce smaller leaves (Fig. 4.2).

For cassava, as for all other crops, vegetative growth and yield performance can be evaluated using two parameters: LAI (the ratio of leaf area to ground area) and net assimilatory rate (NAR: the rate of DM production per unit of leaf area). LAI is closely related to root storage, with an optimum LAI for root bulking rate of between 3 and 3.5 (El-Sharkawy, 2004). The cassava plant should reach such an LAI as early as possible in order to produce high yields. As far as NAR is concerned, after the 4th month, more DM is accumulated in the roots than in the rest of the plant and at harvest (10–12 months after planting) the DM is located mainly in roots, followed by stems and leaves. The NAR and root growth rate are reduced when LAI increases from 3 to 6.

Unlike grain crops, in which the vegetative and reproductive phases are at different times and there is little or no competition for photoassimilates, cassava stems, leaves and roots develop simultaneously and photoassimilates are partitioned between the different organs (Uarrota *et al.*, 2017). High starch accumulation in the cassava roots results from a combination of physiological,

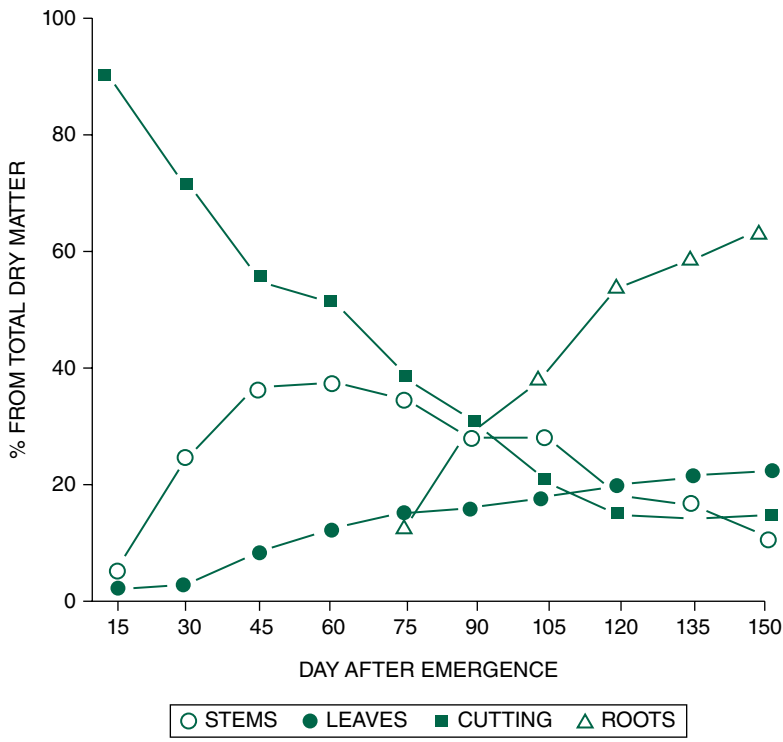


**Fig. 4.2.** Growth of the cassava plant during the first 12 months of the cycle (source: Alves, 2002).

cellular, biochemical and gene expression. Starch accumulation may occur as early as 25–40 DAP and start to occur in the fibrous roots as early as the formation of the root system. Although sucrose, glucose and fructose are the substrates for starch biosynthesis, their contents in the different cassava tissues are not uniform, possibly because they could be interconverted during starch biosynthesis. It has been shown that total sugars content is higher in the distal part of the cassava root compared to the proximal part, which is higher in starch. The distal part is composed of young tissues where sugars accumulate while the proximal part is composed of older tissues where these sugars have already been converted into starch. Maltose, glucose, sucrose and fructose contents also vary within the different parts of the cassava root (Lebot and Kaoh, 2017). High starch accumulation seems to be associated with stronger stem transport of the sugars through high expression of genes encoding glucose transporters and hexose carrier proteins in the phloem–xylem systems of the stems (Li *et al.*, 2016).

This type of partitioning of the DM leads to an optimum LAI value for the growth of roots when there is a balance between DM distribution in the underground and vegetative organs. If more photoassimilates are allocated to the stems and leaves than are used to induce a larger LAI, then less DM will be allocated to root development. It is, therefore, assumed that storage root production is limited by the LAI. Experimental results show that root production is positively correlated with the lifespan of the leaves. The continuous replacement of the leaves involves a metabolic input, resulting in competition with the roots for the photosynthates, and may reduce the root yields (Uarrota *et al.*, 2017). Figure 4.3 illustrates the total biomass of the plant, the shoots and root development as functions of the LAI.

In Colombia, it has been shown that short-stemmed cassava genotypes are superior in producing DM in their storage roots per unit of nutrients absorbed. These genotypes are interesting for soil fertility conservation, while their yields approach those of tall genotypes (but remain, on average, inferior) (El-Sharkawy and De Tafur, 2010). It might be interesting for breeding programmes to focus their selection on efficient short- to medium-stemmed genotypes, since farmers rarely apply fertilizers. Short types can surpass tall types in yields when grown at higher densities (more than 10,000 plants/ha) in order to maximize irradiance interception. In Cuba and in Vanuatu, two countries frequently visited by tropical cyclones, short-stemmed cultivars are also interesting for their tolerance to these violent depressions. Tall types are lodging when winds are above 30–40 knots and this can cause rapid root rots or make the harvest complicated. Short types are more resistant and can be easily intercropped or planted at higher densities.

The formation of storage roots is thought to occur when a subset of fibrous roots receives signals to undergo secondary thickening. The neck of the root, which connects the storage tissues to the basal stem, continues to lay down lignified xylem tissue leading to radial thickening with minimal presence

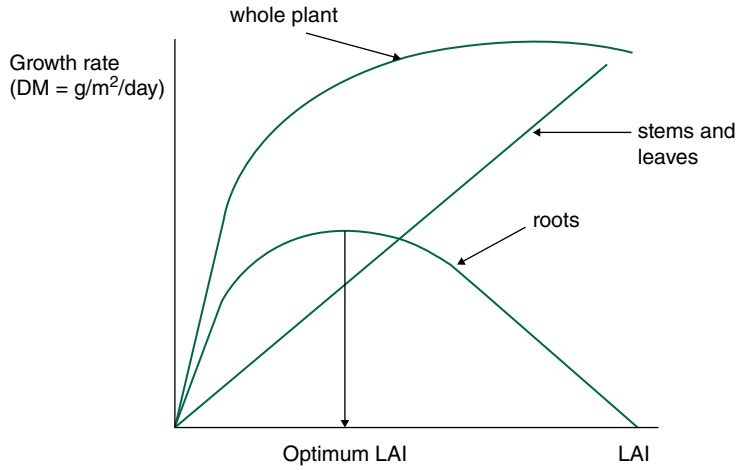


**Fig. 4.3.** Relations between whole plant growth, partitioning of growth between stem and leaves, roots and leaf area index (LAI) (source: El-Sharkawy, 2004).

of starch-containing parenchyma. As the root grows, the cambium still produces xylem, and a larger proportion of the new cells differentiate into xylem parenchyma. It is hypothesized that hormonal signals are sent from the stem to the roots via the phloem (Chaweewan and Taylor, 2015; Khan *et al.*, 2016).

Numerous co-factors are involved, however, and it is risky to assume that the performance of the plant depends on simple correlations between parameters. For example, the nutritional content of the cassava stems are directly influenced by the soil fertility where the mother plants are grown. The nutritional content of the collected cuttings, in turn, affects the yields of the subsequent crops directly, irrespective of their soil fertility status. The root formation and the sprouting rate are influenced by the nitrogen/phosphorus/potassium (NPK) contents in the cuttings, indicating that the nutritional reserves contained in the stem are very important (Molina and El-Sharkawy, 1995). This demonstrates the importance of the quality of the planting material (Table 4.1).

## PHOTOPERIODISM

In the tropics, variation in day length is small (10–12 h) and photoperiod may not limit cassava productivity. Some experiments have shown that the optimal light period is around 12 h, with some differences between genotypes. Long days do promote vegetative growth and do decrease root development. Short days increase root growth and reduce vegetative growth. It is, therefore, assumed that there is an antagonistic relationship between vegetative growth and the development of roots in response to variation of photoperiod.

**Table 4.1.** Effects of the nutrient content of cassava cuttings on the leaf area, fresh weight of foliage, stem and roots of subsequent crops.

| Planting material treatment kg/ha | | | Subsequent crop treatment Unfertilized | | | | Subsequent crop treatment Fertilized* | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| N | P | K | LAI | foliage (t/ha of fresh weight) | stem | roots | LAI | foliage (t/ha of fresh weight) | stem | roots |
| 0 | 0 | 0 | 0.4 | 1.1 | 2.0 | 13.5 | 0.7 | 1.7 | 4.5 | 19.1 |
| 0 | 100 | 100 | 0.5 | 1.0 | 2.6 | 17.5 | 0.8 | 1.6 | 3.6 | 24.7 |
| 100 | 0 | 100 | 0.4 | 1.1 | 3.0 | 14.9 | 0.7 | 1.5 | 4.4 | 23.5 |
| 100 | 100 | 0 | 0.3 | 1.1 | 2.3 | 15.8 | 0.6 | 1.6 | 4.5 | 24.7 |
| 100 | 100 | 100 | 0.9 | 1.7 | 3.1 | 24.2 | 1.3 | 2.1 | 6.2 | 30.2 |

*Fertilized = application of 50, 43 and 83 kg/ha of N, P and K. LAI measured at 3 months after planting. Source: adapted from Molina and El-Sharkawy (1995). NPK, nitrogen, phosphorus and potassium.

Long photoperiods may increase the growth requirements of the shoots, reducing the carbohydrates available for the growth of the roots (Alves, 2002). Stem branching is associated with the onset of flowering, which is promoted, in some cultivars, by long days. At high latitude (for example, at 27° S in Australia), where photoperiods vary from 11 to 14 h, the concentration of the first flowering and branching occurs when days are longer than 13.5 h (Keating *et al.*, 1982).

Cassava is not a shade-tolerant crop. When radiation is reduced by shading, root growth, DM content, root number and harvest index are reduced. Compared to non-shaded control plants, it was found that shade significantly induced the expression of genes involved in light reaction of photosynthesis, light signalling and deoxyribonucleic acid (DNA) synthesis/chromatin structure. In shaded cassava plants, the genes related to anthocyanin biosynthesis, heat shock, Calvin cycle, glycolysis, mitochondrial electron transport, and starch and sucrose metabolisms were dramatically depressed (Ding *et al.*, 2016). Intercropping cassava with perennial plantation crops such as rubber, palm and coconut is fairly common practice throughout the tropics. However, as soon as the shade becomes too dense, the growth of cassava is impacted and the plants have a very thin appearance with long internodes and fewer leaves.

Cassava photosynthesis follows a $C_3$ pathway (De Souza *et al.*, 2017; Gleadow *et al.*, 2009) with a high optimum temperature of 35°C and a wide plateau from 25 to 35°C. Cassava requires high solar radiation for efficient photosynthesis and therefore shade has a considerable effect on cassava growth and production. Under shading, the root bulking process starts later and the number of roots per plant is reduced. Shading increases plant height and there is an increase in leaf area per unit weight (Okoli and Wilson, 1986).

## TEMPERATURE

Temperature has considerable effects on cassava growth (Table 4.2). It affects sprouting, leaf formation, leaf size and therefore general plant growth. Cassava growth is favourable under temperatures ranging from 25 to 29°C, but it can tolerate as low as 12°C and as high as 40°C. At low temperatures, the sprouting of the stem cuttings is considerably delayed and the rate of leaf production is also decreased. At 24°C, the leaf life varies according to the genotype and plant age and is approximately 60–80 days during the first 4 months of growth (El-Sharkawy, 2004). At temperatures lower than 24°C the rate of leaf formation decreases and, at high temperatures, a leaf is fully expanded in 2 weeks. Its size increases with the age of the plant up to 4 months. At temperatures between 15°C and 24°C, leaf life is approximately 200 days but, at higher temperatures, it is only 120 days. At lower temperatures, leaf life may extend up to 200 days.

Sprouting is considerably hastened when temperature increases up to 30°C, but it slows down above 37°C. Again, there are considerable genotype × temperature interactions and different cultivars perform differently, indicating that natural selection is significant in cultivar adaptation to local environments. High temperatures and drought interactions increase the cyanogenic potential of the roots and can increase root toxicity significantly (Brown *et al.*, 2016). It is hypothesized that, in regions where both temperature and drought are forecast to increase, their combined effect on cassava toxicity will lead to an increased need for processing to reduce this toxicity (Uarrota *et al.*, 2017).

**Table 4.2.** Effects of different temperatures on cassava growth.

| Air temperature (°C) | Physiological effects |
|---|---|
| < 15 | Plant growth inhibited |
| < 17 or > 37 | Sprouting impaired |
| < 17 | Reduction of leaf production rate, total and root dry weight |
| 16–38 | Cassava plant can grow |
| 16–30 | Transpiration rate increases linearly and then declines |
| 20–24 | Leaf size and leaf production rate increased and leaf life shortened |
| 25–29 | Optimum for cassava growth |
| 25–30 | Highest rates of photosynthesis in greenhouse |
| 28 | Faster shedding of leaves with reduction in the number of branches |
| 28.5–30.0 | Sprouting faster and optimum |
| 30–40 | Highest rates of photosynthesis in the field |

Source: adapted from Alves (2002).

## NUTRITION

It is often stated that cassava is a heavy feeder that finishes the nutrients that are present in the soil, with a high efficiency in nutrient absorption on low-nutrient soils, leaving them poorer than before. It is also thought that cassava exports more nutrients than most other crops and that it contributes to the decline in soil fertility. It is assumed that this could be the consequence of its powerful root system, which allows the plant to extract nutrients from a thick layer of soil. In fact, Howeler (2002) has shown that a very low percentage of roots reach the deep layers and that they contribute to water absorption only. When comparing average nutrient removal by cassava and various other crops, it appears that its reputation as a heavy feeder is exaggerated and that nitrogen (N), phosphorus (P) and potash (K) removal per tonne of DM is lower than removal by other major crops (Table 4.3).

Nutrient absorption depends on cassava growth rate, which in turn depends on climatic conditions, soil fertility and genotype. The nutrient contents in the roots and in the whole plant tend to be very high when yield is high and low when yield is low. If the nutrients removed are proportional to yield levels, then an average yield of 15 t/ha would remove approximately 35 kg of N, 5.8 kg of P, 46 kg of K and 4.1 kg of Ca. However, the relationship between dry root yield and root nutrient content is not linear so that, at lower yields, nutrient removal is significantly lower. Cassava yields as low as 10 t/ha can be sustained for several cropping seasons, as long as the tops are reincorporated into the soil (Howeler, 2002).

## WATER DEFICIT AND STRESS

Cassava is a drought-tolerant crop but, when deprived of water, plant and root development are affected. This leads to an altered starch biosynthesis,

**Table 4.3.** Comparison between cassava and other crops for their average nutrient removal (in harvested dry matter product).

| Crop/plant part | Yield dry* (t/ha) | N kg/ha | P kg/ha | K kg/ha | N kg/t DM | P kg/t DM | K kg/t DM |
|---|---|---|---|---|---|---|---|
| Cassava/fresh roots | 13.5 | 55 | 13.2 | 112 | 4.5 | 0.83 | 6.6 |
| Sweet potato/ fresh roots | 5.1 | 61 | 13.3 | 97 | 12 | 2.63 | 19.2 |
| Maize/dry grain | 5.6 | 96 | 17.4 | 26 | 17.3 | 3.13 | 4.7 |
| Rice/dry grain | 4.0 | 60 | 7.5 | 13 | 17.1 | 2.4 | 4.1 |

Note: *Assuming cassava to have 38% dry matter, grains 86% and sweet potato 20%. Source: adapted from Howeler (2002).

which is expressed by variation in starch quality whose magnitude depends on the severity of the stress conditions and stage of plant maturity. During the early phases of plant development, water stress delays normal growth, which resumes only when the immature plant receives sufficient water. In mature plants, the starch quality is affected by the environmental conditions, especially the onset of rain after a stress period, which reduces the starch yield (Sriroth *et al.*, 2001).

Cassava responds to water deficit by reducing its evaporating leaf area rapidly by partially closing the stomata. This increases the efficiency of water use. When severe, a drought period can induce diminution of the root yield, depending on the duration of the water deficit and its position in the growth cycle. The critical period is between 30 and 150 DAP, which corresponds to the root initiation phase. During that period, a water deficit of at least 2 months can cause a decrease in root yield from 32% to 60% (Connor *et al.*, 1981).

There are various mechanisms underlying cassava tolerance to water stress. They are related to the sensitivity of its stomata to both atmospheric and edaphic water stress (El-Sharkawy, 2004). In most plant species, a response to water stress is the closure of stomata, which directly decreases photosynthesis and growth. However, cassava stomata partially close when the air humidity is low and the leaf, being protected from dehydration, remains photosynthetically active (Uarrota *et al.*, 2017). When water is available, the cassava plant keeps a high stomatal activity and maintains high internal $CO_2$ concentration. Under water stress, the plant closes stomata and decreases leaf area growth in response to small decreases in soil water. The closure of the stomata and the resulting decline in transpiration protect leaf tissues from desiccation. The leaf area is decreased but expands rapidly as soon as water becomes available again. This response limits cassava transpiration surface during water deficit (Alves, 2002).

Under water deficit, cassava leaves accumulate large amounts of abscisic acid rapidly in young and mature leaves. The young leaves halt their expansion growth and their transpiration rate is decreased. The high abscisic acid levels under water stress are reversed after 1 day of watering and the rapid return to normal abscisic acid levels corresponds to the rapid leaf area growth. The rapid reduction in cassava leaf area growth and stomatal closure is probably due to the ability of cassava to produce and accumulate abscisic acid very early in the water stress phase (Alves and Setter, 2000). During stress, growth cessation involves both cell division and expansion but both are able to recover fully when stress occurs early. It is thought that the developmental and regulatory systems controlling cell division play an important role in the plant's response to stress (Alves and Setter, 2004).

Long leaf life and good leaf retention are two important physiological traits that contribute to yield (Lenis *et al.*, 2006; Uarrota *et al.*, 2017). Cassava leaves can remain photosynthetically active under prolonged water stress over more than 2 months and are able to recover from stress. It has also been shown that the leaf petiole plays an important heliotropic role in orienting the leaf lamina

towards the sun, maximizing light interception. The midribs of the lobes were found to control another leaf movement, which is leaf drooping or folding. This movement makes the leaf bend from the horizontal position it holds in the early morning by folding downward at noon. This occurs irrespective of soil water and leaf water pressure (El-Sharkawy and Cock, 1984). This movement decreases light interception by half compared to horizontal leaves. The outcome is a direct reduction in transpiration water loss, while the leaf keeps a relatively high photosynthetic rate. Consequently, this leaf movement may act as a water stress avoidance mechanism and contributes partly to cassava's drought tolerance (El-Sharkawy, 2004).

It is difficult to identify and measure the most reliable traits to assess the drought tolerance of cassava genotypes. Cassava drought tolerance is a combination of different physiological mechanisms to tolerate dehydration and to maintain its photosynthetic capacity. However, a few traits have been identified: a powerful root system (extending occasionally to up to 2 m long) and a tight stomatal control over leaf gas exchange. During a prolonged water stress, the plant can reduce its canopy by shedding older leaves and producing new smaller leaves, leading to reduced evaporation. The plant will then recover and form new larger leaves as soon as water becomes available. Hence, cassava is able to withstand water stresses during which photosynthesis is reduced, and this strategy is thought to contribute to its drought tolerance (Uarrota *et al.*, 2017).

In Brazil, it has been shown that the use of physiological traits alone was not efficient at predicting fresh root yield in cassava under drought stress. It was hypothesized that the absence of correlation between root yield and some physiological traits under drought stress, such as the leaf expansion rate or the chlorophyll index, may explain why these traits are poor predictors of root yield. A study attempting to identify the most suitable traits compared 49 different genotypes in well-watered and water deficit conditions and the different traits were evaluated using different predictive models. The most important traits for predicting the fresh root yield were found to be the number of roots per plant, the LAI, the number of leaves measured in the 8th month and the shoot yield (Santos Silva *et al.*, 2019).

## CLIMATE CHANGE ADAPTATION

The crop canopy is a yield determinant. The ideal plant type for maximum yield under favourable conditions has been developed with a computer-based simulation (El-Sharkawy, 2004). This ideal plant has the following traits:

- Maximum leaf size near 500 $cm^2$ per leaf blade at 4 months.
- Long leaf life (c. 100 days).
- LAI between 2.5 and 3.5 during most of the cycle.
- A harvest index greater than 0.5.
- Two vegetative shoots originating from the original cutting.

If such an ideal plant could exist, and provided that the growing conditions are optimal, predictions of a computerized model indicate that it could produce in a year 90 t/ha of fresh roots (approximately 30 t/ha DM). Observed yield potential for cassava compares favourably with other major crops and it produces more energy per hectare than maize, sorghum and rice (El-Sharkawy, 2004). An average experimental yield for several improved cultivars of 90 t/ha in 10 months has been measured over an experimental area of 1 ha in Colombia. The climatic conditions, with a high mean temperature (28°C) and high atmospheric humidity (70%), were near optimum. This confirms the validity of the computer-simulated plant type (El-Sharkawy, 2014). The difference between the potential yield and the average farmers' yields is more than six-fold, indicating that the potential of cassava is far from being achieved. This observation reflects a long-standing debate, especially in Asia, to clarify the respective roles of genetic improvement and cropping system intensification, for continuous increase of cassava yields. It seems that suitable agricultural practices can have a significant impact in the short term. It has been shown that the sprouting capacity of the stems is one of the most important traits to adapt to climate change (Ceballos *et al.*, 2011) and there is significant variation between genotypes for this trait.

Cassava yield potential could be increased by enhancing its light interception efficiency and its conversion efficiency. This would involve modifications in the canopy structure and architecture of the plant, and genetic improvement to increase photosynthetic rates in concert with sink capacity of its storage roots. This will involve a combination of genes conferring rapid canopy development in early growth with adequate water, with genes for drought tolerance in later development to deal with seasonally dry environments (De Souza, 2017).

Increasing temperature, $CO_2$ and rainfall will impact directly cassava yield, quality, pests and diseases but will also favour the growth of weeds competing with the crop. The utilization of varieties with stable root DM content and tolerance to herbicides is seen as a suitable adaptation strategy. Integrated pest and disease management is critical and it will rely on the exploitation of diverse sources of genetic resistance (Ceballos *et al.*, 2011). The geographical distribution of allelic diversity to small farmers is considered a cost-efficient system to broaden the genetic bases presently cultivated and to strengthen their capacity to adapt to forthcoming changes (Lebot, 2013).

Increased $CO_2$ in the atmosphere may have a positive impact on cassava growth. The present concentration is around 400 ppm but it could reach 700 or 1000 ppm towards the end of the century. A study conducted in controlled field conditions has shown that after 3.5 months of growth at elevated $CO_2$, above-ground biomass was 30% greater and cassava root dry mass increased over 100%. It is thought that high photosynthetic rates and photosynthetic stimulation by elevated $CO_2$ led to the development of larger canopies and a large sink capacity, and contributed to cassava's growth and yield. Cassava

exhibited photosynthetic acclimatization via decreased Rubisco capacity early in the season prior to root tuberization when sink capacity was smaller. No evidence of increased leaf N or total cyanide concentration in elevated $CO_2$ was detected. Increased $CO_2$ and temperature may have a positive effect on cassava's productivity but there is a need for further field experiments to confirm this (Rosenthal *et al.*, 2012). Other controlled experiments have confirmed that elevated $CO_2$ reduces the impact of water deficit in cassava through reduced stomatal conductance and transpiration rate. Elevated $CO_2$ was found to increase photosynthesis and transpiration efficiency, and biomass production was greater for cassava plants grown under elevated $CO_2$ (Cruz *et al.*, 2016).

When examining the possible impacts that climate change will likely have on cassava itself, based on projections to 2030, results indicate that cassava is actually positively impacted in many areas of Africa. An almost opposite crop–climate response has been observed between cassava and sorghum, suggesting that cassava could replace sorghum in areas where the latter suffers greatly. However, if cassava can adapt to harsher future climates, it is also clear that pest and disease pressure is likely to escalate and, therefore, the priority is to increase resistance and improve crop management practices (Jarvis *et al.*, 2012).

Mature cassava plants are able to tolerate salinity (100 mM NaCl), but young plants suffer when the levels are around 40 mM, and growth is severely impacted. Cassava is not suitable for regions contaminated with low levels of salt (Gleadow *et al.*, 2016).

# 5

# Agronomy

Cassava can be cultivated successfully in areas with an annual rainfall of between 1000 and 2000 mm, but it can tolerate lower rainfall if it is well distributed. The most favourable conditions seem to be in climates with 1500–2000 mm/year and maximum solar radiation. Over the past 25 years in South-east Asia, yields were found to be higher when cassava was planted in the early part of the rainy season, which in most countries is April–May (Aye, 2017). In many countries, however, some cassava is also planted at the end of the rainy season (September–October), a practice which becomes more risky as latitude increases. In Africa, in areas with no marked seasonality, cassava can be planted all year round.

## SEED SYSTEMS AND PROPAGULE SELECTION

Once an improved genotype has been selected, the slow propagation rate is a serious practical constraint. In normal conditions a cassava plant can produce, on average, 10–20 good cuttings of 20–30 cm. Four clonal generations are, therefore, necessary to produce sufficient planting material to establish 1 ha at the most common density (10,000 plants/ha).

Rapid propagation techniques have been developed and are now used widely. The Centro Internacional de Agricultura Tropical (CIAT) has developed a simple practical system of two-node cuttings planted flat, 1 cm deep, in a well-drained substrate, under a screen to preserve sufficient moisture. Young shoots sprouting from these cuttings are then separated as soon as they have two leaves (8–10 cm long) and are placed in plastic tubes of 2 cm in diameter, filled with boiled water. They then develop roots and are ready to be transplanted into the field. Using this system, a normal plant can produce 200 leafy cuttings in 4 months and 12,000–24,000 stakes/year if the two-node cuttings are collected three times a year from the mother plant. Another method for rapid multiplication has been devised using leaves excised with their axillary buds. When transferred to a mist propagator, they start to root and sprout.

The propagules are transplanted 2–3 weeks later into small pots filled with peat then, after 1 month or so, to the field. This method is quite labour intensive but can produce between 100,000 and 300,000 stakes of a selected genotype in 18 months (Vilpoux *et al.*, 2017).

In Africa, the International Institute for Tropical Agriculture (IITA) has developed an efficient rapid multiplication system based on the use of ministem cuttings. Cuttings from the hardwood portion may have 1–2 nodes, those from the semi-mature portion have 4–6 nodes and those from the tip portion may have 6–10 nodes (Fig. 5.1). Sprouting takes place in well-drained nursery beds where the hardwood ministem cuttings are planted horizontally at a spacing of 10 × 10 cm and a depth of 4–5 cm. The semi-mature and the tip-shoot cuttings are planted at the same spacing but vertically, with two-thirds of the cutting (the old end) below the ground and the remaining third (the young tip) above the ground. Transplanting is done in well-prepared fields during the rainy season, or with proper irrigation (IITA, 1998).

*In vitro* culture can speed up the propagation rate greatly with, however, considerable variation between clones. On average, from a single bud it is possible to obtain in only 1 year between 15,000 and 100,000 *in vitro* plantlets. These plantlets have poorly developed cuticles and it is important to provide an environment with high relative humidity, such as a simple humidity chamber made out of plywood and plastic sheeting, for proper acclimatization. Once they have been pulled out of their tubes, the agar substrate is washed out gently and the bare root plantlet is transplanted to a Jiffy® peat or a vermiculite substrate in a small pot. Immediately after transplanting, the plants are placed in the humidity chamber, where they will stay for about 3 weeks before being transplanted to seedbeds at 50 × 50 cm spacing. They will produce semi-hardwood cuttings in 6–8 months (IITA, 2002).

Well-organized seed systems are often lacking for cassava, even in countries where it is an industrial crop. Structured seed systems can be established, but these need to focus on factors including poor-quality planting materials.

**Fig. 5.1.** Cassava ministem cuttings placed horizontally in trays and sprouting 2 weeks after planting (photo: V. Lebot).

The degradation of cassava's planting material leads to declining yields and is caused by systemic diseases (viruses, bacteria, phytoplasma); poor soil fertility and nutrient imbalance; soil salinity; the socio-economic situation of the farmer, which impacts crop management; and the low storage potential of stakes, due to the poor nutritional status of mother plants. There are, however, several encouraging initiatives focusing on quality standards of propagules: age, number of nodes per cutting, pith thickness and sprouting capacity. In India, a seed system based on two-node mini-stakes has been developed and seems promising. Tissue culturing is used for sanitation and propagation of virus-free mother plants but is not really feasible for large plantations, as plants are slow growing. The mini-stake system is used to increase the propagation rate of the planting material and to accelerate the distribution of selected varieties. Two-node mini-stakes are used when there is constant moisture availability for field planting, to produce plants that will be the source of the stem cuttings or to produce shoots and rooted first. The mini-stakes are planted flat on nursery beds in a shade-net house. With light irrigation, they start sprouting in about 1 week and are ready for transplanting about 3–4 weeks after planting. About 50,000 two-node mini-stakes can be transplanted on 1 ha of land and will produce at maturity, depending on the variety, approximately 60,000 cassava stems for further propagation. Each stem can produce approximately 3–4 good cuttings for direct field planting (George and Sunitha, 2017).

In Brazil, it has been observed that new cassava varieties may produce well initially but then their performance tends to decline owing to the accumulation of viral particles. It has been difficult to develop tissue culture propagation systems which are economically viable. However, when used in combination with other conventional propagation techniques, they can contribute to the establishment of healthy seed nurseries. The use of two-node mini-stakes is very efficient in increasing the propagation rate, but it has been observed that their use outside research stations is limited (Vilpoux *et al.*, 2017).

In East Africa, where cassava brown streak virus (CBSV) is a major disease, several experiments were conducted to select the most appropriate planting material to avoid the rapid decline of the yields due to the viral load. It has been observed that cuttings taken from upper stems of diseased plants can produce virus-free clones compared to middle or lower parts of the same stems. This unusual propagation system could be exploited to develop strategies to control the spread of CBSV in East Africa (Mohammed *et al.*, 2016). It has also been observed that the fields of East African farmers can produce sufficiently clean material if rogueing is properly practised, leading to successful CBSV suppression. Well-managed fields were found to maintain low disease levels but multiplication sites should be established in areas of low disease pressure and vector population density. Finally, the increase in plant propagation rates can have an impact on site sustainability (McQuaid *et al.*, 2016). In Ivory Coast, West Africa, a simple technique for rapid production of cuttings is used for live plants (and different heights of where to cut the plant have been tested).

It is possible to cut cassava plants at 10 cm from the soil surface 7 months after planting without affecting yield and dry matter (DM) in tuberous roots, and this produces a higher number of cuttings per plant. Cutting plants higher up, at 35–60 cm, causes significant losses (N'Zue *et al.*, 2007).

When a cassava stem cutting is planted in the upright position, with the older end in the soil, a mass of callus tissue forms at this older end and, within a few days, roots are produced. Roots also develop at any submerged nodes. It is preferable to cut stakes at a right angle to prevent splitting, which may provide entry for pathogens. Stems that are cut at a sharp angle induce a grouped development of roots and, when this is combined with an inclined planting, it allows the localization of the roots in one area of the soil and consequently the grouping of the roots together, easing the harvest. The vertical planting of stems which have been cut at a right angle induces the roots to radiate around the plant. Farmers tend to favour one or the other, depending on the type of soil: heavy and wet or light and dry.

Stems used to prepare cuttings should be sufficiently lignified and the young branching tips avoided. They produce plants with early branching and flowering, and are fragile, presenting difficulties in becoming established in the field. The over-lignified portions from the basal stems of old plants should also be avoided as they are poor in nutritive reserves and are more prone to infection with viral particles. Stakes are at the right stage when the diameter of their pith is half the total diameter of the stake.

Higher yields are obtained in South-east Asia when stakes are cut from the mid- and lower part of stems taken from mother plants that are about 8–12 months old. Many viruses, fungi and bacteria do not produce clearly visible symptoms, but stakes should be inspected to select the best and to detect insect infestation. Postharvest chemical treatment of stakes with mixtures of systemic and contact fungicides, and with an insecticide when necessary, can protect and extend stake life during storage (Leihner, 2002). The selected planting material should be developed with mature and healthy stems kept in good storage conditions to minimize losses. Stored stakes should be as long as possible, and not cut, as this increases dehydration.

How long stakes can be stored depends on the variety and climatic conditions during storage. Where there are periods of the year when planting is not advisable, cassava stakes may have to be stored for several months. Viability is excellent for 1 month and it is, in some exceptional cases, possible to conserve stakes up to 5 months. There are significant differences between stakes stored vertically or horizontally.

In India, healthy, mature stems approximately 1.2–1.5 m long from three different cultivars were stored for 5 months in hot, dry weather conditions, under different treatments, and comparing different positions and techniques. The stems stored vertically under tree shade and buried in a sand bed and watered every 2 weeks retained moisture content (68%–71%), had the greatest percentage of fresh stem (90%–92%), had the greatest starch content

(256–270 mg/g dry stem) and showed the greatest percentage of sprouting (91%–95%). However, the plants obtained from these stems showed a lower reduction in yield (2.6–3.6 t/ha) compared to root yield of plants from fresh stems. It is, therefore, recommended that cassava stems be stored vertically with the bottom portion (2–3 cm) buried in a sand bed and watered every 2 weeks, under open conditions with appropriate plant protection measures, over a period of 5 months under hot, dry weather conditions (Ravi and Suryakumari, 2005).

In the Philippines, it has been observed that stems can be stored in a vertical position in the open and covered with coconut palm fronds for up to 4 months without affecting the yield of the subsequent crop. In subtropical climates, such as in the cassava-producing provinces of China, the stems need to be cut before the first frost and stored in trenches at least 1 m deep and covered with straw and soil to prevent frost damage. It appears that some varieties are more tolerant to low temperatures than others (Howeler and Tan, 2001).

The deterioration of the planting material is related to respiration and dehydration of the stems. Fresh stems continue to metabolize during storage, losing carbohydrates and valuable reserves, which will reduce sprouting vigour after planting. The percentage of sprouting can fall from 100% to only 30% when stem cuttings are stored for only 2 weeks at 24°C in the sun. On the other hand, if long stems are stored in the shade with 72% relative humidity and chemical (fungicide and insecticide) protection, over 95% of sprouting is obtained after 201 days of storage. These stakes need further chemical treatment before planting to provide extra protection and stimulate growth (Leihner, 2002).

The size of the cutting is important and, in West Africa, cuttings measuring 40–50 cm give a higher yield than those measuring only 15–20 cm (Onwueme and Charles, 1994). However, using long cuttings requires a large quantity of planting material and they are cumbersome to handle. Amerindians in Brazil use cuttings 50–60 cm long in non-mechanized cropping systems but, in the same country, modern and mechanized farms use 15–20 cm cuttings in mechanical planters. The most suitable length of cutting is found to be 15–20 cm in Thailand, 20–25 cm in Malaysia and 25–30 cm in India; short cuttings are recommended in the Philippines for horizontal planting and longer cuttings for vertical planting.

The number of nodes on the cutting is, however, equally important. Cuttings should have at least 5 nodes. When planting material is scarce, it is possible to use short cuttings of only 2–3 nodes placed for about 1 week in wet paper to produce sprouts and roots before planting. In Kerala, India, 2–3-node cuttings are planted close together in moist sand in a nursery for 20 days before transplanting, and this method is particularly useful in areas with a short rainy season. In the large commercial plantings of Indonesia, about 50 stems are bundled together with rubber bands and are cut with a circular power saw. The top of each bundle is dipped in red ink to facilitate planting (Howeler and Tan, 2001).

## SOIL PREPARATION

Depending on soil type and drainage, the field may be prepared as mounds, ridges, flat-tilled or not tilled. Drainage conditions determine the size of the ridges or mounds. In many areas, cassava is still cultivated in slash-and-burn traditional cropping systems where the plot is cleared from existing vegetation, exposing high organic matter soil content. The only soil preparation used is the loosening of the soil locally with a sharp spade, or even a planting stick. The soil is opened and the cutting is inserted, vertically, inclined or flat. This no-till soil preparation produces a texture sufficiently loose to allow good establishment of the stake, initial root penetration and, later, root thickening. In these conditions, farmers find that better soil preparation does not necessarily produce higher yields. They will put considerable effort into preparing the soil for their yams but not for cassava, as it can perform remarkably well with minimal soil preparation.

Under more permanent cropping systems, cassava requires a thorough loosening of the soil to produce a well-drained and aerated substrate for the roots to develop and function adequately. In South-east Asia, land preparation is usually carried out using a hoe or an animal-drawn plough, but in Thailand, Malaysia, Tamil Nadu (India) and much of South Vietnam, land is now prepared by tractor, usually on contract (Aye, 2017). In most countries, the best yields are obtained by two ploughings, followed by one discing and ridging, but ridging is not advisable if planting occurs during the dry season. In Thailand, land preparation is done with a three-disc plough, a seven-disc harrow and a ridger. Some farmers use a simple two-wheel tractor with a small disc plough or a rotavator (Aye and Howeler, 2017). Cassava is particularly susceptible to waterlogging and succumbs easily to excess water in the soil. In areas of high rainfall or in heavy soils, drainage is obtained by preparing mounds, ridges or beds. Planting on ridges is better during the rainy season and planting on the flat is better during the dry season. Soil preparation can be reduced when mulching is applied. Mounds may range in height from 30 to 60 cm and cassava grown on mounds gives higher yields than that grown on unploughed land. Mounds also improve ease of harvesting. When mounds are prepared far ahead of planting, nutrients are leached from the loose soil (Howeler, 2017a).

Continuous cassava cultivation leads to the breakdown of soil structure combined with increased erosion, which can occur after just two cycles. On relatively steep slopes, cassava is planted by only preparing planting holes with a hoe, to minimize erosion. Zero tillage with herbicides has produced good results in Thailand but zero tillage is easier when the land comes out of bush fallow, which prevents excessive weed growth. In very weedy plots or where the soil is compacted, zero tillage results in low yields and serious difficulty when planting, weeding and harvesting. To counter the soil-degrading effects of mechanical soil preparation, efficient techniques of conservation tillage probably require a combination of minimum tillage and the use of herbicides in pre- and post-emergence (Aye, 2017).

## PLANT DENSITIES AND CROP ESTABLISHMENT

When root production is the only objective, the optimal density is 10,000 plants/ha (1 × 1 m), which is adequate for commercial-size fresh roots. Planting densities depend on the growth habit of the cultivar (erect or low branching, early or late maturing), soil fertility, rainfall and temperature. The combination of these factors affects the development of the cassava plant canopy.

Higher plant densities can be used if the average size of the root is not important to achieve a higher yield (of smaller roots) per unit of area. Lower densities (5000 plants/ha) can be used when vigorously branching cultivars are grown; and high densities (20,000 plants/ha) can be used with less vigorous cultivars under low fertility conditions. If the only objective is the production of stakes, a density as high as 40,000 plants/ha (0.5 × 0.5 m spacing) can be used (Leihner, 2002). When some planted cuttings do not germinate, the surrounding plants will grow over the empty space and their yield will compensate for the missing plants. Thus, if less than 30% of the plants are missing, it is not necessary to replant the missing plants. However, if replanting is carried out, it should be before the plants are more than 2 weeks old.

Vertical planting provokes a rapid establishment and development of a good canopy cover. Horizontal planting has the advantage that there is no need to worry if the cutting is upside down and the shallower root system allows for easier harvest. Mechanical planters in use today are designed to plant horizontally: the machine opens a furrow in which the cutting is dropped flat and covered with soil. In Asia, new mechanical planters are now designed to allow vertical planting (Aye and Howeler, 2017). In fact, in regions with adequate rainfall (1000–2000 mm), the cutting position does not matter, but in areas with sandy soils or poor rainfall, vertical planting is safer (Leihner, 2002). In the Philippines, in areas with heavy rainfall, planting vertically on ridges is recommended and, in dry areas, planting horizontally on flat soil or in furrows.

The depth of planting also depends on the local climatic and soil conditions. On dry, sandy soils, cuttings should be planted deeper and on wet and heavy soils, they should be planted shallower. Depth of planting may vary from 5 to 15 cm and it is often observed that deeper planting produces better yields than shallow planting in the dry season. In some cases, however, deeper planting may cause some difficulties at harvest, especially if it is done manually. Cassava planting is mechanized in some parts of Thailand, Brazil and Colombia, but manual planting is still the rule throughout Africa and Asia, even in large commercial plantings. However, in Africa, recently developed mechanical planters can plant from 1 to 6 rows. On farms of more than 20 ha, four-row planters are economically viable. However, if a two-row planter is available, with a 60 hp tractor, it is possible to plant 5–7 ha per day when African farmers and their families would spend more than 8 days to plant a field of 1 ha (Marechera and Muinga, 2017). Experienced crews in Thailand can plant cuttings in straight lines using only 8 man-days/ha (Howeler and Tan, 2001; Aye and Howeler, 2017).

In any case, and because of cassava's high sprouting rate, it is recommended that only one cutting be used at each planting hole. In some traditional cropping systems, farmers often plant more than one cutting per hole. In doing so, they intend to favour a rapid establishment of ground cover and some control of weeds which are, in many systems, removed by hand. This practice is also a safety measure to ensure that at least one will sprout, or that they will harvest sufficient roots per plant. This is not recommended, however, as it causes a waste of planting material and produces multistem plants, which are less efficient.

Spatial arrangements and planting patterns depend on the cropping system and are adapted according to the characteristics of the harvester (in mechanical cultivation) and of intercrops (in traditional cultivation). Different spatial arrangements can be adopted to satisfy the needs of different systems. One can, for example, use a wider than normal spacing between the cassava lines while narrowing the distance between the plants on the line. Such an arrangement facilitates the establishment of intercrops and reduces competition.

Cassava is often established on sloping land because of its minimal requirements for land preparation. However, it has been demonstrated that planting on slopes can result in severe erosion. *Stylosanthes guianensis* and *Vetiveria zizanioides* (vetiver grass), used as live barriers and hedgerows on slopes planted with cassava, reduce soil erosion considerably. Contour ridging is sometimes applied on gentle slopes but up-and-down ridging is more common when the land is prepared by tractor. In these areas, contour hedgerows interfere with tillage in straight lines. Closer spacing (0.8 × 0.8 m), combined with minimum tillage, mulching and planting at the end rather than at the beginning of the rainy season, also contribute to the reduction of soil erosion. In Vietnam, more farmers are adopting contour ridging than contour hedgerows but, in the northern districts, more farmers are still planting hedgerows of *Paspalum atratum*; these serve to stop erosion and also feed their cattle and water buffaloes (Aye and Howeler, 2017).

## INTERCROPPING

More than one-third of the cassava grown in the world is intercropped. It is often found in mixed stands with a variety of food and cash crops, and this system minimizes risk, optimizes the land and maximizes labour inputs per unit of area and time. Under trees such as mature coconut, oil palm or rubber, cassava tends to suffer from shading and production can be very low. Most intercropping systems associate cassava with long- and short-season crops such as maize, cowpea and beans. The association with grain legumes is interesting because of their soil-improving (N-fixing) characteristics. There are particular cassava functional traits that make some varieties more suitable

for intercropping. These include leaf nutrient content and litter quality; leaf retention and longevity; plant architecture; timing of carbon allocation to storage roots; rooting depth, its extension and branching; and interaction with mycorrhizal fungi (Kuyper, 2017). In many countries, some landraces already combine all these traits. It has been observed that cassava with an erect growth, late branching and medium vigour produces less shade over the associated crop and is the most suitable for intercropping with low-growing annual species (Mutsaers *et al.*, 1993).

The yield of cassava can be reduced significantly if the intercrop creates strong competition for light, water and nutrients. When the aim is to establish another species in an already planted stand of cassava, light is the limiting factor. However, cassava intercepts less light towards the end of its growth cycle and, if the initial spacing is suitable, it is possible to establish a quick crop during the last months of cassava's life. Although the productivity of an under-crop in these conditions is lower than when both crops begin their cycle together, its contribution to the protection of the soil is an advantage (Leihner, 2002).

Intercropping cassava with upland rice, maize and grain legumes is a common practice in Indonesia. Intercropping with groundnut is more common in northern Vietnam and China, and vegetables are profitable intercrops in Tamil Nadu, India. Intercropping is not much practised in Thailand, Malaysia and Kerala (India), except for when cassava is intercropped in young rubber and coconut plantations. Grain legumes (common beans, cowpea, mung bean, groundnut) are grown simultaneously with cassava in Java, Indonesia. They have a significant soil protection role and a positive effect on income (Howeler and Tan, 2001; Aye and Howeler, 2017).

If cassava is planted in an already established cover crop (such as *Dolichos* or *Glycine*), soil protection is good but cassava yield decreases due to competition from the legume in the critical establishment phase. With less invasive legumes, such as *Arachis pintoi*, the loss is tolerable but, with *Stylosanthes guianensis*, it is considerable (Leihner, 2002). Despite the positive contribution of cover crops, their adoption by smallholders is difficult because seed supply is always problematic, establishment in the fields is labour intensive and their impact on cassava yield is not always significant.

Mulching under cassava offers soil protection against erosion but its adoption by farmers is minimal as there are serious constraints: the necessary biomass may not be readily available, the labour involved may be costly and there may be some competition with the biomass need for animal feed. Numerous cover crops (such as *Glycine*, *Pueraria*, *Mucuna*) are useful only within a rotation because of their weedy and vigorous behaviour. Experiments have been conducted with N-fixing legume species to assess their potential as dead mulches when sprayed with herbicide prior to planting, and the first results are very encouraging, especially with *Mucuna pruriens*. The mulch controls the weeds during the first two phases of the growth cycle and the soil is enriched in nitrogen, favouring early vegetative growth. For healthy growth, cassava

depends on mycorrhizal symbiosis and the regular insertion of a legume in the cropping systems has been shown to increase spore counts by 36% at the end of the rotation. Rotation with green manure leads to balanced nutrient extraction, enhances soil life and reduces vulnerability to erosion (Leihner and Lopez, 1988).

The application of mulch made of the leaves of *Flemingia macrophylla* was found to have a positive effect on the root yield of cassava in South Benin, West Africa (Böhringer and Leihner, 1997), but it represented an important input. In Asia, green manuring and alley cropping have not been adopted, except for the use of *Tephrosia candida* as an erosion control in northern Vietnam. When species such as *Leucaena* are planted in alleys, there are no important shading effects from these species if they are pruned two to three times a year. Depending on the size of the plot, this work represents a significant investment in working man-days, which is not necessarily rewarding. *Leucaena* contributes high amounts of N but competes strongly for K. Considering the moderate N but high K requirements of cassava, such alley cropping may result in the unbalanced development of leaves and stems and low harvest indices and root yields.

## WEEDING

Hand weeding is the most common technique, using hoes, shovels or machetes; but, in some places, pulling weeds out by hand is preferred. The major weeds affecting cassava production are the grasses *Andropogon* spp., *Imperata cylindrica*, *Panicum maximum* and *Pennisetum* spp. and the broadleaves *Commelina* spp., *Mimosa invisa* and *Mucuna pruriens*, but many others can cause problems. *Imperata cylindrica* competes for water and also pierces the roots, providing entry to pathogens. The earliest growth stage, until the canopy closes completely, is the most critical period and it should be kept weed free during the first two phases of the growth cycle: stem cutting sprouting and canopy establishment. Weeding should start 3 weeks after planting (WAP) and should be repeated as often as necessary until the canopy closes. Weed competition during the first 2 months can reduce yield by 50%. Weeding after 4 months will not necessarily increase yield and late weed infestations occurring before harvest appear to have little impact on yield, though this can disturb the harvest and lower the quality of the stakes of the future crop.

Weeding requires between 20 and 200 man-days/ha, making it one of the highest costs. Use of bullocks and pre-emergence herbicides, combined with intercropping, mulching or planting in the dry season, may all reduce weeding costs. No herbicide has been developed especially for cassava, but the substituted ureas (diuron, fluometuron and linuron) are suitable and are moderately selective for the control of broadleaf weeds. Gramoxone™ and Paraquat™ (0.5 kg/ha of active ingredient (a.i.)) are commonly used between rows.

Diuron has been shown to be effective at 1.6 kg of a.i./ha, atrazine at 2 kg a.i./ha and fluometuron at 2 kg a.i./ha. For grasses, highly selective herbicides such as alachlor, butachlor and glyphosate (1 kg a.i./ha) are recommended, while oxyfluorfen can control both broadleaf weeds and grasses. Spraying can be carried out immediately after planting, within 4 days and before sprouting. In Thailand, the best results are obtained with pre-emergence application of metolachlor (1.56 kg a.i./ha) with or without post-emergence spraying of Paraquat™ (0.5 kg a.i./ha), with glyphosate (4–4 l/ha) as a cost-efficient alternative. If the treatment cannot be done at this very early stage, then protective shields must be used to avoid contact with shoots because, even with small amounts of glyphosate, the damage on young leaves can be serious. Glyphosate is, therefore, recommended once the canopy has developed and the lower leaves have disappeared. Spray hoods can be used with knapsack sprayers to protect the plants (Hauser and Ekeleme, 2017). No transgenic varieties of cassava with herbicide tolerance are available yet (Zhang *et al.*, 2017).

The more vigorous and early-branching cultivars are often preferred by farmers because they tend to develop a canopy rapidly and higher densities will also contribute to early formation of cover. However, early growth vigour might be the first criterion and some experiments have shown that non-branching but vigorous erect types can out-yield low-branching types in cases of early weed infestation. Canopy density and internode length seem to be more important than branching.

Fallow management is important and plant cover crops such as *Mucuna* (60 × 40 cm, two seeds per hill), *Crotalaria* (drill at row spacing at 60 cm) and *Calopogonium* (drill at row spacing at 30 cm) are very useful in degraded and weed-infested fields for one season, followed by cassava (Leihner and Lopez, 1988; Leihner, 2002). Aggressive legume species such as *Mucuna pruriens* are efficient in controlling the weed population (especially *Cyperus rotundus*) and to reduce its density and impact after planting with cassava. This system is now adopted in central Africa and parts of Asia (Hauser and Ekeleme, 2017). However, to be manageable, the large seeds of *Mucuna* need to be collected at the end of the fallow or they will germinate once cassava cuttings are planted and will cover the young plants. Such cover crops can be beneficial to soil fertility, if properly incorporated after slashing, but need close supervision to avoid invasion in cassava fields.

Motorized tools are increasingly used for cassava crop maintenance. The most common ones are the brush cutter with a fast rotating horizontal blade or a nylon string, and the roto-tiller with vertical rotating blades. These machines are light and efficient but represent a significant investment, and need regular maintenance and the replacement of their blades depending on weed densities and species. Both machines, however, necessitate gentle use and expertise or they will damage the crops: the brush cutter can cut the base of the stems if handled too close. The roto-tiller can damage the storage roots if its blades are penetrating the soil surface too deeply.

## FERTILIZATION AND NUTRIENT DISORDERS

Cassava cultivation on the same plot leads rapidly to nutrient depletion as a result of nutrient absorption by the plants and its removal with the harvested product, roots and stakes. Nutrient removal is higher when yields are high because, when fertility is high, the plant has a higher nutrient concentration. To prevent nutrient depletion, an application of approximately 80 kg N, 9 kg P and 50 kg K/ha is recommended when the expected yield is approximately 15 t/ha if all the stems and the leaves are to be removed from the area (Howeler and Tan, 2001). However, it has been shown in Thailand that if tops are returned to the soil after 19 years of cultivation, the yield is about 10 t/ha (twice as high as when tops are removed). With adequate fertilization, high yields of at least 20 t/ha are maintained during 19 years of continuous cropping (Howeler, 2002). It has been observed that the yield of maize planted after cassava was higher than when it followed other crops, such as cowpea. The positive effect of cassava was thought to be due to the high concentrations of N resulting from the fallen cassava leaves and from the crop residues incorporated into the soil after the harvest (Howeler, 2017a).

If crop yields are low and if other potential causes have been ruled out (e.g. pests, disease, shade, low temperatures), cassava may be suffering from nutritional deficiencies. A diagnostic can be done by combining different techniques. Visual identification of mineral deficiencies is a quick and cheap method. Many symptoms have been described with colour photos (Susan John *et al.*, 2006). Soil analysis is quite advantageous because it can detect deficiencies before planting and, if necessary, elements can be applied to correct the problem during growth. In order to do so, representative soil samples are collected and mixed together, finely ground, screened and sent to a testing laboratory. The results are then compared with published data. Table 5.1 presents the ranges corresponding to the nutritional requirements of cassava (Howeler, 2017a).

The blade of the youngest, fully expanded leaf is the most suitable sample for indicating the crop's requirements. Normally, it is the fourth or fifth leaf from the top and only the blades are analysed, not their petioles. Approximately 20 leaf samples should be collected from a single plot, 4 months after planting, when the nutrient concentrations have stabilized. The leaves should be dried as soon as possible in an oven to around 60–80°C for 24–48 h. Once ground, the dried leaves are preserved in vials until analysis. The diagnosis of nutritional disorders is done by comparing the values obtained from the laboratory to those given in Table 5.2, or with other levels presented in the literature (Howeler, 2017a). Other techniques, such as the missing element technique, can be used in pots in a greenhouse or in the field. All nutrients (i.e. N, P, K) are applied to all treatments with rates known to be non-limiting, except one nutrient which is missing in each treatment. The treatments exhibiting the poorest growth are those indicating which element is deficient.

**Table 5.1.** Levels of soil nutrients relative to cassava production.

| Soil characteristic | Very low | Low | Medium | High | Very high |
|---|---|---|---|---|---|
| pH (in soil water) | < 3.5 | 3.5–4.5 | 4.5–7 | 7–8 | > 8 |
| Organic matter (%) | < 1 | 1–2 | 2–40 | > 4 | |
| Al saturation (%) | | | < 75 | 75–85 | > 85 |
| Salinity (mS/cm) | | | < 0.5 | 0.5–1 | > 1 |
| Na saturation | | | < 2 | 2–10 | > 10 |
| P (µg/g) | < 2 | 2–4 | 4–15 | > 15 | |
| K (meq 100/g) | < 0.1 | 0.1–0.15 | 0.15–0.25 | > 0.25 | |
| Ca (meq 100/g) | < 0.25 | 0.25–1 | 1–5 | > 5 | |
| Mg (meq 100/g) | < 0.2 | 0.2–0.4 | 0.4–1 | > 1 | |
| S (µg/g) | < 20 | 20–40 | 40–70 | > 70 | |
| B (µg/g) | < 0.2 | 0.2–0.5 | 0.5–1 | 1–2 | > 2 |
| Cu (µg/g) | < 0.1 | 0.1–0.3 | 0.3–1 | 1–5 | > 5 |
| Mn (µg/g) | < 5 | 5–10 | 10–100 | 100–250 | > 250 |
| Fe (µg/g) | < 1 | 1–10 | 10–100 | > 100 | |
| Zn (µg/g) | < 0.5 | 0.5–1 | 1–5 | 5–50 | > 50 |

Source: adapted from Howeler (2002, 2017a).

**Table 5.2.** Average nutrient concentrations in youngest, fully expanded leaf blades of cassava corresponding to different nutritional states of the plants.

| Nutrient | Very deficient* | Deficient | Low | Sufficient | High | Toxic |
|---|---|---|---|---|---|---|
| N (%) | < 4 | 4.5 | 5 | 5.4 | > 5.8 | n.a. |
| P (%) | < 0.25 | 0.3 | 0.37 | 0.45 | > 0.5 | n.a. |
| K (%) | < 0.85 | 1 | 1.3 | 1.65 | 2.1 | > 2.4 |
| Ca (%) | < 0.25 | 0.35 | 0.45 | 0.65 | 0.8 | > 0.88 |
| Mg (%) | < 0.15 | 0.18 | 0.23 | 0.27 | > 0.29 | n.a. |
| S (%) | < 0.2 | 0.25 | 0.28 | 0.33 | > 0.36 | n.a. |
| B (µg/g) | < 7 | 11 | 17 | 23 | 50 | > 64 |
| Cu (µg/g) | < 1.5 | 2.5 | 5.4 | 8 | 12 | > 15 |
| Fe (µg/g) | < 100 | 105 | 115 | 130 | 170 | > 200 |
| Mn (µg/g) | < 30 | 35 | 45 | 100 | 200 | > 250 |
| Zn (µg/g) | < 25 | 28 | 34 | 36 | 90 | > 120 |

*Very deficient = < 40% maximum yield (m.y.); deficient = 40%–80% m.y.; low = 80%–90% m.y.; sufficient = 90%–100% m.y.; high = 100% m.y.; toxic = < 90% m.y. Source: adapted from Howeler (2017a).

Excess N induces an overproduction of leaves and stems and a poor root yield. It is important to apply the right amount, but also the right balance between the various nutrients. Fertilizers are best applied as a band on one or both sides of the rows. Spot placement just beside the planting site is also effective. Broadcasting the fertilizer is discouraged as the nutrients are not readily accessible to the newly planted cassava and will favour weeds rather than the crop.

N deficiency reduces plant growth and yield of roots but there are no clearly observable symptoms or chlorosis. Stunting of cassava plants can occur without remarkable changes in leaf colour. It is sometimes observed in very sandy soils with poor organic matter. To compensate for deficiency, applications should be made at planting and again 3 months later at a low rate of 50–100 kg/ha. If cassava is grown for forage production, with green tops cut every 4 months, high rates of 200–300 kg/ha N have to be applied.

P deficiency produces leaves darker in colour with the purple coloration of the petioles more pronounced, but severe deficiency can also cause yellowing and necrosis of young leaves. All P fertilizers should be applied to the soil at planting as 200–400 kg/ha of $P_2O_5$. Mycorrhizal symbiosis around the cassava roots increases significantly the plant's ability to absorb P (Howeler, 2002).

K deficiency reduces the height of the plant without causing spectacular chlorosis. Plants have leaves with narrow and fewer lobes. Cassava has high requirements for K and, in many soils where K level is low, the response to N and P fertilizers is poor (Onwueme and Charles, 1994). K should be band applied as 100–200 kg/ha of $K_2O_5$ at planting and again 3 months later.

In some cases, Mg, S, Zn, Cu, Fe, Mn and B deficiencies can produce remarkable chlorosis but can be corrected with proper fertilizer applications. Cassava is very tolerant to soil acidity and, in most growing areas, the crop does not respond to the application of lime. When responses are reported, as in India and China, they may be due to Ca deficiency rather than to the neutralizing effect of lime itself. Significant variety differences in tolerance to Fe and Zn have been observed, and a change of cultivar is often a more practical solution than correcting applications of micronutrients (Howeler, 2017a).

In Asia, it is recommended that P be applied fully at the time of planting, while N and K can be applied at 30 DAP. Alternatively, all fertilizers can be applied together at 30 DAP. In China, the highest yields are reported with application split at 30 and 90 DAP. In India, the best results are reported with application of all N and K shortly after planting; and in the Philippines there are no significant differences between different split applications occurring between planting and 60 DAP. In Latin America, no significant differences were found between the application of all three nutrients at planting and the split application of N, P and K at planting, 30 DAP and 60 DAP. In Ghana, it is recommended that 400 kg NPK (15–15–15)/ha of 40 g per plant be applied and that the application is split. The first application should occur 30 DAP (spot placement and covered) and the second at 60 DAP (spot placement but not covered). Slow-release fertilizers (lime, manures, rock phosphates) can be broadcasted and incorporated in the soil before planting, but highly soluble fertilizers should be band applied just after planting so that the young roots can absorb nutrients.

In traditional farming systems, smallholders apply animal manures to cassava with good results, but optimum rates and methods of application have

not been tested experimentally. Rates vary from 5 to 10 t/ha of pig manure in Vietnam and south China, to 9 t/ha of cattle manure in Indonesia and 4–5 t/ha of chicken manure in Colombia (Howeler, 2002). In areas of Brazil where there are large cattle populations, there is a simple system where cattle are enclosed in plots in which cassava is to be planted.

Cassava does not extract more nutrients than other crops; when only roots are removed from plots, the NPK ratio is about 2:1:4. However, the symptoms of deficiencies are difficult to observe and, consequently, farmers are often unaware that their low yields are due to these deficiencies (Howeler, 2017b). When cassava is grown continuously on the same field, K will become the most limiting nutrient. On poor soils, cassava responds well to fertilizers, with significant economic return for farmers.

In Mozambique, the roots of cultivars planted in mixed cropping systems were well colonized by arbuscular mycorrhizal fungi. The difference in colonization rates was thought to reflect differences in the fungal inoculum potential of the different soils and could explain the higher concentrations of some nutrients in the plants in some villages compared to others. The potential of these mycorrhizal fungi should be considered in efforts seeking to improve the nutrition of plants in low-input farming systems (Burns *et al*., 2012).

Soil fertility is also restored by the incorporation of legume cover crops such as *Dolichos*, *Glycine*, *Pueraria* or *Mucuna*. These organic materials should be incorporated into the soil before planting. Since most cassava farmers often live in areas where fertilizers are too expensive or not available, varieties that make better use of nutrient supply, which can produce more root DM when fertility is declining, are the most attractive alternative for farmers, if they are available (Howeler, 2017c).

## HARVESTING

Although the harvest can be spread over time, it is the most expensive operation and can represent between 30% and 50% of the total cost in any cropping system. Young roots contain a limited amount of starch, while old roots contain a high proportion of lignified and fibrous matter. It is best to harvest when the starch content of the root is at its maximum. For most cultivars, this occurs at around 10–12 months but, for early-maturing varieties, it can be as early as the 7th month. However, the gains in yield that are obtained after 10 months of growth are quite significant. If there is no special reason for an early harvest, it is wise to leave cassava in the ground for a few more months as, at this stage, the crop does not require extra care. The cassava root deteriorates rapidly, in 36–48 h, so that farmers harvest only what is needed, leaving the remaining plants to continue growing until they are wanted. This is especially true in traditional cropping systems, but also in intensive and commercial ones where lines of the field are harvested one after the other, depending on handling capacity.

Hand harvesting is the rule. A machete is used to cut off the stems approximately 20–30 cm above the ground. If the ground is sufficiently loose, a strong pull at the base of the remaining portion of the stem is sufficient to lift out the roots, and this is especially easy if the plant has been planted on ridges. If the soil is hard and compact, it might be necessary to loosen it with a tool before pulling, so the rapidity of the harvest depends on the compactness of the soil. On compact soils, a man can harvest 500 kg fresh roots/day and double this (1 t/day) on loose soils. Harvesting during the dry season is more difficult than during the wet season. This is unfortunate as many farmers involved in some form of postharvest processing prefer to sun-dry their roots during the dry season. To save labour, some farmers replant cassava while harvesting. Once the roots have been lifted, stem cuttings of the same plant are established in a hole next to it. By the time the field has been harvested, it has again been replanted, although the differences in age between the first and the last plants can vary by up to 6 months. This practice should not be encouraged as it exhausts soil fertility rapidly.

A simple tool has been invented in Thailand to ease hand harvesting. It is made of a metal plate with a cut-out V-shape, welded in a metal cylinder mounted on a stick. Farmers use the power of leverage to uplift the cassava stumps out of the ground (Aye and Howeler, 2017). This tool has been tested successfully in Ghana and it is hoped that it will be rapidly adopted (Amponsah *et al.*, 2017).

Mechanical harvesting has been tried in various countries of Asia, Africa and South America but has encountered serious difficulties, one of which being the considerable power needed for lifting. The tops that are removed can be shredded mechanically for subsequent incorporation into the soil, or kept as a source of planting material. Once the tops have been removed, the lifting has to be done within a few days or the plants will mobilize their reserves and initiate new shoots, reducing the quality of the roots. Several uplifting devices have been designed and tested. A cassava root digger is pulled by an 80-hp tractor, ensuring that the roots are brought to the soil surface. This device facilitates pulling the roots out of the soil and heaping them ready for loading in trucks. In Africa, improved cropping systems with adequate mechanization have been compared with traditional (manual) systems (Table 5.3) (Marechera and Muinga, 2017).

Transport of the roots can also be mechanized. A belt conveyer behind the lifting device transfers the roots into a trailer. Finally, the roots are separated from each other, and the parts of the peduncle or fragments of stem which are still attached are eliminated. At this stage, the roots are screened and the ones not wanted are discarded. Harvesting requires between 20 and 40 man-days/ha, with transport being the most costly operation. The efficiency of harvesting depends on the soil texture and climatic conditions, but also on the weed population and the depth and shape of the roots. The development of varieties with compact root mass will make harvesting easier.

**Table 5.3.** Comparison of inputs per hectare for manual and mechanized cassava cropping systems in Africa.

| Process | Manual | Mechanized |
|---|---|---|
| Land preparation | 30 man days (240 h) | 1 h |
| Cuttings preparation and planting | 8 man days (64 h) | 45 min |
| Weeding | 12 man days (96 h) | 30 min |
| Weeding cost (US$) | 300 (by hand) | 50 (with herbicides) |
| Harvesting | 43 man days (320 h) | 3 h |
| Cost reduction | | 60% |
| Yields | 7–9 tonnes | 30–45 tonnes |
| Income (US$) | 700–900/ha | 3000–4500 |
| Market linkages | Traditional brokers and middlemen | Linked to processors |

Source: adapted from Marechera and Muinga (2017).

Cassava leaves are high in protein, with a favourable balance of amino acids, and can be used for animal feeding after proper drying and ensiling. In Asia, numerous experiments have been conducted with pigs, poultry, and dairy and beef cattle and have shown very encouraging results. New varieties may need to be developed for this harvestable product. A combination of different techniques, plant spacing, fertilization and pruning times may allow farmers to increase the value of their harvest (leaves and roots) per hectare.

# 6

# Pests and Diseases

Cassava is attacked by numerous pests and diseases that cause significant losses, especially in South America, its area of origin. Some pathogens attack only the stakes and invade the vascular system, constituting primary sources of infection, while others attack only foliar or root tissues. The vegetative nature of cassava propagation contributes to pest build-up and dissemination among countries and continents. Because of its long growth cycle, the cassava plant is almost always present in farmers' fields or backyards, contributing to the maintenance of pathogen populations and inoculums. The present shift towards large-scale planting to satisfy demand may contribute to the emergence of new or worse pest and disease problems.

## PESTS

No fewer than 200 species have been reported to attack cassava. The pests vary greatly between the three major producing regions, indicating that severe quarantine measures should prevent the introduction of pests from the Americas to Africa, Asia and the Pacific. In Asia, none of the major American pests have become endemic and native arthropods are not causing serious crop damage (Bellotti *et al.*, 1999). Several pests endemic to the Americas (hornworms, mites, lace bugs, whiteflies and stem borers) could cause devastating losses if introduced accidentally to Africa or Asia. Some species considered to be minor pests in America could become major predators in geographical areas where they have no natural enemies (Table 6.1).

Pests damage cassava indirectly as they feed on the leaves or stems, reducing the canopy area of the plant, the leaf life and therefore its photosynthetic capacity. Arthropod pests appear to be more damaging during the dry season and do not seem to cause significant losses in humid areas with high rainfall. Because most pests prefer the younger and tender leaves, their feeding during the dry season causes the greatest yield losses. When the

**Table 6.1.** Geographical distribution of important pests of cassava.

| Pest | Species | America | Africa | Asia–Pacific |
|---|---|---|---|---|
| Mites | *Mononychellus tanajoa* | × | × | |
| | *M. mcgregori* | | | × |
| | *Tetranychus urticae* | × | | × |
| | *T. yusti* | | | × |
| | *T. marainae* | | | × |
| Mealybugs | *Phenacoccus manihoti* | × | × | × |
| | *Phenacoccus herreni* | × | | |
| Whiteflies | *Aleurotrachelus socialis* | × | | |
| | *Aleurodicus dispersus* | × | × | × |
| | *Aleurothrixus aepim* | × | | |
| | *Bemisia tabaci* | × | × | × |
| | *Bemisia afer* | × | × | |
| Hornworm | *Erinnyis ello* | × | | |
| | *Erinnyis alope* | × | | |
| Lace bugs | *Vatiga illudens* | × | | |
| | *Vatiga manihotae* | × | | |
| Burrower bugs | *Cyrtomenus bergi* | × | | |
| Thrips | *Frankliniella williamsi* | × | × | |
| | *Scirtothrips manihoti* | × | | |
| Scales | *Aonidomytilus albus* | × | × | × |
| Fruit flies | *Anastrepha pickeli* | × | | |
| | *Anastrepha manihoti* | × | | |
| Shoot flies | *Neosilba perezi* | × | | |
| | *Silba pendula* | × | | |
| Gallmidge | *Jatrophobia* (*Eudiplosis*) *brasiliensis* | × | | |
| White grubs | *Leucopholis rorida* | × | × | × |
| | *Phyllophaga* spp. | × | × | × |
| | Several others not identified | × | × | × |
| Termites | *Coptotermes* spp. | × | × | × |
| | *Heterotermes tenuis* | × | | |
| Stem borers | *Chilomina clarkei* | × | | |
| | *Coelosternus* spp. | × | | |
| | *Lagochirus* spp. | × | × | × |
| Leaf-cutter ants | *Atta* spp. | × | | |
| | *Acromyrmex* spp. | × | | |
| Root mealy bugs | *Pseudococcus mandioca* | × | | |
| | *Stictococcus vayssierei* | | × | |
| Grasshoppers | *Zonocerus elegans* | × | × | |
| | *Zonocerus variegatus* | × | × | |

Source: adapted from Bellotti *et al*. (1999); Graziosi and Wyckhuys (2017).

plant enters a wet season, it has the capacity to recover rapidly as it can produce a new leaf canopy and therefore increase its photosynthetic rate in the newly formed leaves.

## Mites

Of the 40 species reported, two are the most frequent: *Mononychellus tanajoa* and *M. mcgregori* originate in South America but are now present in Africa and Asia. *Tetranychus urticae* is present in South America and Asia (with *T. yusti* and *T. marianae*). The neotropical green mite *M. mcgregori* has been identified in Vietnam and might already be present in China and Cambodia (Graziosi and Wyckhuys, 2017). These green mites attack the growing point, feeding on young leaves and the tender portions of the stems. Infested leaves lose their normal colour, develop yellow spots and are deformed. Severe damage can stunt plant growth and induce branching. The continued use of acaricides is not feasible and control measures focus on host plant resistance and biological control. The Centro Internacional de Agricultura Tropical (CIAT) has succeeded in developing varieties with an improved level of resistance and has released them to farmers (Bellotti, 2002). Some predators, phytoseiid species from South America, have been identified. Of the 66 species collected, 13 are known to occur frequently. Phytoseiid species have been introduced in Africa and, after several massive releases, *Typhlodromalus aripo* has contributed to the biological control of the green mite (*M. tanajoa*) in Africa (Yaninecк *et al.*, 1992, 1993) with, however, non-lasting results. A fungus (*Neozygites tanajoae*) pathogenic to the cassava green mite has also been tested but it seems that the mite succeeds in avoiding this pathogen (Hountondji, 2008).

## Mealybugs

Approximately 15 species of mealybug have been reported feeding on cassava but only *Phenacoccus manihoti* and *P. herreni* are economically important. The nymphs and adults feed on the leaves, causing yellowing and malformation. *P. herreni* is found in northern South America and high populations cause serious yield losses. These populations peak during the dry season; however, the rains reduce them and permit the recovery of the crop. *P. manihoti* was introduced accidentally into Africa in the 1970s but has been biologically controlled successfully through the introduction of a parasite, the predator wasp *Apoanagyrus lopezi* from South America, wherever it was released in Africa. In Brazil, in the states of Bahia and Pernambuco where cassava was suffering from *P. herreni* attacks, this mealybug was controlled successfully by the introduction of parasites, *Acerophagus coccois*, *A. diversicornis* and *Aenasius vexans*,

the last showing a strong preference for *P. herreni* (Bellotti, 2002). The cassava mealybug, *P. manihoti*, was introduced into South-east Asia in 2012 (Parsa *et al.*, 2012; Graziosi and Wyckhuys, 2017).

## Whiteflies

The whitefly *Bemisia tabaci* is known to transmit the cassava mosaic virus (CMD) in Africa, India, Sri Lanka and South-east Asia. Whiteflies cause direct damage to cassava by feeding on the phloem of the leaves, inducing leaf chlorosis and fall, which results in a reduction in root yield. Intercropping cassava is known to control the spread and development of whitefly populations efficiently, but this technique depends on the intercropped species for success. Biological control might be feasible using a group of microhymenopteran parasites. *Encarsia hispida* seems to be the most frequent parasite observed on the whitefly *Aleurotrachelus socialis* in South America, but its real efficiency in controlling populations is not known (Evans and Castillo, 1998). The whitefly *Aleurodicus dispersus* was introduced into South-east Asia in 1987 (Graziosi and Wyckhuys, 2017).

## Lepidoptera (hornworms, stem borers, burrower bugs, lace bugs)

Attacks by the hornworm *Erinnyis ello* and the stem borer *Chilomina clarkei* are the most devastating. The hornworm (*E. ello*) has a geographical range from Paraguay to the Caribbean. The larvae feed on the leaves, leaf buds and young stems. When attacks are severe, they cause complete defoliation of the plant, but it recovers, especially if rainfall is good. Pesticides can control hornworm populations if they are detected at an early stage. Biological control is complicated by the fact that the release of predators has to be synchronized with the early stages of the hornworms, preferably the egg or the first to third larval instars. CIAT has developed a cheap, storable, biological pesticide consisting of a virus species of the family Baculoviridae. Infested larvae are collected from the field, macerated in a blender, filtered and mixed with water then sprayed on hornworm-infested fields (Bellotti, 2002).

Populations of stem borers (*C. clarkei*) are highest during the rainy season and, when more than 35% of cassava plants show stem breakage, yield losses of up to 60% can occur. Once the larvae have entered the stem, control is quite impossible, but the early larvae are more vulnerable. Several studies attempted to introduce *Bacillus thuringiensis* (*Bt*) genes through *Agrobacterium*-mediated genetic transformation into the embryonic tissues of cassava in an attempt to develop transgenic varieties resistant to *C. clarkei* but, so far, none has been released (Zhang *et al.*, 2017). The soil bacterium (*Bt*) carries a set of *cry* genes encoding insect-specific endotoxins that are efficient in combating a wide range of insects (Taylor *et al.*, 2004b).

*Cyrtomenus bergi*, the cassava burrower bug, feeds directly on the roots of the plant, causing economic losses in Costa Rica, Panama and Venezuela. The nymphs and adults feed on cassava roots by penetrating the peel using their strong stylet. Several soil pathogens (*Aspergillus*, *Fusarium* and *Pythium* spp.) then enter through the lesions and root rot develops. The rainy season greatly favours adult and nymph activity, while the dry season increases nymphal mortality. It appears that cultivars with low cyanogenic glucoside (CG) content are more susceptible and that cultivars with high CG content are resistant to *C. bergi* damage. Control is difficult and several costly pesticide applications are necessary.

In South America, a prolonged dry season is favourable to the development of lace bug (*Vatiga illudens* and *V. manihotae*) populations. Adults and nymphs feed on the lower surface of the leaves. They cause economic losses in Brazil.

### Thrips

Thrips (*Frankliniella williamsi*, *Scirtothrips manihoti*) attack cassava in South America during the dry season, and damage the growing points. The young leaves are distorted and produce deformed older leaves with yellow spots. They also cause wounds on the young stems and the internodes are shortened. When the attack is severe, the plant can be reduced to a witch's broom appearance. Some cultivars are resistant but systemic insecticides such as dimethoate (160 cc active ingredient (a.i.)/ha) give good control.

## NEMATODES

Nematodes are often responsible for indirect damage as they open the way to various bacterial or fungal infestations. The most frequently encountered belong to the genera *Meloidogyne*, *Pratylenchus*, *Helicotylenchus*, *Rotylenchulus*, *Criconemoides*, *Scutellonema* and *Xiphinema* (McSorley *et al.*, 1983; Jatala and Bridge, 1990). The lesion nematode *P. brachyurus* causes serious damage in South America. The most widely reported nematodes are the root-knot nematodes, which are found on cassava in all continents, including the Pacific Islands (Bridge, 1988). The most important species are *M. incognita* and *M. javanica*. Females live in the roots and lay their eggs while feeding on the tissues. The tissues are disorganized and galls are produced on the roots. There are remarkable differences between cultivars, ranging from resistance to susceptibility. Root yield losses have been reported in Africa. When the infestation is severe, the root system is reduced considerably and causes stunting of the plant. The most serious effect of infestation is on storability, and important postharvest losses are reported (Hillocks and Wydra, 2002). The use of less-susceptible cultivars and proper crop rotation can avoid infestations.

## BACTERIA

The cassava bacterial blight (CBB) is one of the most serious diseases affecting cassava and is caused by *Xanthomonas campestris* pv. *manihotis* (or *X. axonopodis* pv. *manihotis*). It is found on cassava and related species (*M. apii*, *M. glaziovii* and *M. palmata*). The bacterium is of South American origin and was observed in Brazil as early as 1912. It caused severe epidemics following its introduction into Africa, but the disease is minor in Asia. In the Republic of Congo, the introduction of the disease led to total loss of planting material but, after the introduction of resistant varieties, the disease was contained, though there are some indications that CBB still occurs sporadically in the rainforest zone. In West Africa, CBB is present in all producing countries and severe systemic infections cause significant losses in leaf biomass, root yield and in planting material. Most strains appear to be highly virulent (Wydra *et al.*, 2001).

The symptoms start with the presence of water-soaked angular spots and the total or partial wilting of the leaves and branches. The spots enlarge and turn brown with a circular necrotic area around them. There are gum exudates on the young stems and petioles, which are more pronounced during the rainy season. When the infection is severe, the shoots die back, giving a candlestick appearance to the plants. Various control measures have been recommended, from crop rotation to break the life cycle of the bacteria, to the burying or burning of infected plant material during the dry season. Grasshoppers are vectors of the disease and their control in fallow, around or in cassava fields, is another adequate control measure. Mixed cropping and the application of potash fertilizer are also recommended to lower the incidence of the disease. Improved varieties with resistance to CBB now exist in CIAT and the International Institute for Tropical Agriculture (IITA) and have been released to farmers. It has been observed, however, that some varieties lose their resistance over time, probably because of the development of more virulent strains.

Deoxyribonucleic acid (DNA) fingerprinting of CBB strains has shown that there are no correlations between virulence and DNA groupings, but that there are five clusters in South American grouping strains from climatic zones, while the African population is more uniform, reflecting its recent introduction. In Colombia, where CBB is severe, amplified fragment length polymorphism (AFLP) fingerprinting of 160 isolates reveals a complex population structure and confirms migratory processes in the Caribbean region. Virulence tests show that the most cultivated varieties are susceptible to the majority of isolates (Trujillo *et al.*, 2014). Great care should be taken when introducing material from South America to Africa (Verdier *et al.*, 1993). The selection of non-infected planting material is essential. Seeds are not *X. campestris*-free and this should be taken into account in the international exchange between South America and Africa, as new strains can be introduced. Seeds can be heat treated and tested for contamination.

Angular leaf spot (also called bacterial necrosis) is another bacterial disease of cassava caused by *X. campestris* pv. *cassavae*. This disease has been reported in Malawi, Uganda, Rwanda, southern Africa and Niger. The symptoms are angular leaf spots with bright yellow exudates during periods of high humidity. Bacterial necrosis can lead to the complete defoliation of the plant. The disease occurs mostly on poor soils and after heavy rains (Hillocks and Wydra, 2002).

In South America, *Erwinia carotovora* ssp. *carotovora* causes the internal rotting of stems and branches with dark lesions and necrosis of the roots. The disease is characterized by a discoloration of the woody portion of the plant. In Colombia, the spread of these bacteria appears to be due to fruit flies (*Anastrepha* spp.) and the insects make holes on the stem surface. These holes are easy to distinguish by the exuding latex where the stem has been perforated. The planting of uninfested, healthy stakes of varieties known to be resistant to fruit fly damage, and the appropriate use of insecticides, is the recommended measure.

## FUNGI

Reportedly, close to 250 species of fungi have been found infecting cassava but only a dozen or so seem to have an economic importance. They can cause damage to the leaves, stems or roots (Table 6.2).

The super-elongation disease (SED) caused by *Sphaceloma manihoticola* is one of the major diseases affecting cassava in South America and in the Caribbean. SED can cause losses of more than 80% in Colombia if susceptible varieties are used. The most effective control measure is the use of disease-free cuttings. Resistant genotypes are being selected by CIAT in the eastern savannah region of Colombia where high levels of infection allow reliable assessment (Legg and Alvarez, 2017).

The brown leaf spot caused by *Cercospora henningsii* is one of the most common diseases in cassava. This disease has a worldwide distribution and almost always occurs in plantings located in areas with high temperatures. The optimum conditions for spore production are when free water on the surface of the leaves reaches a temperature of between 25 and 32°C. The older leaves are more susceptible than the younger ones. The disease is more widespread and severe when the plants are 5 months old. This disease is characterized by angular, uniformly brown spots located on both surfaces of the leaf. As the disease advances, the leaves become yellow, dry and finally fall. If susceptible cultivars are used, cassava plants can be severely defoliated at the end of the rainy season. This defoliation, especially when it is followed by the dry season, can cause yield losses of up to 20% on individual plants. The use of resistant varieties and of wider spacing between plants to reduce humidity are simple control measures. Fungicides are not economical.

**Table 6.2.** Some of the most common fungi causing damage to cassava.

| Species | Disease name | Leaves | Stems | Roots |
|---|---|---|---|---|
| *Cercospora henningsii* | Brown leaf spot | × | | |
| *C. caribaea* | White leaf spot | × | | |
| *C. vicosae* | Diffuse leaf spot | × | | |
| *Phyllosticta* spp. | Ring leaf spot | × | | |
| *Oidium manihotis* | Ash disease | × | | |
| *Uromyces* spp. | Rust | × | × | |
| *Colletotrichum gloeosporioides* | Anthracnose | | × | |
| *Glomerella cingulata* | *Glomerella* stem rot | | × | |
| *Botryodiplodia theobromae* | *Botryodiplodia* stem rot | | × | |
| *Ophiobolus manihotis* | | | × | |
| *Phomopsis manihot* | | | × | |
| *Sphaceloma manihoticola* | Super-elongation disease | | × | |
| *Elsinoe brasiliensis* | | | × | |
| *Cochliobolus lunatus* | | | × | |
| *Phytophthora dreschleri* | *Phytophthora* root rot | | | × |
| *P. erythropseptica* | | | | × |
| *P. richardii* | | | | × |
| *P. parasitica* | | | | × |
| *Pythium schleroteichum* | | | | × |
| *Fomes lignosus* | White thread disease | | | × |
| *Sclerotium rolfsii* | *Sclerotium* root rot | | | × |
| *Armillariella mellea* | Dry root rot | | | × |
| *Fusarium monoliforme* | | | | × |
| *F. oxysporum* | | | | × |
| *F. semitectum* | | | | × |
| *Phaeolus manihotis* | | | | × |
| *Sphaerostilbe repens* | | | | × |

Source: adapted from Hillocks and Wydra (2002); Legg and Alvarez (2017).

White leaf spot is caused by *C. caribaea*, a species with worldwide distribution. This disease is commonly found in humid but cool growing areas and causes defoliation of susceptible genotypes. Sporulation occurs on the surface of the leaf lesions during humid weather and the conidia are distributed from plant to plant by rain and wind. The lesions are small, angular and yellowish brown, and the spots enlarge to reach 3–5 mm and have a purple border. The diffuse leaf spot caused by *C. vicosae* also has a worldwide distribution and is prevalent in warmer and humid areas, especially in Brazil and Colombia. The symptoms are distinct from the two previous *Cercospora* leaf spots; this species produces large and diffuse infections without definite borders, which may cover one-third of a leaf lobe. Control measures are by the use of resistant varieties.

*Phoma* (or *Phyllosticta*) spp. are associated with leaf lesions causing ring leaf spot disease. It is characterized by large brown spots visible on both

surfaces of the lamina that are circular, with a diameter of approximately 1–3 cm, and located on the edges of the lobes. The disease is quite common in Latin America but has also been reported in India and Africa. The spread of the disease seems to be favoured by temperatures below 22°C and is common during cool periods of wet weather. The disease can defoliate susceptible cultivars, cause dieback of the young shoots and sometimes kill the plant. Except for the use of resistant cultivars, no control measures are known.

Cassava anthracnose occurs worldwide and is common in the humid tropics. In Africa, it is more common in lowland rainforest than in the savannahs. It is caused by *Glomerella manihotis* but the *Colletotrichum* state (*C. gloeosporioides* f. sp. *manihotis*) is more commonly referred to. The symptoms are leaf spots of 10 mm in diameter produced at the base of the leaves, but the stems can be attacked as well, causing cankers and damaging planting material. Spore dispersal is mainly by wind and water but sap-sucking insects may contribute to the infection. IITA has identified resistant cultivars (Ikotun and Hahn, 1994). Methods for the control of anthracnose include: crop rotation and the destruction of crop debris, fallow period to reduce the inoculum build-up and clean planting material; a biological approach involving *Pseudomonas aeruginosae* has also been tested (Legg and Alvarez, 2017).

Several *Phytophthora* species are associated with cassava root rots and they often occur with some soilborne fungi such as *Pythium* or *Fusarium* spp. Root damage favours infections. The *Fusarium* species are a significant component associated with cassava root rot. Numerous and diverse species are associated with rotted cassava in Nigeria and Cameroon. The use of AFLP markers allowed the main species (*F. oxysporum* and *F. solani*) to be distinguished, but species distribution varied among countries and among locations within a country. This suggests that genotype resistant at one location may not be resistant at another. The pathogens can be spread by cuttings (Bandyopadhyay *et al.*, 2006). In wet areas next to drainage ditches, or in waterlogged soils, the losses can reach 80%. Symptoms are the dieback of terminal shoots, leading to sudden wilting of the plant. In Central Africa, most root rot disease is caused by *Fomes lignosus* but is significant only in fields cleared recently from the forest, where stumps have been left to rot. In West Africa, *Sclerotium* spp. affect old plants and the disease is identified by the white mycelium, which penetrates the root epidermis and causes necrosis and rot.

## VIRUSES

Root crop species such as cassava tend to accumulate, through successive clonal generations, various viruses in their tissues and in planting material. So far, no fewer than 29 different viruses have been isolated and characterized, and it is very likely that new ones also will be identified soon as virologists now have access to more sophisticated and accurate tools (Table 6.3). All

**Table 6.3.** Viruses affecting cassava.

| Geographic region | Virus | Taxonomic group |
|---|---|---|
| South America | Cassava common mosaic virus (CsCMV) | *Potexvirus* |
| | Cassava virus X (CsVX) | *Potexvirus* |
| | Cassava vein mosaic virus (CsVMV) | *Caulimoviridae* |
| | Cassava symptomless virus (CsSLV) | *Potexvirus* |
| | Cassava Colombian symptomless virus (CsCSLV) | *Potexvirus* |
| | Cassava Caribbean mosaic virus (CsCAMV) | *Potexvirus* |
| | Cassava American latent virus (CsALV) | *Comoviridae: Nepovirus* |
| | Cassava frogskin associated virus (CsFSaV) | *Ozyzavirus* |
| | Cassava torrado-like virus (CsTLV) | Unassigned |
| | Cassava new alphaflexivirus (CsNAV) | *Alphaflexvirus* |
| | Cassava polero-like virus (CsPLV) | Unassigned |
| Africa | African cassava mosaic virus (ACMV) | *Geminiviridae: Begomovirus* |
| | East African cassava mosaic virus (EACMV) | *Geminiviridae: Begomovirus* |
| | South African mosaic virus (SACMV) | *Geminiviridae: Begomovirus* |
| | Cassava brown streak virus (CBSV) | *Potyviridae: Ipomovirus* |
| | African cassava mosaic Burkina Faso virus (ACMBFV) | *Geminiviridae: Begomovirus* |
| | East African cassava mosaic Cameroon virus (EACMCV) | *Geminiviridae: Begomovirus* |
| | East African cassava mosaic Zanzibar virus (EACMZV) | *Geminiviridae: Begomovirus* |
| | East African cassava mosaic Kenya virus (EACMKV) | *Geminiviridae: Begomovirus* |
| | East African cassava mosaic Malawi virus (EACMAV) | *Geminiviridae: Begomovirus* |
| | Cassava mosaic Madagascar virus (CMMGV) | *Geminiviridae: Begomovirus* |
| | Cassava common mosaic virus (CCMV) | *Potexvirus* |
| | Cassava Ivorian Bacilliform virus (CIBV) | *Anulavirus* |
| | Cassava Kumi viruses (CKV) | Unassigned |
| | Cassava 'Q' virus (CQV) | Unassigned |
| Asia and the Pacific | Cassava common mosaic virus (CCMV) | *Potexvirus* |
| | Indian cassava mosaic virus (ICMV) | *Geminiviridae: Begomovirus* |
| | Sri Lankan cassava mosaic virus (SLCMV) | *Geminiviridae: Begomovirus* |
| | Cassava green mottle virus (CGMV) | *Comoviridae: Nepovirus* |

Source: adapted from Calvert and Thresh (2002); Legg and Alvarez (2017); Lozano *et al*. (2017).

Begomoviruses are transmitted by the whitefly *Bemisia tabaci*. Interestingly, none of the economically important viruses in Africa are present in South America. The whitefly (*B. tabaci*) which transmits all viruses in Africa and Asia is not impacting cassava in South America, and *B. tabaci* genotypes occurring in South America differ from those in Africa and Asia (Legg and Alvarez, 2017).

These viruses belong to different taxonomic groups and they have a localized geographic area of distribution. In Central and South America, several viruses found on cassava do not produce symptoms and deleterious effects. The three viruses causing diseases that are economically important are the cassava common mosaic virus (CsCMV), the cassava vein mosaic virus (CsVMV) and the cassava frogskin virus (CsFSaV) (Calvert and Thresh, 2002).

### Cassava common mosaic disease (CsCMD)

The symptoms are a leaf mosaic and chlorosis, which are more severe during cool periods, where yield losses up to 60% have been reported. CsCMD is most prevalent in southern Brazil and Paraguay. There are no known vectors and the primary source is infected planting material. It can be spread by mechanical transmission on knives used to prepare the planting material. The most efficient control measure is the elimination of plants showing CsCMD symptoms.

### Cassava vein mosaic disease (CVMD)

CVMD is very common in the semi-arid zone of north-eastern Brazil, although there are also reports of occurrence in other states of Brazil. When a recently planted infected stem cutting sprouts, the first five leaves exhibit vein chlorosis in a chevron pattern, or as ring spots on the lamina. Leaf deformation is common. The symptoms are more pronounced in the semi-arid areas but, except for the period just after sprouting, CVMD does not affect plant vigour. The virus spreads through a field, suggesting that there is a vector, but it has yet to be identified. The elimination of infected plants is an efficient control measure.

### Cassava frogskin disease (CFSD)

CFSD was first reported in Colombia but it is spreading, and it has also been reported in Panama and Costa Rica. In most genotypes, the leaves are symptomless. Severity depends on the age of the roots and climatic factors. Hot and dry conditions inhibit the symptoms, while cooler temperatures enhance them. The characteristic root symptoms are ridges and corky layers forming raised fissures on the surface of the root periderm. Severely infected roots do not accumulate starch. The initial dissemination of CFSD is through infected

planting material and, within a field, the vector is the whitefly *B. tuberculata*. The problem is that stems and leaves do not provide signs of infection and, to make matters worse, infected stems are thicker than those of healthy plants and tend to be selected by farmers as stakes for subsequent planting. CFSD can, however, be controlled by careful selection of stems from harvested plants with symptomless roots (Calvert and Thresh, 2002).

## Cassava mosaic disease (CMD) in Africa

CMD caused by the African cassava mosaic virus and the cassava brown streak virus disease are the two most important virus diseases in Africa. The mosaic virus causes the plant's leaves to wither, retarding root growth. The brown streak virus destroys leaf tissue and makes cassava roots corky and inedible. CMD occurs in all the growing areas of Africa, including the neighbouring islands of Capo Verde, Seychelles, Zanzibar, Madagascar, Reunion and Mauritius (Fauquet and Fargette, 1990). The disease is recognized as a major threat in many African countries. The situation can change dramatically in a timescale of only 5 years and can move from benign (less than 20% incidence) to epidemic (when CMD is spread by the whitefly vector, *B. tabaci*) and farmers experience severe losses. The symptoms of CMD are the green and yellow mosaics. Leaves affected by the green mosaic have contrasting areas of green and light green on the lamina; these symptoms are not normally associated with a decreased leaf area or yield. Leaves affected by yellow mosaic have contrasting areas of green and yellow, with a remarkably distorted lamina. CMD-resistant varieties do not express symptoms as much as susceptible varieties. IITA has released numerous resistant varieties and the seeds have been distributed widely or used in breeding programmes in many African countries. Unfortunately, in many cases, farmers continue to grow local varieties that have no resistance to CMD. The reasons for this paradoxical situation are not fully understood (Calvert and Thresh, 2002).

Some strains of the virus are more virulent than others. Symptoms also depend on climatic factors. The most efficient approach to reducing the incidence and severity of the disease is to use resistant varieties and sanitation, involving the destruction and removal of diseased plants. Cropping practices can also reduce the incidence of the disease. For example, some planting dates can avoid exposing young plants to large populations of whiteflies. Other techniques, such as intercropping with different species, are quite efficient in reducing the incidence. The use of virus-free planting material is a basic approach to the control of CMD. However, even if farmers are aware of this, it is difficult for them to distinguish uninfected plants at the time stem cuttings are prepared because the plants are often leafless following drought or pest attacks and, therefore, CMD symptoms are not apparent. The most interesting source of resistance comes from *M. glaziovii*. DNA sequencing has shown that

many landraces now cultivated in Africa have *M. glaziovii* genes and their resistance to CMD is most likely the main reason for their widespread cultivation (Bredeson *et al.*, 2016).

## Cassava mosaic disease (CMD) in India

CMD is the only disease known to be important in Asia, but it was restricted to India (mostly Kerala and Tamil Nadu) and Sri Lanka until an isolated outbreak in Cambodia in late 2015 (Wang *et al.*, 2016). The symptoms of mosaic disease reported in India are similar to those observed in Africa. The Indian isolates are serologically distinguished from the African ones and are therefore regarded as different strains. CMD in Asia is caused by two cassava mosaic begoviruses: Sri Lankan cassava mosaic virus (SLCMV) and Indian cassava mosaic virus (ICMV) (Legg and Alvarez, 2017) (Table 6.3). CMD spreads naturally in India and the vector is the whitefly *B. tabaci*. Experiments conducted in India have shown, however, that the high incidence of the disease is due to the use of infected plant material rather than by rapid spread by whiteflies. The high productivity of cassava in India is associated with the limited use of intercrops, weed control, application of fertilizers and use of irrigation whenever

**Fig. 6.1.** Upper part of a cassava plant (Trivandrum, Kerala, India) showing symptoms of Indian cassava mosaic virus (*Geminiviridae: Begomovirus*) (photo: V. Lebot).

**Fig. 6.2.** The symptoms of cassava mosaic disease in India; the leaves have contrasting areas of green and yellow mosaics, with a remarkably distorted lamina (photo: V. Lebot).

necessary. However, farmers give limited attention to the selection of healthy planting material.

The use of true seeds might be a solution. In India, two promising parents – a CMD-resistant exotic accession (MNga-1) and a local cultivar ('Ambakadan') with profuse fruit setting, seed output and male sterility – have been studied for their seed production. The hybrid progenies of these two parents reveal a higher percentage of CMD-free seedlings and first clonal progenies in the evaluation trials conducted over 2 years in two different locations. A nearly homogeneous hybrid population resistant to CMD can be obtained by systematic rogueing at seedling and first clonal stages. In the open pollinated (OP) progenies of 'Ambakadan', the CMD infection increased drastically due to secondary spread of the pathogen (Rajendran *et al.*, 2005).

## Cassava brown streak disease (CBSD)

CBSD occurs in Uganda, Tanzania, Mozambique, Kenya, Malawi, Zimbabwe and Zambia. The virus affects leaves, stems, roots and even fruits. The disease is named after the brown elongated necrotic lesions that develop on the young green tissues of affected plants. CBSD causes necrosis of the roots,

which develop characteristic constrictions. The main effect of the disease is on the quality of the root produced and not in root number or yield. Necrosis decreases the commercial value of the roots produced, which become unusable and unmarketable when damage is extensive. In most cases, farmers have to harvest prematurely before serious deterioration of the roots occurs, which naturally lowers the yield. There is evidence of natural spread between plants as clones, and plants obtained from true botanical seeds introduced from West Africa have become infected in eastern Africa. The spread is attributed to an arthropod or other vector as yet unidentified.

A new method using a combination of tissue culture, chemotherapy and thermotherapy has been developed to clean cassava plants from viral infections that cause cassava mosaic and brown streak diseases. Infected plants of resistant or tolerant varieties from East Africa were cleaned in the UK. In the first cycle of the virus-indexing procedure, 27 of the 31 varieties were cleaned and after an additional three cleaning cycles, all plants were virus-free. The virus-free tissue-cultured plants were shipped back to East Africa for distribution to farmers (Maruthi *et al.*, 2019).

## INTEGRATED PEST AND DISEASE MANAGEMENT

It is often observed that failure to adapt cultural practices can contribute to pest and disease outbreaks and more crop damage (Graziosi and Wyckhuys, 2017). Preventive measures are recommended to farmers and include:

- Use of disease-free stem cuttings.
- Use of resistant or tolerant cultivars.
- Avoidance of soils infested with soilborne pathogens and insects, or postponement of planting until the pathogen population is low.
- Use of selective pesticides or fungicides to avoid the destruction of pest enemies.
- Application of selective insecticides only when damage is severe and the plant cannot recover without the aid of the application.
- Observation of quarantine measures to avoid the dissemination of pests and viruses in areas where they do not yet occur.

Interestingly, traditional cropping systems, involving different varieties associated and intercropped with different food crop species, are presenting natural pest management control measures represented by the existing 'filters' established between cassava and various pests and diseases. Pesticide use is always minimal among smallholders as the cassava crop cycle is long and necessitates several applications to be effective. As cassava shifts to commercial planting, there may be a tendency to apply pesticides. There is potential to use biopesticides instead of chemical pesticides (e.g. the effectiveness of spraying the hornworm baculovirus), but further research is necessary to develop new biopesticides.

Cultural practices such as intercropping have been shown on many occasions and in different countries to be effective in reducing pest populations. Unfortunately, on commercial plantations where mechanization is a standard practice, farmers are often reluctant to adopt intercropping, although profuse data indicate that they should. Other measures, such as mixing different varieties, burning plant debris, proper crop rotation, changing planting dates and use of high-quality pest-free cuttings contribute to an ideal combination. The implementation of an efficient integrated pest management (IPM) system combining biological control and varietal resistance is essential for sustaining good yields (Bellotti *et al.*, 1999).

Cropping system diversification enhances and restores the resilience of local cassava cropping systems when under heavy pest and disease pressure. Intercropping can contribute to whitefly control by favouring natural enemies. It has been shown that different intercropping systems lower whitefly populations in cassava fields. In Asia, CIAT has already introduced germplasm collection varieties known to be resistant to whiteflies but they are not deployed yet in the fields (Graziosi and Wyckhuys, 2017).

In East Africa, efforts to improve yield have tended to focus on single constraints, and particularly on specific pests and diseases (control of CMD, green mites and mealybugs). However, it is thought that a new approach should be favoured, focusing on the development and on-farm participatory evaluation of a range of new technologies for IPM. These include improved germplasm, soil fertility management, early weed control, and water capture and use efficiency. Dissemination of improved varieties is a strength in any new package because the introduction of new varieties is the ideal entry point for the promotion of alternative crop management options (Fermont *et al.*, 2009).

The decision to use IPM should be based on detailed agrosystem studies and proper identification of problems, and preference should be given to those IPM components that are most appropriate under smallholding conditions. Consequently, the approach should be decided on a case-by-case basis (Hahn and Caveness, 1990).

# 7

# Postharvest Quality and Marketing

## CHEMICAL COMPOSITION

Compared to other plant food groups, cassava roots are a good source of energy, an average source of minerals and vitamins, and the poorest source of proteins. Cassava leaves provide an excellent source of calcium and a good source of proteins. The use of edible cassava leaves as a green vegetable is popular in Africa and Madagascar. The composition of the leaves is highly variable and there is a wide spread of values for moisture percentage, vitamin C and iron (Montagnac *et al.*, 2009). Cassava is, on average, the driest root crop (highest dry matter, DM) (Table 7.1). Roots and leaves are good sources of K and Mg. Leaves also have high levels of carotenoids.

Compared to other root crops, cassava varieties present on average the lowest nitrogen content (2.3% DM), lowest total minerals (2.5%) and highest starch (85.6%). There is, however, significant variation between varieties, even when these are planted on the same day and harvested on the same day from the same plot, to avoid the influence of environmental factors (Table 7.2) (Lebot *et al.*, 2013). Cassava roots have a very low protein content (N equivalent), which is of concern for people whose diet is based on cassava, especially if no complementary source – such as green leaves, beans or animal protein – is readily available. There are significant differences in the chemical composition of different cultivars of cassava grown in the same environment. There are differences in moisture, starch, energy, protein, dietary fibre and sugar between cultivars, and the characterization of these differences is a necessary prerequisite for breeding programmes (Table 7.3). There is now great interest in enhancing the nutritional value of cassava through breeding. Reports on the variability of carotene content of cassava germplasm indicate that the intensity of root colour is highly correlated with carotene concentration (Fig. 7.1). The carotene content in the fresh root varies from less than 0.77 mg/100 g dry root up to 4.69 mg/100 g dry root. The genotypes with the highest concentration in the fresh roots

**Table 7.1.** Comparison between cassava and other uncooked foods.

| | Cassava root | Sweet potato root | Yam tuber | Taro corm | Rice, polished, raw | Beans, dried | Cassava leaves |
|---|---|---|---|---|---|---|---|
| Moisture content % | 63 | 71 | 74 | 69 | 12 | 12 | 75 |
| Energy (kJ/100 g) | 610 | 460 | 414 | 490 | 1500 | 1200 | 230 |
| Protein % | 0.5 | 1.4 | 2.0 | 1.1 | 6.5 | 22 | 6 |
| Energy from protein* % | 1.5 | 5.3 | 8.5 | 3.9 | 7.2 | 31 | 44 |
| Dietary fibre % | 1.5 | 1.6 | 1.2 | 1.5 | 2.4 | 22 | 7 |
| Ca | 20 | 29 | 8 | 32 | 4 | 100 | 350 |
| Fe | 0.2 | 0.4 | 0.8 | 0.5 | 0.5 | 8 | 2.8 |
| Vitamin A (retinol equiv.) | Traces | 0.01 | 0.02 | 0.01 | 0 | 0.008 | 1.4 |
| Vitamin C (ascorbic acid) | 15 | 24 | 20 | 15 | 0 | Trace | 80 |

*An indication of the food as a source of protein is obtained by calculating the % of the total energy of the food provided by the protein. Source: adapted from Bradbury and Holloway (1988).

**Table 7.2.** Comparison of flour from 112 cassava varieties with other root and tuber crops. Compounds are in % dry matter (with minimum and maximum values).

| | Cassava | Sweet potato | Greater yam | Taro | Cocoyam |
|---|---|---|---|---|---|
| | *n = 112* | *n = 225* | *n = 219* | *n = 306* | *n = 117* |
| Nitrogen | 2.3 (1.1–5.6) | 5.7 (2.7–10.0) | 10.3 (6.3–21.1) | 4.6 (2.1–14.8) | 5.8 (3.2–10.7) |
| Minerals | 2.5 (1.2–3.5) | 3.5 (1.4–8.2) | 4.8 (2.7–8.2) | 4.2 (1.5–8.9) | 3.7 (1.4–7.1) |
| Starch | 85.6 (78.1–91.2) | 68.7 (45.0–83.8) | 77.4 (58.8–85.0) | 78.9 (55.9–89.0) | 82.2 (70.5–86.4) |
| Sugars | 4.1 (0.9–10.1) | 11.3 (1.5–28.1) | 1.8 (0.1–10.1) | 3.8 (0.2–21.8) | 0.7 (0.0–2.97) |
| Cellulose | 3.0 (1.5–7.0) | 5.2 (2.4–15.8) | 5.0 (1.1–11.8) | 3.1 (1.4–7.3) | 2.7 (1.55–6.1) |

Source: adapted from Lebot *et al*. (2013).

are not those with the highest concentration after processing. High levels of carotene can be recovered after boiling and this recovery varies greatly, depending on the genotype (Iglesias *et al*., 1997). A traditional cultivar of cassava with a lycopene content of up to 5 mg/kg has been collected in the Amazon Basin, showing that there is potential to improve cassava for such secondary metabolites. Lycopene occurs in tomato, guava, watermelon and pink grapefruit and is thought to counteract the incidence of degenerative diseases (Pires *et al*., 2007). In Africa, breeding efforts have released biofortified varieties with higher carotenoid content in the roots. In Nigeria, it is

**Table 7.3.** Composition of cassava roots and leaves.

| Composition for 100g | Roots (FW*) | Leaves (FW) |
|---|---|---|
| Food energy (kJ) | 526–561 | 209–251 |
| Dry matter (g) | 30–40 | 10–30 |
| Protein (g) | 0.3–3.5 | 1.0–10.0 |
| Lipid (g) | 0.03–0.5 | 0.2–2.9 |
| Carbohydrate (g) | 35–38 | 7.0–18 |
| Dietary fibre (g) | 0.1–3.7 | 0.5–10.0 |
| Ash (g) | 0.4–1.7 | 0.7–14.5 |
| Vitamin B1 (thiamine) (mg) | 0.03–0.28 | 0.6–0.31 |
| Vitamin B2 (riboflavin) (mg) | 0.03–0.05 | 0.21–0.74 |
| Vitamin B3 (niacin) (mg) | 0.6–1.1 | 1.3–2.8 |
| Vitamin C (ascorbic acid) (mg) | 15–50 | 60–370 |
| Vitamin A (carotenoids) (µg) | 5–35 | 8300–11800 |
| Calcium (mg) | 16–176 | 37–708 |
| Phosphorus (mg) | 6–152 | 27–211 |
| Iron (mg) | 0.27–14.0 | 0.4–8.3 |
| Potassium (g) | 0.25–0.27 | 0.35 |
| Magnesium (g) | 0.03 | 0.12 |
| Copper (ppm) | 2.0 | 3.0 |
| Zinc (ppm) | 14.0 | 71.0 |
| Sodium (ppm) | 76.0 | 51.0 |
| Manganese (ppm) | 3.0 | 72.0 |

*FW: fresh weight basis (source: adapted from Montagnac *et al*., 2009; Bechoff, 2017).

**Fig. 7.1.** A carotene-rich cassava variety presents an attractive bright orange colour after cooking. In most tropical countries, consumers prefer sweet-type orange-fleshed varieties, either for direct consumption after boiling or after processing into traditional dishes (e.g. *fufu* or *gari*) (photo: V. Lebot).

estimated that about 30% of children under 5 years are vitamin A-deficient, so these varieties represent a great hope in tackling this problem (Bechoff, 2017; Parkes and Aina, 2017).

Some health problems have been associated with cassava consumption and with the absorption of residual cyanogens in processed foods. These problems include toxicity and chronic neurological diseases, including tropical ataxic neuropathy (TAN) and Konzo. TAN is a neurological disease associated with extreme poverty and cassava-based diets, although some co-factors may be involved. Konzo disease has been reported in different countries in Africa where bitter cassava dominates the diet. Death can occur rapidly if an excessive amount of hydrogen cyanide (HCN) is ingested. Fatalities are, however, an exception because of the low levels of HCN in processed foods obtained with techniques aiming at detoxifying cassava (Dufour, 2007). The traditional products made from cassava roots can be separated in two categories: those which are not fermented and are prepared from sweet-type varieties, and those which are fermented and prepared from bitter-type varieties. The choice of the product is mostly based on the cyanogenic potential of the variety (Bechoff, 2017).

## PHYSIOLOGICAL DISORDERS IN FRESHLY STORED ROOTS

The postharvest physiological deterioration (PPD) of cassava is very fast compared to other root and tuber crops. The roots are perishable and start to deteriorate between 1 and 6 days after harvest, depending on the genotype, temperature and storage conditions. The appearance of blue spots and streaks in the xylem vessels is the first stage of deterioration and suggests that an endogenous enzymatic activity is responsible. The bluish streaks gradually become more prominent and turn black after 1 week or so. It is suggested that vascular discoloration is caused by local stress produced by high rates of water loss at damaged sites.

Ethylene is produced in the cassava root after 16–18 h of incubation (Ravi and Aked, 1996). Cultivars susceptible to postharvest deterioration produce more ethylene than resistant cultivars, so it is likely that there is a relationship between ethylene and the deterioration in cassava root tissues. Of course, PPD is enhanced by root injury. PPD resembles a wounding response with insufficient healing of the attacked sites. In fact, wound healing occurs, but is probably too slow. When healing occurs, it is able to halt physiological deterioration (Wenham, 1995).

Polyphenol oxidase (PPO), an enzyme, has been found in the cortex tissue of cassava roots undergoing vascular discoloration. PPO and peroxidase enzyme systems increase during cassava deterioration. The greatest activities of peroxidase and PPO are related to high amounts of phenolic compounds. There is a

rapid accumulation of phenolic compounds such as coumarins, catechins and flavonoids, which probably contribute directly to deterioration (Buschmann *et al.*, 2000). Hydroxycoumarin, scopoletin and its glucoside scopolin were identified during PPD, as well as trace quantities of esculetin and its glucoside esculin (Bayoumi *et al.*, 2010). PPD was found to correlate negatively with phenolics and carotenoids, and positively with anthocyanin and flavonoid content (Uarrota *et al.*, 2014).

There is a need to understand the pathways, genes and physiological mechanisms involved in PPD tolerance. There are interactions among three factors: the degree of postharvest deterioration, the respiratory rate and the weight loss of the root. Genotypes with higher respiratory rate and weight loss develop faster postharvest deterioration. Deterioration tends to decrease with plant age and vascular discoloration is stimulated by the attack of a number of pathogens. Processes that inhibit PPO can prevent vascular streaking and deterioration; these are heat treatment, cold storage, anaerobic storage and dipping the roots in solutions of antioxidants (e.g. ascorbic acid, sodium metabisulfite) (Uarrota *et al.*, 2017).

The conventional breeding of varieties having longer shelf lives is a practical approach to solving the perishability problem in cassava. The introduction of a genetic modification into its metabolism might be another approach, although more data are needed to assess its potential (Zhang *et al.*, 2017). Not much information is available on the biochemical pathways associated with cassava postharvest deterioration. The use of improved storage techniques remains the most practical approach.

## MARKETING AND QUALITY STANDARDS

Ethnic markets in the EU and the USA exhibit a relatively consistent demand for fresh roots, with slight rises occurring during some cultural and ethnic holidays. Improvements in postharvest storage and marketing of waxed roots have resulted in increased consumption, especially in US cities with Hispanic American residents. Quality and promotional programmes conducted by Caribbean companies have broadened the market for fresh and frozen cassava in the USA. The leading exporting country to the USA is Costa Rica. In the EU, demand is mostly the result of a large African population.

Fresh cassava exports are required to be of excellent quality. The roots must be mature; fleshy; not fibrous; free from major deformities; fresh in appearance; free from soil, softness and decay, cuts and bruises; and the whole roots should have a clean and intact skin. Whole roots should be not less than 20 cm in length and 5 cm in diameter at the thickest end. Varieties with brown to golden brown skin colour are preferred and white- and yellow-fleshed roots are popular. Greyish flesh colours are not acceptable. Exported cassava must meet the quarantine and phytosanitary requirements of the

importing countries. Consequently, the roots have to be free from soil, pests, disease and other foreign matter. So far, no chemical treatments are required in the USA and in the EU. There are Codex Alimentarius (FAO/WHO) quality standards for sweet and bitter-type cassava and detailed procedures to export to Europe are available (CBI, 2019).

## STORAGE METHODS

The success of storage methods depends on the condition of the cassava roots. Damaged roots deteriorate more rapidly and have a shorter postharvest life. Mechanical damage occurs during the harvesting of the roots, when they are pulled out of the ground, because of the breaking off of the root tip and bruising of the neck of the root where it is attached to the plant. Deterioration starts at such sites of physical damage. Cultivars with compact, cylindrical or conical roots with a well-developed peduncle and no longitudinal splits are better adapted to conservation techniques. Those with a short peduncle are difficult to separate from the main stem.

The simplest way of preserving cassava is in the ground until the crop is harvested, but different genotypes have different optimum ages after which there is a loss in yield or an alteration in quality. Several techniques have been described for preserving harvested roots buried in sand or in the soil for 1 or 2 months without noticeable deterioration. These involve the harvest of undamaged bunches with a portion of the main stem and the preparation of pits under shade (Ravi and Aked, 1996). In India and South-east Asia, cassava roots can also be stored in clamps built by laying down a round bed of paddy straw or dried grass approximately 1.5 m diameter and 15 cm thick. A heap of 300–500 kg fresh roots is then piled on it in a conical shape and covered with straw and a thick layer (15 cm) of soil, which is collected from around the clamp while digging the drainage ditch. These simple clamps, often built in the field, are known to preserve roots for as long as 1 month, although ventilators made of bamboo or fibres may be necessary in the hot season. These ventilators are placed through the layer of soil to allow respiration of the stored roots when temperature increases. Wire netting has to be placed around the clamps to prevent rodent attack.

Box storage, with sawdust, coconut husk or moist coir dust, is also effective for 4 weeks in suitable temperatures (approximately 22–24°C). The main cause of losses in the boxes is drying of the packing material and its limitations are the cost of the box and the extra labour required. Cassava roots can also be preserved in polyethylene film for up to 3 weeks with microbial and fungicide treatments. One limitation, however, is the high cost of polyethylene bags and fungicide. Without fungicide, and using simple woven bags, stored roots can last 7–10 days.

Cassava roots have been found to store best at 3°C, with 14% loss after 2 weeks and 23% after 4 weeks. If the roots are stored between 0°C and 2°C, an internal browning occurs. At temperatures above 4°C, roots rapidly show blue

mould infections and are rejected after only 2 weeks. If cassava roots are stored at low temperatures, they deteriorate rapidly as soon as they are shifted to room temperature. Deep-freezing in polyethylene bags or in plastic boxes is feasible and afterwards cassava roots are quite palatable, although with a spongy texture. Considerable volumes preserved in this way, peeled, pre-cut and frozen, are widely available in supermarkets in many countries.

A waxing treatment is also commonly used to extend shelf life and currently is the most common way of preserving cassava for the export niche markets of fresh roots (e.g. in the EU or the USA). Cassava roots are dipped in a 2.2% aqueous emulsion of fungicidal wax with 17% triethanolamine and 5% *O*-phenyl-phenol for 1 min and then drained, dried and stored at room temperature. This allows for an acceptable loss of 10% after 2–10 days. Roots dipped in ordinary paraffin wax for 45 s at 90–95°C can be stored for 1 month, and this is now adopted commercially. Such roots are found in EU supermarkets.

Dried cassava products are easier to store than fresh roots but there is often deterioration caused by fungi, bacteria, insects and rodents. Some insects, however, such as the larger grain borer *Prostephanus truncates*, have been introduced into Africa and are now major pests and economically significant losses are reported (Westby, 2002). Storage life can also be extended by removing surface bacteria through immersion in very hot water for varying periods of time, but recontamination must be prevented, normally by immediate aseptic packaging. This is expensive since it requires a sterile handling area fully equipped with automatic or semi-automatic handling equipment. Peeled and chopped cassava roots are also vacuum-packed in plastic bags immersed in boiling water for 2 min to destroy surface bacteria. This product is not fully sterile since water immersion at 90–95°C is not sufficient to destroy the heat-resistant spores of organisms such as *Bacillus* or *Clostridium*. Such treatment is, however, sufficient to shock spores and these can then be destroyed the following day by re-immersion in a boiling water bath. This technology has the advantage that it is very inexpensive to set up and the process can be carried out with just a plastic bag sealer, although it is more efficient with a vacuum sealer.

## TRADITIONAL PROCESSING TECHNIQUES

With the rapid spread of sweet-type cultivars, cassava is now increasingly consumed boiled directly after harvest. However, the age of the plant and environmental conditions may affect the texture and taste of boiled cassava roots. Analyses conducted in West Africa show that the sensory taste (sweet or bitter) of boiled cassava roots cannot be correlated with sugar content and cyanide potential, and hence bitterness is not a good indicator of the poisonous character of boiled cassava roots. It is also observed that rainfall before harvest reduces DM content and the mealiness of boiled roots. Pectins were suspected to be the major biochemical cause of cassava mealiness (Hongbété *et al.*, 2011).

Throughout West Africa, *fufu* is made by steaming or boiling peeled roots and pounding them into sticky dough, which is eaten with soups and sauces. In the Philippines, fresh cassava roots are squeezed and, once the juice is expelled, the pulp is made into pellets known as *landang*, or 'cassava rice'. In Vanuatu, the fresh roots are ground into a paste and steam cooked to produce *laplap*, a pudding. In many countries, however, cassava is often processed into various forms before being consumed. The various processing techniques aim at enhancing the culinary qualities of the resulting foods, but also at reducing cyanogens (Bechoff, 2017).

Cassava roots are peeled before processing. Peeling is a laborious process and mechanical peelers have been developed in Brazil, India and the Philippines. The roots are then grated and there are many different designs of graters, including metallic plates punched with nails or wooden planks pierced by nails. Some machines have been developed for grating in the starch extraction process. Once finely grated, cassava is easy to sun-dry but, depending on the location, sun-drying can be a fairly slow process and, in many countries, it goes through pressers first to extract water from the pulp. It takes, on average, 3 days during the dry season and 1 week in the wet season to sun-dry cassava properly. The growth of moulds occurs during the wet season and can lead to the development of mycotoxins, rendering the product non-marketable. In fact, fungal growth occurs not only during sun-drying but also during storage when conditions are humid. In such cases there is the possibility of mycotoxin formation and the involvement of different *Aspergillus*, *Cladosporium*, *Fusarium* and *Penicillium* species (Westby, 2002). Various simple techniques exist to improve the sun-drying process, including different sizes and shapes of cassava pieces and different pressers (hydraulic or manual) (Sanni *et al.*, 2006).

The fermentation of grated roots is important in many West African countries. Grated roots are allowed to ferment in bags for 3–5 days and this causes lactic acid fermentation and a decrease in pH to less than 4. Pre-mould fermented roots are inserted during grating as starter colonies to inoculate and activate the process. This is the case for roasted granules (*gari* in Nigeria), steamed granules (*attiéké* in Ivory Coast) and fermented pastes (*agbelima* in Ghana and *placali* in Ivory Coast). Fermentation of cassava roots can also be done under water and different products are made as wet pastes (*akpu*, *fufu*, *chikwangue*) and dried flours. Fermentation softens the roots, which are then easily broken into small pieces and sieved to remove fibres. Traditional processing and fermentation or sun-drying techniques also aim at reducing the cyanogens in the cassava products (Table 7.4).

In the case of *casabe*, the flat bread used as a dietary staple by indigenous groups in the Amazon region, the grating causes an extensive disintegration of tissues and, therefore, contact between the enzyme (linamarase) and the cyanogenic glucoside (linamarin). As the inner peel is grated with the pulp, hydrolysis is activated because the enzyme activity is higher in the peel (Dufour, 2007). For *gari*, the basis of the Nigerian diet, the roots are peeled and grated

**Table 7.4.** Efficacy of six traditional processing techniques to remove cyanogens.

| Food | Region | Processing steps | Days | Cyanogens, removed % |
|---|---|---|---|---|
| Casabe | South America | Scrape, grate, wash, separate starch, ferment, drain, cook | 3 | 97 |
| Gari | West Africa | Peel, grate, ferment, drain, toast | 4 | 93 |
| Farinha d'agua | South America | Peel, soak, grate, ferment, drain, toast | 8 | 99 |
| Bâton de manioc | Africa | Peel, chop, soak, drain, pound, wrap, boil | 5 | > 99 |
| Fermented flour | East Africa | Sun-dry, ferment, crush, sun-dry, pound, sieve | 6 | 95 |
| Sun-dried flour | Africa | Sun-dry, pound, sieve | 17 | 66 |

Source: adapted from Dufour (2007).

and the mash is allowed to ferment for several days before it is drained off and toasted. The initial grating is, once again, the most important stage in the detoxification process. In Brazil, *farinha* is made following a very similar process. *Farinha d'agua* follows a slightly different preparation process because the whole roots are first soaked in water for several days. They are then grated, mashed and allowed to ferment for several days. *Bâton de manioc* is a fermented and cooked paste served with soups and stews in central Africa. The roots are first peeled, chopped, soaked in water for 2 days, drained off, pounded and then ground into a fine paste before being wrapped in leaves (*Megaraphrynium macrostachyum* or *Marantaceae* species) and boiled (Bechoff, 2017). The final cooking is important in removing the cyanogens.

Fermented flours are produced following a lengthy process where the peeled roots are sun-dried for 3 days, piled in heaps and covered for several days, scraped to remove any moulds, crushed, sun-dried again for 3 days, pounded and finally sieved into flour. The first sun-drying phase is a sort of curing serving to inhibit bacterial growth, while the heap phase extends the time for enzymatic degradation. The efficiency of the final sun-drying is important in removing residual volatile cyanogens (Dufour, 2007).

The roots, stems and leaves of cassava are used for animal feed. Roots have a low amylose content compared to other starchy foods and the high energy value of cassava makes it a very attractive ingredient in animal feed. Fresh cassava roots are sometimes fed raw or boiled to cattle but, depending on the variety and on the cyanogen concentration, feeding fresh roots may cause toxicity. The low protein content is, of course, a disadvantage and necessitates additives to balance a cassava-based diet. The aerial parts of the plants, on the other hand, have a high protein content (as high as 17% DM) and the green

foliage can be pruned after only 4 months and every 60 days to yield up to 4 t/ha/year of crude protein (Balagopalan, 2002). Pigs are very often fed fresh leaves, but farmers are sometimes reluctant to feed ruminants with cassava leaves because of the possible toxic effects and limited knowledge of the high protein content of the leaves. Cassava silage is made after chopping the plant into smaller pieces with mechanical choppers. One problem is the release of considerable volumes of silage effluents containing essential nutrients. Silage can be prepared in pits near animal sheds and silage made of grass mixed with cassava can be stored for off-season use.

## INDUSTRIAL PROCESSING

Small-scale processing includes: peeling, grating, starch extraction, fermentation, de-watering, frying, pounding, drying, grinding, milling and sieving. For all these operations, a wide range of relevant equipment exists in Nigeria (Sanni *et al.*, 2006) and elsewhere. In South-east Asia, fresh roots are sliced into chips with mechanical choppers and sun-dried for 2–3 days. The chips are spread (4–6 kg/m$^2$) on a cement floor and turned 4–5 times a day with rakes. Drying takes approximately 2–3 days. Before rain arrives, chips are piled up and covered with plastic sheets. The final moisture content is around 14% (2.4–2.5 kg of fresh roots can give 1 kg of chips). Cassava chips are used as substitute for broken rice or maize in animal feed. For the starch industry, the moisture content of the dried chips has to be reduced to 14% maximum. The standard specifications are 65% minimum for starch, 5% maximum for raw fibre and 3% maximum for sand or dust. The dried chips can be preheated with steam, passed through a die (7–8 mm) when they are still soft and warm and are then cooled down to harden into pellets. These dust-free, hard pellets are produced with industrial machines. The pellets are easier to transport and conserve due to volume reduction and density increase.

Several organisms and techniques can increase the protein content of cassava products using solid-state fermentation involving the fungus *Trichoderma pseudokoningii*. An increase in protein content, from 1.3 g/100 g initially to 14.3 g/100 g after the enrichment process, was observed using cassava flour as the solid ingredient (Balagopalan, 2002).

The constraints being faced by cassava processors are the relatively high cost of the roots, appropriate and affordable equipment, poor product qualities, the absence of producer and processor organizations and high energy costs.

Industrial processing aims mostly at extracting cassava starch. Starch represents between 70% and 85% of the root DM and is easily extractable because cassava roots contain low levels of fat and protein. The starch grains are oval with a flat surface on one side and measure between 5 and 40 μm. Glucose is the only monosaccharide in cassava starch and its amylose content ranges from 13% to 24% (Richard *et al.*, 1991). On average, it takes 4.4 kg of fresh

roots (with 25% starch content) to produce about 1 kg of starch. The peels of the roots can be used as fertilizer or as a substrate for mushroom production (Piyachomkwan and Wanlapatit, 2017).

After rasping, the fresh pulp is pumped on to a series of flat vibrating screens of decreasing mesh size, which retain the coarse fibres and the fine particles. The process is conducted under a gentle flow of water to separate starch from the fibres. The starchy milk is channelled for sedimentation and then filtered again through a fine nylon or stainless steel screen. A cake is then obtained containing 30%–40% moisture, cut into pieces and sun-dried. In larger factories, high-pressure water jets, combined with the abrasion of the roots against drum walls and against each other, remove most of the skin. Static mill screens working in series sprayed with the slurried pulp then cause the smaller starch granules to pass through slots, while the fibres are separated in a continuous flow. Mechanical dehydration is then done either by vacuum filters or centrifuges, and hot air drying is carried out at 150°C, where dried starch granules are separated and transformed into a fine powder of 10%–13% moisture (Balagopalan, 2002).

Cassava starch is used as thickener, binder, texturizer, stabilizer, filler, sweetener and fat replacer by the industry in canned foods, frozen foods, dry mixes, baked goods, snacks, dressings, soups, sauces, noodles and even infant food. Cassava gum is ideal for food packaging because of its excellent cohesiveness and bland flavour. It is obtained by cooking starch in a stainless steel container until it gelatinizes. The paste should flow freely in a continuous stream and, on cooling, become more viscous. Although gums can be prepared without additives, various chemicals are added to increase viscosity. These gums are very useful for laminated papers, wallpapers and pasting labels. Dextrin can be used at a higher concentration than starch as a gum for envelopes, bottle labels, postage stamps and cardboard boxes, and it dries faster.

Cassava starch can be converted into glucose by acid hydrolysis or enzyme hydrolysis. Glucose syrup is used in the confectionery, pharmaceutical and food industries. The conversion of glucose to fructose can be done by alkali or by the enzyme, glucoisomerase. Fructose syrup is gaining in importance; fructose is twice as sweet as sucrose and four times sweeter than glucose. Maltose, a reducing sugar, can be obtained commercially from cassava starch by enzyme treatments using β-amylase or fungal α-amylase. Maltodextrins, produced by the action of α-amylase on starch, are partially hydrolysed starch and are approved as a food ingredient (Balagopalan *et al.*, 1988).

Modified starches are also produced to improve their functionality for industrial applications so they can be cooked properly at higher concentrations. Their viscosity is reduced so that their dispersion is improved. Acid-modified starches are clear and stable and may be used for adhesives, gum tapes or bag adhesives. Oxidized starches are used in the paper industry, for wrapping cotton or synthetic textiles. Cross-linked starches, acetylated starches and

cationic starches find their application in starch paper coatings, water-resistant adhesives and coating binders (Balagopalan, 2002; Piyachomkwan and Wanlapatit, 2017).

Industrial processing of starch generates considerable waste in solid or liquid form. The brown peel of the cassava root, the periderm, can represent up to 5% of the roots, but it can be used for animal feed. The problem comes from the liquid residues resulting from the large quantities of water used during the process – the effluents – which pose problems to life in rural areas. The concentration of cyanoglucosides in the effluents is a threat to groundwater. It is therefore necessary to settle and filter the effluent through sand and charcoal to reduce pollution (Balagopalan, 2002).

Biodegradable plastic made from starch is increasingly popular among responsible consumers. The process involves mixing and blending starch with synthetic polymers and stabilizing, gelatinizing and plasticizing agents. Films can be blown that are 40% starch and are biodegradable. Cassava starch can also be incorporated into synthetic polymers to improve plastics

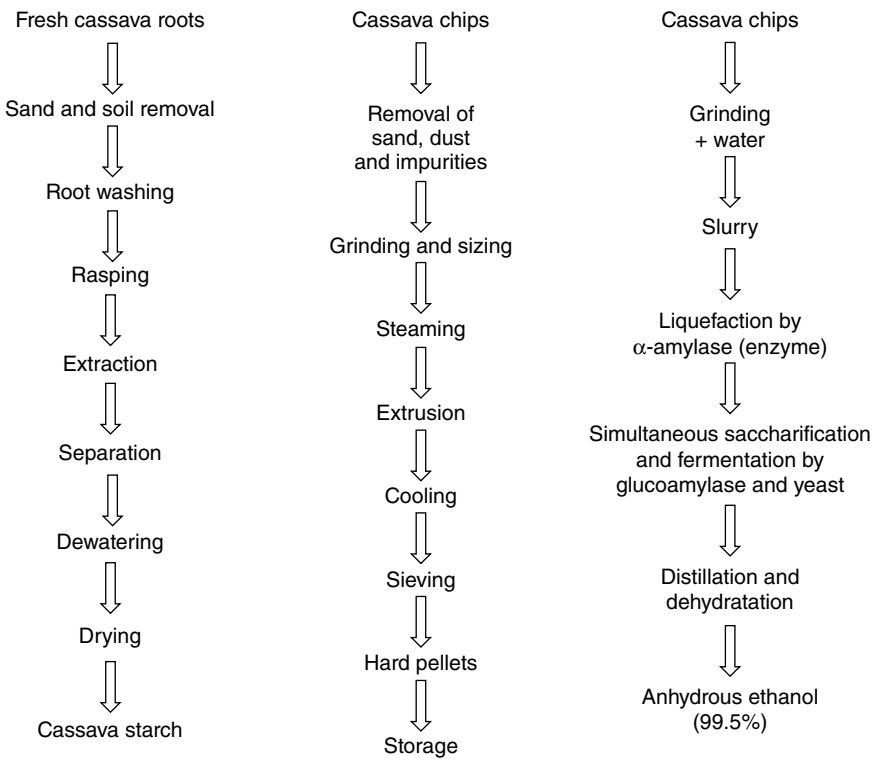


**Fig. 7.2.** Cassava starch, chips and bioethanol manufacturing processes in Thailand (Source: Piyachomkwan and Wanlapatit, 2017).

for specific uses, such as biodegradable agricultural plastic mulches and single-use disposable packaging.

In South-east Asia and China, the demand for monosodium glutamate made from cassava is increasing constantly to satisfy the growing needs of the fast-food industries. The market for cassava starch is, therefore, expected to grow to meet this demand. There is at present tremendous interest in producing ethanol and biofuel from cassava roots; but in tropical countries, cassava has to compete with sugarcane, and in temperate countries with maize. However, a simple process of making bioethanol is presented in Fig. 7.2. Chips are ground into a fine powder and mixed with water (but fresh roots can also be used). The slurry of ground cassava is then cooked at 85°C and the starch is converted to dextrin using enzymes (α-amylase). Glucose is then converted to ethanol by yeast (*Saccharomyces cerevisiae*) fermentation at 30–32°C. The simultaneous saccharification and fermentation (SSF) is now used by most factories to reduce production time and energy consumption. The average conversion rate is around 2.5 kg of dried chips per litre of pure ethanol. In a similar process, citric acid can be produced from sugar or starch substrate through a fermentation process with *Aspergillus niger*. Cassava chips are mixed with water (65%–70%) by soaking, and are sterilized by steaming. They are then inoculated with *A. niger* at 30°C and the fungus uses its own enzymes to grow and to develop the fermentation of the slurry. Citric acid is then recovered through precipitation with calcium hydroxide (Piyachomkwan and Wanlapatit, 2017).

# Section II
# Sweet Potato

Sweet potato (*Ipomoea batatas* (L.) Lam., *Convolvulaceae*, Dicotyledons) is ranked fifteenth in world crop statistics, just after cassava. Its roots are rich in carbohydrates and vitamin A and its leaves are rich in proteins. It can produce more edible energy per hectare and per day than wheat, rice or cassava. It has diverse uses ranging from consumption of fresh roots or leaves to processing into animal feed, starch, flour, noodles, natural colourants, candy and alcohol. The underground storage organs of the sweet potato plant are storage roots, as for cassava. Unlike yams, *I. batatas* does not produce tubers which correspond to subterranean stems or part of a stem that thicken and contain stored reserves. Sweet potato produces storage roots which present a cellular arrangement identical to a primary root with a radial vascular bundle.

# 8

# Origin and History

## DOMESTICATION

Sweet potato originated on the American continent. Based on the number of related species and analysis of their morphological variation, the geographical centre of origin of *I. batatas* and its wild relatives has been thought to be between the Yucatan peninsula in Mexico and the Orinoco River in Venezuela (Austin, 1987). It seems that the oldest remains of dried sweet potatoes are from the caves of the Chilca Canyon in Peru, which have been radiocarbon dated to 8000 BC (Engel, 1970; Ugent and Peterson, 1988; Woolfe, 1992; Piperno, 2011). Sweet potato roots have also been excavated from an archaeological site located in the Casma Valley of coastal Peru, dating between 1785 and 1120 BC (Ugent *et al.*, 1981). An analysis of their starch granules revealed that they were significantly smaller in size compared to the modern cultivars but that they were definitely from the species *I. batatas* (Perry, 2002) (Fig. 8.1).

Morphological analysis of the various related species indicates that *I. trifida* is the closest wild relative to the sweet potato (Austin, 1987) but *I. tabascana* is also morphologically very close (Austin and De La Puente, 1991). Several hypotheses have been formulated to discuss the botanical and geographical origins of the sweet potato. Using chromosome numbers and genome analysis, Nishiyama (1971) defined a *Batatas* group of related species composed of four American species: *I. batatas*, *I. trifida*, *I. littoralis* and *I. leucantha*. He proposed that sweet potato could have originated from the diploid species, *I. leucantha*, from which the tetraploid, *I. littoralis*, has been derived through polyploidization. The hybridization between these two species could have produced *I. trifida*, a hexaploid species generated by natural doubling of the triploid interspecific hybrid. Further cross-pollinations between these wild species, followed by selection and domestication of interesting genotypes, could have produced the hexaploid species, *I. batatas*.

This hypothesis has been challenged by a taxonomic revision of the *I. batatas* complex, where Austin (1987) observes that there are, in fact, no

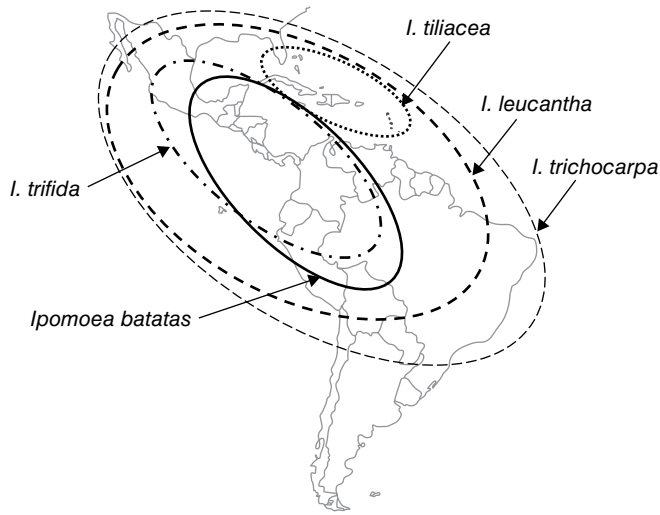


**Fig. 8.1.** The geographical centre of origin of *Ipomoea batatas* and its closest wild relatives.

fewer than 13 American *Ipomoea* species that can be assumed to be closely related to the sweet potato (Khoury *et al*., 2015). He also suggested that natural hybridization between *I. trifida* and *I. triloba* resulted in the generation of the wild ancestors of the present *I. batatas*. Autopolyploidy of *I. trifida* and the occurrence of 2*n* gametes might also have been involved in the origin of sweet potato, allowing natural interconnection between species of different ploidy levels (Shiotani, 1987). It has been shown that 2*n* pollen is produced by the diploid *I. trifida* and some genotypes of *I. batatas*, and that polyploidization through fertilization by non-reduced gametes could allow gene flow between different *Ipomoea* species (Orjeda *et al*., 1990; Freyre *et al*., 1991).

McDonald and Austin (1990) believe that true wild populations of *I. batatas* do exist and that, unlike those escaped from cultivation, they have dehiscent capsules with four seeds, and stems that lack adventitious roots at most nodes. Living populations of *I. batatas* var. *apiculata* have been described in the state of Veracruz, Mexico. This botanical variety is distinguished from *I. batatas* by indehiscent capsules. Interestingly, these authors maintain that the indehiscent character is important for seed dispersal. The capsules have been floated in water for several days without opening and sinking. Apparently, their seeds are still viable after being in salt water for 1 week. Wild tetraploid *I. batatas* exist in Mexico, Guatemala, Colombia and Ecuador (Bohac *et al*., 1993).

Molecular markers (RFLPs, RAPDs and microsatellites) have been used to clarify affinities between related species and they have confirmed the

relationship of *I. batatas* with *I. trifida* (Jarret *et al.*, 1992; Jarret and Austin, 1994; Buteler *et al.*, 1999; Roullier *et al.*, 2011). Restriction analysis of chloroplast DNA also indicates that *I. trifida* is probably one of the ancestors of *I. batatas* (Huang and Sun, 2000).

Molecular cytogenetic techniques such as fluorescence *in situ* hybridization (FISH) have been used. Among various diploid species studied, *I. trifida* appears to be the closest relative to *I. batatas*. Chromosome organization shows that hexaploid *I. batatas* is more closely related to *I. trifida* than to *I. tabascana* (Srisuwan *et al.*, 2006). This very close genetic relationship between these three species has also been revealed using the *exon* and *intron* $\beta$-amylase gene sequences, which indicate that *I. batatas* is closer to *I. trifida* than it is to *I. tabascana* and, in fact, this latter species might have derived through hybridization between the first two (*I. batatas* and *I. trifida*) (Rajapakse *et al.*, 2004). Cytogenetic investigations using FISH, however, conclude that more than one progenitor is involved in the phylogeny of the sweet potato and that the allopolyploid hypothesis supported by cytology should be retained, suggesting that the sweet potato genome is composed of three different genomes, two from closely related species and one from a distant relative (Srisuwan *et al.*, 2006).

Because the natural distribution of *I. trifida* is between Peru and Mexico, it is logical to assume that the domestication of the sweet potato occurred within this vast geographical region. The question is, therefore, where exactly the domestication process first occurred, and on which side of the Panama isthmus. Central America is a region rich in related species, with great diversity within *I. trifida* and *I. batatas*, and is therefore the favourite candidate. Molecular markers used to study the diversity existing within the CIP (Centro Internacional de la Papa) collection indicate that Central America presents the highest total number of alleles and of region-specific alleles and heterozygosity, while the Peru–Ecuador region presents the lowest values on all three counts. These results confirm previous molecular marker studies and support the hypothesis of Central America as the primary centre of diversity and the most likely centre of origin of the sweet potato (Gichuki *et al.*, 2003). The lower molecular diversity in the Peru–Ecuador region suggests distribution from the primary centre of origin, so that the Peru–Ecuador region should be considered as a secondary centre (Zhang *et al.*, 2000, 2001).

However, chloroplast haplotypes and nuclear simple sequence repeat (SSR) data favour two different domestication events in Central and South America through autopolyploidization of distinct populations of *I. trifida*. It is likely that sweet potato domestication occurred over a period of time and more than once within both regions. Gene flow occurs between cultivated varieties and wild sweet potato, or between varieties and plants escaped from cultivation and surviving in the wild. Genetic recombinations occur over a long period of time and outstanding individuals can be captured through cloning (Roullier *et al.*, 2011).

## DISCOVERY OF THE CROP BY WESTERN EXPLORERS

Columbus introduced the plant to Western Europe on his return from his first voyage to the New World in 1492. From records made by Columbus in Hispaniola, by the various Spanish explorers and missionaries in Mexico and Peru, and by the Portuguese in Brazil, it was apparent that sweet potato was cultivated widely throughout Central and South America before the first European contact.

The sweet potato has a long cultivation history in Oceania but the origin of the crop in the Pacific has long been a mystery. When Captain James Cook arrived in Tahiti and Hawaii, the sweet potato was already well established and widely cultivated. Polynesians being expert sailors and navigators, it is possible that they could have reached South America and brought back with them this remarkable plant species. Barrau (1957) was the first to propose three possible routes for the introduction of this vegetatively propagated crop to the Pacific Islands: the so-called *kumara*, *batatas* and *kamote* lines.

The hypothesis that there was a direct prehistoric transfer by Peruvian or Polynesian voyagers from South America to Polynesia has been a controversial issue. Linguistic affinities between the Quechua name for sweet potato (*kumal*) and the Polynesian word *kumara* suggest a human transfer, but it is not known if Peruvian or Polynesian voyagers were involved (Yen, 1974). Archaeological data obtained throughout the Pacific tend to consolidate the history of successive waves of settlements from the west and that there was no Peruvian input into Polynesian culture. It is therefore assumed that the distribution of the sweet potato, from South America and throughout the Pacific, was the result of Polynesian migrations and colonization of the most remote islands (Ballard *et al.*, 2005). Carbonized remains of sweet potato from Easter Island and the island of Hawaii pre-date western contact. The sweet potato could have reached Hawaii possibly by about AD 1100 or 1200, Easter Island by AD 1300, the Cook Islands around AD 1000–1100 and from there could have been distributed to New Zealand by AD 1150–1250, where it was the staple of the Maori people.

In Vanuatu, the word used in local vernacular languages is *kumala*, but it is not known if the sweet potato is a secondary Polynesian introduction on this Melanesian archipelago or if it could have been introduced with other staple foods from the Solomon Islands by early migrants.

Based on palynological and soil depositional evidence (Golson, 1977; Gorecki, 1986; Haberle, 1998), it is suggested that the sweet potato could have arrived in the New Guinea Highlands by 1200 BC. It could also, however, have reached New Guinea much later, during the earliest contacts between European explorers and the Melanesian peoples. The dense populations encountered by the Europeans during the 1920s discoveries of the Papua New Guinea (PNG) Highlands appeared to western scientists as exceptionally dependent on *I. batatas*, both for the people and as fodder for their pigs. It has

been argued that this plant was responsible for an '*Ipomoean* revolution' in this isolated region, allowing it to be densely populated (Ballard *et al.*, 2005). Deoxyribonucleic acid (DNA) analysis shows that PNG cultivars have diverged significantly from their ancestors in South America after a long, isolated evolution in a particular agroecological environment (Roullier *et al.*, 2013a).

Two other lines could be responsible for the introduction of the sweet potato into this part of the world. The *batatas* line is based on the hypothesis that Portuguese explorers could have transferred West Indian cultivars grown in Europe to Africa, India and the East Indies. The *kamote* line assumes that Spanish galleons voyaging between Acapulco and Manila spread sweet potato clones from Mexico to the Philippines while trading across the Pacific (Yen, 1974). DNA fingerprinting has been used to clarify the debate and to study genetic similarities between cultivars from Oceania and the Americas. Significant gene transfers between Mexico and Oceania were revealed. In contrast, there is little relationship between the Peru–Ecuador germplasm and that of Oceania, which suggests that this region may not be the origin of the Oceanian material. Human dispersal from Mesoamerica via the *kamote* line is, therefore, the most probable of these two alternatives (Rossel *et al.*, 2001). Nuclear data show that New Guinea landraces are principally derived from the Northern neotropical genepool (*kamote* and *batatas* lines, from the Caribbean and Central America).

The possible introduction of the sweet potato into New Guinea via the *kamote* or *batatas* lines during the 16th century could have come about through Indonesia and the present Irian Jaya. Sweet potato was already present in Java by 1610, probably introduced by the Portuguese, and in eastern Indonesia by 1633, where it was most likely introduced by the Spanish. During the 16th and 17th centuries, there were extensive trading routes between the Moluccas (now Sulawesi) and New Guinea, so it is likely that the sweet potato reached New Guinea shortly after it reached the Moluccas (Ballard *et al.*, 2005). However, chloroplast data show that South American clones (early *kumara* clones) were also introduced and recombined with existing genotypes. It has been hypothesized that sexual recombinations between the three different sources have played a predominant role in the diversification of sweet potato in New Guinea (Roullier *et al.*, 2013a). This confirms an ancient presence on the big island of New Guinea (Fig. 8.2).

Ocean current simulations also suggest that sweet potato capsules simply could have drifted away from South America to the distant islands. It is, therefore, possible that the natural dispersal of fruits could have been responsible for its introduction (Montenegro *et al.*, 2007). Even if this fourth alternative is theoretically feasible, it is difficult to imagine the various steps involved in such dispersal and its subsequent adoption by human populations. Other *Convolvulaceae* species are able to disperse naturally and to establish wild populations on the shores of oceanic islands (*I. pes-caprae* or *I. littoralis*, for example), but wild populations of *I. batatas* or *I. trifida* have never been observed by

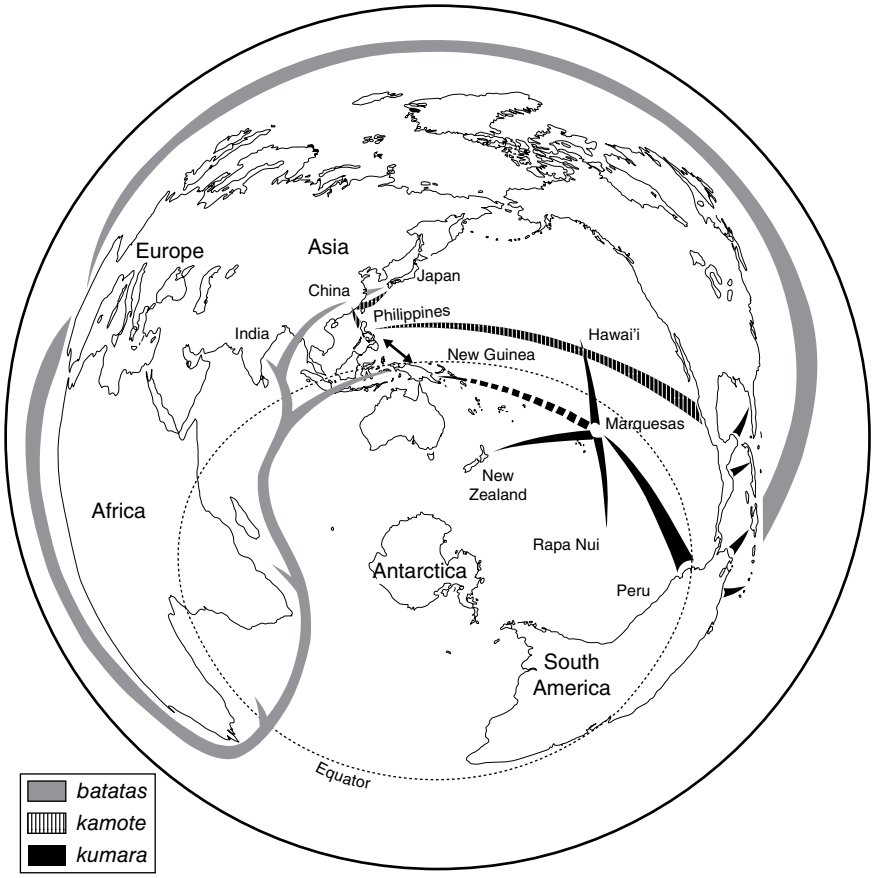


**Fig. 8.2.** The three possible routes for introduction of the sweet potato into Oceania (source: Ballard *et al.*, 2005, after Yen, 1974).

botanists in the Pacific, and pollen remains have never been identified in archaeological sites.

After AD 1500, with the exploration and colonization of Africa, Portuguese explorers transferred West Indian clones collected around Hispaniola directly to Africa, India and the East Indies in the 16th century. Spanish explorers carried the plant, probably in the form of storage roots, in easterly and westerly directions. First, it was taken from South America to Spain and to other European countries (Belgium, England, France and Holland), where growth was not satisfactory because of the low temperatures. It was then taken to the warm coastal regions of Africa, where it spread rapidly. By the mid-19th century the plant was widely grown from Zanzibar to Egypt. The Spanish explorers carried the crop from Mexico to the Philippines. From there, the Portuguese introduced the plant to India and Malaysia. Fukiense sailors took the storage

roots from the island of Luzon in the Philippines to Fukien in South China in AD 1594, but also from Fukien to Taiwan and to the Okinawa islands and Japan in AD 1674 (Yen, 1974). Sweet potato has often been a lifesaver: before the First World War, the Japanese used it when typhoons demolished their rice fields. The plant kept millions from starvation in famine-plagued China in the early 1960s.

The dissemination of the plant to North America was by explorers and traders travelling on land from Mexico to the southern USA, or by sea from the West Indies to colonies on the US east coast. The sweet potato was grown by European settlers in Virginia as early as AD 1648, in Carolina by AD 1723 and in New England by AD 1764. In the latter part of the 18th century it was cultivated throughout the southern states (Smith *et al.*, 2009).

## PRESENT GEOGRAPHICAL DISTRIBUTION

Sweet potato is now cultivated in more than 100 developing countries. It is typically a smallholder crop grown on marginal soils with limited inputs. In these countries, yields are well below the average for developed countries, so improvement is readily feasible (Table 8.1.).

The sweet potato is a dry-land crop tolerant of a wide range of edaphic and climatic conditions. It is more tolerant of cold than other tropical root and tuber crops, and so can be grown at altitudes as high as 2500 m. It has become the staple of many communities living in the highlands of Uganda, Rwanda and Burundi in East Africa, and PNG.

Asia is the world's largest producing region, with more than 80 million t of fresh roots produced annually. China alone produces more than 71 million t and accounts for 65% of sweet potato production worldwide. In China, sweet potato is a major source of animal feed and raw material for food processing industries, and new uses are generating more demands for the crop (Fig. 8.3). Sichuan and Shandong are the two largest sweet potato-producing provinces (Zhang *et al.*, 2009). Nearly half of Asian production is for animal feed, with the remainder used primarily for human consumption, either as fresh (boiled roots) or processed products (noodles).

The average annual per capita consumption of fresh roots (FAO, 2017) is estimated at 10 kg in Africa, 20 kg in Asia, 5 kg in Latin America, 7 kg in Japan and only 2 kg in the USA, but is more than 75 kg in Oceania (PNG and the Pacific Islands) (Iese *et al.*, 2018). Within these geographic regions, however, consumption can vary greatly. In Africa, for example, the annual per capita consumption is estimated at more than 160 kg in Rwanda and more than 100 kg in Burundi. African farmers produce only about 25 million t of sweet potatoes annually and most of the crop is cultivated for human consumption. African yields are low, about one-third of Asian yields, indicating huge potential for future growth.

**Table 8.1.** Major countries in the world producing sweet potato in 2017.

| Region | Country | Production (thousand t) | Area (thousand ha) | Average yield (t/ha) |
|---|---|---|---|---|
| Africa | Malawi | 5,472 | 271 | 20.1 |
| | Tanzania | 4,244 | 800 | 5.3 |
| | Nigeria | 4,013 | 1,620 | 4.2 |
| | Ethiopia | 2,008 | 246 | 8.1 |
| | Angola | 1,858 | 207 | 8.9 |
| | Uganda | 1,620 | 392 | 4.2 |
| | Madagascar | 1,141 | 139 | 8.1 |
| | Rwanda | 1,079 | 185 | 5.8 |
| | Mali | 1,021 | 59 | 17.2 |
| | Burundi | 711 | 73 | 9.8 |
| | Mozambique | 700 | 66 | 10.7 |
| | Kenya | 667 | 71 | 9.4 |
| | Egypt | 432 | 13 | 33.0 |
| Asia | China | 71,796 | 3,363 | 21.4 |
| | Indonesia | 2,023 | 113 | 17.9 |
| | India | 1,460 | 128 | 11.4 |
| | Vietnam | 1,353 | 121 | 11.1 |
| | Japan | 807 | 35.6 | 22.6 |
| | Philippines | 537 | 85 | 6.3 |
| | North Korea | 443 | 34 | 12.7 |
| | South Korea | 331 | 23 | 14.1 |
| | Bangladesh | 263 | 26 | 10.2 |
| America | USA | 1,617 | 65.5 | 25.1 |
| | Brazil | 776 | 53 | 14.3 |
| | Haiti | 630 | 105 | 6.0 |
| | Cuba | 517 | 48 | 10.8 |
| | Argentina | 343 | 24 | 14.5 |
| | Peru | 256 | 14 | 18.1 |
| | Mexico | 77 | 3.8 | 20.4 |
| Europe | Spain | 51 | 2 | 25.5 |
| | Portugal | 23 | 0.9 | 24.9 |
| | Italy | 9 | 0.4 | 21.2 |
| | Greece | 3 | 0.2 | 21.1 |

Source: adapted from FAO (2017).

In Latin America and the Caribbean, production and area planted are important in developing countries such as Cuba and Haiti. In Peru, production and yields rose spectacularly over the last decade as this country hosts CIP, the world's leading international research institute on sweet potato, and local farmers are benefiting directly from the Institute's results.

More than 65,000 ha of sweet potato are grown annually in the USA, where production is concentrated in North Carolina, Louisiana, Texas,

**Fig. 8.3.** Different varieties of sweet potato for sale in a street market in Hong Kong, China (photo: V. Lebot).

Mississippi and California. A typical sweet potato farm in the USA is approximately 150 ha and a grower needs this large area to rationalize the investment in machinery, storage and packing facilities. The crop is capital intensive and growers must invest between US$1 and 2 million in their farm to purchase machinery designed for sweet potato, the prime objective being labour cost reduction (La Bonte and Cannon, 1998; Smith *et al.*, 2009).

In Europe, sweet potato consumption and cultivation are in constant increase. Sweet potato is mostly cultivated in Spain, Portugal, Italy and Greece, but many countries in Europe are now successfully testing its production (France, Slovenia, Serbia, Hungary, Bulgaria, Macedonia, Romania and Poland). The market is driven by the growing demand for gluten-free and organically grown healthy foods. There is scope for greater diversification in the EU market, presently evaluated at €350 million per year with more than 300,000 t imported annually and demand increasing at 12% per year.

# 9

# Taxonomy and Botany

## CLASSIFICATION

The *Convolvulaceae* is a family of herbaceous and woody, often climbing species, which is well distributed throughout temperate and tropical latitudes in a wide range of habitats. Many species have long, trailing stems and are typical of rich vegetation, or open drier places, including sand dunes. The woody species are characteristic of tropical regions and, in open woodland, large trees up to 10 m high can occur. *Convolvulaceae* species have alternate and simple leaves; their flowers are bisexual with five free sepals, five fused petals and five stamens fused at the base of the corolla tube. The fruit is a dehiscent capsule. The characters of the ovary, styles and stigmas are used to differentiate up to ten tribes of genera (Heywood, 1985).

*Ipomoea* is a large genus composed of approximately 400 species. Most of them are annual and perennial herbaceous vines, with a few erect shrubs found in the tropics. This large genus is subdivided into several subgenera and sections. A number of African and Australian species are collected from the wild as emergency foods. In South-east Asia and Melanesia, *I. aquatica* is cultivated for its delicious leaf tops, eaten like spinach and rich in proteins.

## MORPHOLOGICAL DESCRIPTION OF *IPOMOEA BATATAS* (L.) LAM.

*I. batatas* is a vine-like, perennial herb, treated as an annual when cultivated. It has trailing or twining stems and containing latex in all its parts. The stems can be prostrate or ascending, often twining, thin (3–10 mm in diameter), with internodes varying from 2 to 20 cm long, glabrous or pubescent and light green to purple in colour. The long, thin stems that creep on the surface produce roots where nodes make contact with the soil. Stem length ranges from 1 to 5 m, depending on genotype. The epidermis of the stem is composed of a

thin layer of cells, and stomata and hairs are present. Under the epidermis is the cortex, composed of several layers of cells containing chlorophyll. Latex ducts are also present in the stem cortex and an abundant white latex exudes when the stems are cut. The endodermis is under the cortex. The vascular bundles have phloem on the outside and inside, and xylem in between. The centre of the stem is occupied by the pith, composed of large cells.

The leaves are highly variable, sometimes on the same plant, depending on their age. They are arranged spirally with a 2/5 phyllotaxy. They are simple and exstipulate, with petioles measuring between 5 and 30 cm long. Their laminas are mostly ovate and can be entire to deeply digitately lobed, with their base usually cordate. Their tips can be acute or obtuse and the leaves can be glabrous, or with variable pubescence. Their colour is also highly variable, from light green to deep purple, sometimes with purple stain at their base, or with green or purple veins beneath (Fig. 9.1).

The flowers are solitary or in clusters of up to 22 buds, growing out of the leaf axils. Their peduncles vary from 3 to 15 cm long. Each flower bud has five sepals, five petals, five stamens and a compound pistil. There are two bracteoles, small and lanceolate; the calyx are deeply five-lobed (1–2 cm long); and the corolla has a typical funnel shape measuring from 3 to 6 cm long and 2 to 5 cm in diameter. Colours vary from light pink to deep purple in the throat and are paler at their margins. Five stamens are attached at the base of the corolla

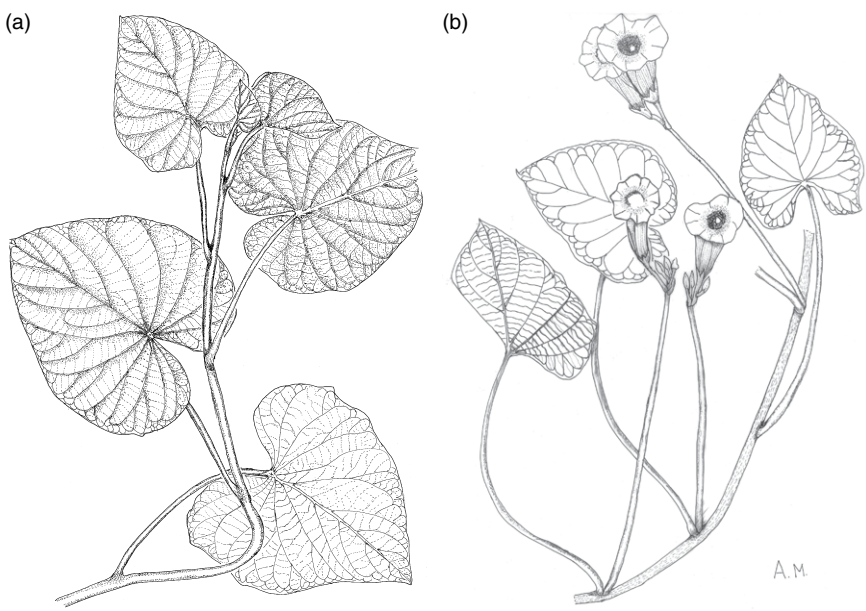


**Fig. 9.1.** a and b. Sweet potato stem, leaves and flowers.

and are of variable length. The filaments and the anthers are white, and the two-celled ovary is surrounded by an orange nectary.

Sweet potato fruits are glabrous or hirsute, dehiscent capsules measuring 5–10 mm in diameter. They contain up to four seeds, but usually only one or two are fully developed. These seeds are brown or black, glabrous, angular and measure approximately 2–3 mm long. Their testa is very hard and the cotyledons are bi-lobed. They are flat on one side and convex on the other. If their coat is scarified, either mechanically or chemically, and the seeds are subjected to favourable conditions for germination, the embryo grows rapidly. Thus, the embryo does not appear to have a dormancy period. After germination, the radicle appears first and grows downwards, developing into the primary root system. The hypocotyl brings the cotyledons above the surface of the substrate. The two cotyledons grow on opposite sides of the stem and the epicotyl develops into a primary shoot stem.

*I. batatas* produces an extensive, fibrous root system which develops from the nodes of the cutting. Five to ten storage roots are produced per plant by the thickening of adventitious roots. They develop below and at a short distance from the level of the basal stems. Cultivars vary in the colour of the skin (called the periderm) and in the colour and chemical composition of the flesh. Within the same cultivar, they vary in number per plant and in size and shape within the same plant, as well as between plants of the same clone growing next to each other in the same field. The principal tissues of the storage root are the periderm; the secondary vascular bundles underneath the periderm; and the tracheids, sieve tubes and laticifers interspersed among storage parenchyma. The structure of the storage root is complex and includes conducting tissues, parenchymatous storage cells, latex vessels, an epidermis and the outer periderm. These roots can be fusiform, globular, round or ovate, with a smooth, ridged or rough surface. The root skin colour varies from white to yellow, orange, red, purple or brown and the flesh colour may be white, yellow, orange, reddish or purple.

The root growth in diameter is due to the activity of three distinct cambia: the cork cambium, the vascular cambium and the anomalous cambium. The cork cambium produces several layers of cork cells on the outside and a layer of living cells on the inside. The vascular cambium arises from parenchyma cells and, very early in the life of the root, it forms a continuous ring producing secondary phloem on the outside and a large amount of storage parenchyma on the inside (Fig. 9.2).

Cassava has a storage root similar to a normal root, except for storage parenchyma produced by xylem tissues. In contrast, sweet potato storage root growth comes from the combined activity of primary, secondary and tertiary meristematic layers associated with xylem tissues. The sweet potato storage root, however, has some anatomical differences from a normal root: the initiation of a storage organ and the capacity to produce buds and sprouts on the root skin.

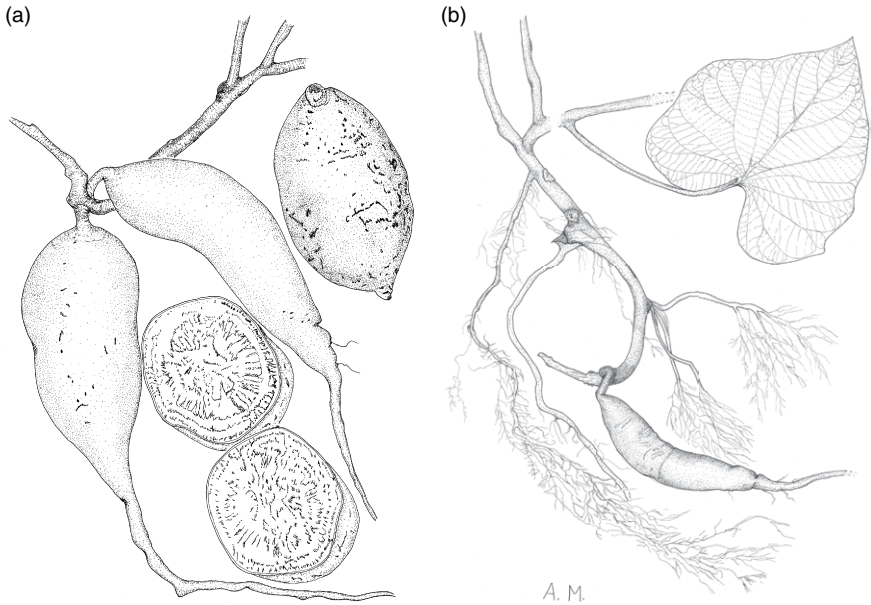


**Fig. 9.2.** a and b. Sweet potato storage roots.

## RELATED SPECIES

According to McDonald and Austin (1990) and Khoury *et al*. (2015), the taxonomy of the *Batatas* section includes 16 taxa (Table 9.1).

It is sometimes difficult to identify accurately all accessions belonging to one species because there is a continuum of variation, including sepal characters, which have been considered by Austin (1987) for the taxonomy. The sweet potato, *I. batatas*, is distinct from the other species in chromosome number, cross-compatibility and the formation of edible roots. It is assumed that a number of species showing ability to intercross with sweet potato should have a common genome, even though the ploidy level is different. It is often difficult to distinguish members of the *I. batatas* group from other species in the *Batatas* series by morphological observation (Nishiyama, 1982).

Tuberous, root-forming diploids have been found in *I. trifida* and, when they are recombined, some sweet potato varieties produce seedlings that never form tuberous roots (Kobayashi, 1984). This trait has probably arisen from hexaploid *I. trifida* by successive mutations of several genes. Several wild communities of *I. trifida* were studied *in situ* along the coast of Santa Marta, Colombia. *I. trifida* vegetatively propagates naturally, as well as by true seeds. Seed setting is not high compared to flowering number, indicating an allogamous behaviour. Tetraploid and hexaploid *I. trifida* are found in the wild and can be differentiated on the basis of their morphological characters. In general, they have larger

**Table 9.1.** The species of the *Batatas* section (adapted from Khoury *et al.*, 2015).

| Species | Ploidy | Geographical range |
|---|---|---|
| *Ipomoea batatas* (L.) Lam. | 6x | American tropics |
| *I. cordatotriloba* Dennstedt | 6x | American tropics |
| *I. cynanchifolia* Meisner | 2x | Brazil |
| *I. gracilis* R. Brown | 4x | Australia |
| *I. grandiflora* (Dammer) O'Donnell | 2x | South-east South America |
| *I. lacunosa* L. | 2x | Eastern USA |
| *I. leucantha* Jacquin | 2x | Widespread in the tropics |
| *I. littoralis* Blume | 4x | Pacific Islands, Mexico, Madagascar, Asia |
| *I. ramosissima* (Poir.) Choisy | 2x | Central and South America |
| *I. splendor-sylvae* House | 2x | American tropics |
| *I. tabascana* MacDonald & Austin | 4x | Mexico |
| *I. tenuissima* Choisy | 2x | Caribbean Islands |
| *I. tiliacea* (Willd.) Choisy | 4x | Caribbean |
| *I. cordatriloba* Denst. | 2x | North and South America |
| *I. trifida* (HB & K) G. Don. | 2x, 4x, 6x | Central America, Mexico |
| *I. triloba* L. | 2x | Caribbean and Central America |
| *I. umbraticola* House | 2x | Costa Rica, Mexico, Nicaragua |

leaves, thicker vines and fewer flowers than diploids. It is often necessary to confirm field observations with cytological counts in order to avoid doubts. Austin (1987) however, thinks that the so-called *I. trifida* hexaploids are, in fact, feral *I. batatas* (escaped from cultivation). He also believes that wild *I. trifida* tetraploids are the result of crosses between *I. trifida* diploids and *I. batatas* hexaploids.

*Ipomoea* species richness is greatest in the south-eastern USA, central Mexico, Central America and northern Andean region with about nine *Ipomoea* species present in Mexico (states of Veracruz through the Yucatan peninsula). The Mexican and Central American regions represent a possible centre of origin and primary diversity. *I. littoralis* is also found in coastal areas of Madagascar, South and South-east Asia, Australia and the Pacific (Khoury *et al.*, 2015).

Wider phylogeny issues would also have to consider another interesting group of edible *Ipomoea* species, including *I. gracilis*, which have been domesticated by the Australian aborigines in northern Australia. Although it is difficult to imagine how they could have contributed to the evolution of the sweet potato, their adaptation to drought might be interesting for breeding purposes (Yen, 1982).

## CYTOLOGY

Within the *Ipomoea* species, the base number of chromosomes is 15 and some are di-, tri-, tetra- or hexaploids with, respectively, 30, 45, 60 or 90 chromosomes.

The genomic composition of *I. batatas* has been debated extensively. Molecular work based on the tetrasomic inheritance of microsatellite markers (simple sequence repeats, SSRs) supports the hypothesis that sweet potato is an allo-auto-hexaploid with two non-homologous genomes (Zhang *et al.*, 2001). Fluorochrome banding and fluorescence *in situ* hybridization (FISH) techniques have suggested an allohexaploid composition of the sweet potato genome (Srisuwan *et al.*, 2006) and ITS (Internal Transcribed Spacer) sequences and nuclear SSR markers favour the occurrence of two autopolyploidization events (Roullier *et al.*, 2013b). By using a novel haplotyping method and phylogenetic tree analysis of homologous chromosomes, it was possible to estimate the time of two whole-genome duplication events as occurring about 0.8 and 0.5 million years ago. It is, therefore, suggested that sweet potato originated from a cross between a diploid progenitor and a tetraploid progenitor, followed by a whole-genome duplication event (Yang *et al.*, 2017).

For mitotic chromosome studies, cuttings of old stems are prepared and put in water to produce roots. The young root tips are then pre-treated with an antimitotic (8-hydroxyquinoline) for 4 h at 16°C and are fixed in 3:1 ethanol–acetic acid for 48 h. In diploid wild *Ipomoea* species, the karyotypes constitute metacentric and submetacentric chromosomes. It is quite difficult to obtain evenly spread metaphases for *I. batatas* mitosis (on root tips) and to observe the 90 chromosomes clearly and independently. Observing where the centromeres are located on the chromosomes of the sweet potato is, therefore, challenging. Multivalents appear to be low in number, indicating that the ancestral parents were not closely related, supporting the hypothesis of an allopolyploid origin. This hypothesis is also supported by the tetrasomic inheritance of $\beta$-amylase in the storage roots of sweet potato (Kumagai *et al.*, 1990).

Other cytogenetic studies have, however, suggested that the sweet potato and *I. trifida* polyploids are autopolyploids with the genome of the *I. trifida* diploid. Synthetic hexaploids (artificially induced with colchicine) and hybrids present almost complete pairings at metaphase I (meiosis), with rare univalents. The raw colchicine hexaploids are partially fertile in crosses with sweet potato cultivars. The chromosome configurations are almost complete in the synthetic hexaploids and their hybrids with sweet potato, indicating that they have the same genome structure as *I. batatas* cultivars. The predominant multivalent formation in both hexaploids is also an indication that there is gene exchange between the chromosomes of the two species (Shiotani and Kawase, 1987). Cytogenetic studies have also reported unreduced gamete formation in diploid *I. trifida*, in triploid hybrids from diploid and tetraploid crosses between the sweet potato and diploid *I. trifida*. Unreduced gametes may present practical interest in which hexaploid genotypes could be produced through crosses between triploid or tetraploid hybrids (Oracion *et al.*, 1990). These various studies confirm that *I. trifida* is the closest relative to *I. batatas* (and may be conspecific), and that it can be used in breeding programmes.

# 10

# Breeding and Genetics

The sweet potato is almost always self-incompatible and this, combined with other seed-limiting processes, has impaired the understanding of its breeding. Several physiological problems also impede seed production. The practical consequences of self-incompatibility and sterility have been recognized by different researchers in different countries (Martin, 1988; Wilson *et al.*, 1989; Mihovilovich *et al.*, 2000). It is difficult to produce seeds by self-pollination. Hand-pollination cannot produce more than four seeds, and often only one or two. Because of its polyploidy, the sweet potato is not a suitable species for Mendelian genetics, and the segregation ratios are quite complex.

Despite these practical constraints, breeding programmes were implemented in the 1970s, but mostly in temperate climates in the USA, Japan or China, and in subtropical Taiwan. Various programmes have been conducted in the tropics since the early 1980s.

## OBJECTIVES AND SELECTION CRITERIA

The sweet potato is a versatile plant offering various products: fresh food, processed starch, alcohol and foliage for animal feed. Throughout the world, farmers are looking for earliness, either for commercial production or for subsistence. However, for subsistence cropping systems, varieties should also be able to produce well during an extended harvest season. Throughout the world, breeders are attempting to improve traits sought by various markets. It is accepted that a good variety should have a high number of commercial storage roots per plant (4–6) and be of medium size (8–23 cm long) and uniformity (5–9 cm in diameter) (Firon *et al.*, 2009).

Among the numerous characteristics that breeders want to improve is the short shelf life of the sweet potato after harvest, which is a serious constraint. If this could be extended, it would improve the potential for transporting and trading sweet potatoes. In most countries where sweet potato is consumed as a staple, high dry matter (DM) content in the storage roots is an important

characteristic as it is often associated with good eating quality and long shelf life. High DM corresponds to processing efficiency, and is therefore important in countries where the crop is processed, and for starch extraction. Farmers using sweet potato foliage for animal feeding look for vigorous canopy development. The importance of pests and diseases varies significantly from one region to another but, in most cases, is a priority for breeders. Scab (*Elsinoe batatas*) is important in the humid tropics of Asia and the Pacific; viruses are important in Africa; and weevils (*Cylas* spp.) are the most serious pests on all continents. Finally, the most important environmental stresses are drought, poor soil fertility, excess moisture and cold in high altitude.

When considering regional variation in needs for new sweet potato varieties, it is important to decentralize germplasm evaluation and breeding work. The Centro Internacional de la Papa, Peru (International Potato Center, CIP) has developed a fully decentralized network for sweet potato breeding, encouraging strong collaboration with partners in national programmes in order to select locally for diseases, pests, abiotic stresses and market needs. In fact, the quarantine problems associated with the movement of germplasm are such that centralized breeding would not achieve much in terms of improved variety dissemination (Grüneberg *et al.*, 2015; Mwanga *et al.*, 2017).

## SEXUAL REPRODUCTION, INCOMPATIBILITY AND STERILITY

Each flower opens only once, just after sunrise, and starts to fade by noon. When the stamens are shorter than the pistil it is fairly easy to hand pollinate the stigmas, but when they are about the same length, or taller, it is difficult to find the stigma and hand-pollination is time consuming. Hand-pollinated flowers usually produce capsules with only two seeds and open-pollinated ones produce capsules with one to three seeds. Sweet potato is outcrossing, with cross-pollinations being done mostly by honeybees and many other insect species. In most cases, however, very few capsules and seeds are produced. This is caused by two distinct phenomena: self-incompatibility and sterility.

Self-incompatibility in sweet potato has been shown to conform to the multi-allelic sporophytic type (pollen dependent) that also exists in the *Asteraceae* and *Brassicaceae* families. Seed setting failure is often associated with pollen germination failure. The inhibition of pollen germination is therefore the physiological basis of incompatibility in sweet potato. A series of multiple alleles controls this incompatibility and these alleles act sporophytically to determine the pollen phenotype. Since the sweet potato is a hexaploid, it is assumed that the incompatibility loci have been duplicated, or even triplicated, during its evolution.

Several days after anthesis, the ovaries of pollinated flowers begin to develop. During the process, all ovules grow together up to the third day. One

or two fertilized ovules increase rapidly, whereas the growth of the others is arrested. As the good seeds continue to grow, the aborted ovules are compressed on one side of the capsule, and die. When the fruit dries, the mature seeds shrink to approximately 3 mm in diameter, about one-half of their size when green and mature. The aborted ovules dry to appear as scales of approximately 0.5–1.5 mm long. Large seeds germinate more rapidly than smaller seeds. Small seeds, however, can represent up to 50% of the total number of seeds obtained, depending on the genotypes involved.

It is likely that sterility is caused by high polyploidy. It can be triggered by accidents occurring in meiosis, resulting in defects and recombination that lead to an unbalanced gene distribution, producing embryos with a defective combination of genes that cannot function properly. It is possible that open-pollination practised over several generations may favour fertile plants that tend to flower freely. Martin and Jones (1986) have shown that flowering increased up to 300% in only six generations of open-pollinated crosses. It is thought that sweet potato is becoming more compatible with continuous breeding (Grüneberg *et al.*, 2015).

## CROSSING TECHNIQUES AND TRUE SEED PRODUCTION

Flowering intensity and seed set are controlled by genotypes, photoperiod, stress and trellising. Most sweet potato genotypes flower naturally within the tropics and it is not necessary to use grafting, girdling or day-length control, which breeders in temperate countries have to use to induce flowering during long days. Parent clones, planted in crossing blocks isolated from other flowering sweet potatoes, are open-pollinated by naturally occurring insects. Sweet potato flowers best during short days and, in tropical countries, the cool season is the best period for producing seeds. In the southern hemisphere, for example, the crossing block is planted during the first 2 weeks of April. Flowering begins 6 weeks later and continues for 3–4 months. Seeds are harvested from June to September (Lebot, 2010) (Fig. 10.1). In Taiwan, in the northern hemisphere, the best season for pollination is from the beginning of November to the middle of December, when the average daily temperature is between 20°C and 25°C, with a maximum seed set occurring when the mean daily temperature is about 23.9°C.

The vine cuttings of the parent clones are planted at 1 × 1 m, with two cuttings per planting position. Usually, ten plants of each genotype are enough, although more may be needed for genotypes with poor flowering. Usually, the climbing vines of four plants are mixed together on a pyramid-like system with four 2-m-high stakes tied together. Eventually, wires connect the pyramids to allow trellising of the vines, which promotes flowering. Staking facilitates hand-pollination and insect pollination, but such plants can be damaged easily by strong winds. It is not recommended that crossing blocks be fertilized with

**Fig. 10.1.** Sweet potato flowers are easily visited by pollinators, mostly bees, and because of self-incompatibility seeds of half-sib progenies can be produced in polycross blocks (photo: V. Lebot).

N as this promotes lush and leafy vines without flowering. Various insects and diseases can reduce flowering, especially scab (*E. batatas*) in the wet tropics.

When hand pollinating, it is necessary to ensure that the flowers are well protected from pollination by insects. The buds and flowers due to open the following morning are prevented from opening by clipping the tip of the corolla. The best time to clip flowers is during the afternoon or the evening of the day before hand-pollination. The flower from the male parent is carried to the female parent and the clip is removed gently without destroying the corolla. The petals are then spread and the anthers of the male parent are rubbed gently over the stigma of the female parent. In order to prevent pollen contamination, the corolla of the pollinated flower is tied together so that insects cannot reach the stigma. Another technique uses 2 cm-long pieces of drinking straw, which are pushed on the unopened corollas 1 day before anthesis. After hand-pollination the corolla is rolled again, and once more pushed into the straw.

For genetic studies, the female parent flowers are emasculated by hand to eliminate all possibility of pollen pollution. Success rates depend on the weather and the health of the plants used, but approximately 50% of the pollinated flowers produce two seeds. It is possible, however, to improve this rate with better nursery techniques. For example, in Japan, bi-parental crosses are made and grafted onto *I. nil* to promote flowering. Hand-pollination is conducted inside a glasshouse, with great care being taken to isolate the plants from pollinating insects. Seeds mature between 4 and 6 weeks after pollination. Each capsule is harvested by hand when it is fully brown and the pedicel has dried (Fig. 10.2). It is necessary to collect them in the crossing block every morning as mature capsules fall off easily or dehisce and release their seeds while opening. Seeds are then extracted and those that are lightweight, deformed or with insect or fungus damage are discarded. An easy way of selecting the healthy seeds is to put them in a container with water and to eliminate those that float. Once properly dried, they can be stored and remain viable for up to 20 years if the

**Fig. 10.2.** Sweet potato capsules are dehiscent and need to be harvested before they release their seeds (photo V. Lebot).

storage conditions are well controlled (18°C, 50% relative humidity) and for at least 5 years in a simple desiccator with silica gel lodged in a refrigerator.

Since sweet potato seeds have a very hard coat, they germinate slowly and irregularly. The most practical way of scarifying substantial volumes of seeds is to soak them in concentrated sulfuric acid (98% $H_2SO_4$) in a glass beaker for 20 min. The seeds are then rinsed under running water for 5–10 min. This technique gives about 95% germination success (Wilson *et al.*, 1989). It is also possible simply to soak the seeds overnight in water and this improves germination, although it will be irregular, occurring over several weeks. Immediately after scarification or soaking, the seeds are placed individually in Jiffy® pots or equivalent, and germination occurs readily. Seedlings are planted at 0.5 × 0.5 m and are ready to harvest at 10 weeks. Cuttings are then replanted for the first 'three hills trial' (Lebot, 2010) (Figs 10.3 and 10.4).

## SELECTION METHODS AND PROGRAMMES

Phenotypic recurrent selection appears to be suitable for sweet potato breeding as it permits minor and recessive genes to be expressed and selected with a progressive increase in population. With this type of mass selection, the capture of additive effects is straightforward, consisting of the selection of a number of genotypes for one or more desirable traits and their hybridization in a polycross block by honeybees. Numerous seedlings are screened for desirable traits and the best are used, with or without the best parents, in a new polycross block for a second cycle of natural hybridization. This technique results in the rapid accumulation of suitable genes. A study conducted with deoxyribonucleic acid (DNA) markers has confirmed the usefulness of a polycross breeding strategy, in spite of frequent cross-incompatibility. Moreover, the high level of genetic

**Fig. 10.3.** Sweet potato seeds before their treatment in sulfuric acid, necessary for scarification (photo: V. Lebot).

**Fig. 10.4.** Sweet potato seeds germinated in Jiffy® pots will be transplanted when they reach the three-leaves stage (photo: V. Lebot).

variation in polycross breeding lines can certainly assist in selecting elite material (Hwang *et al.*, 2002) (Fig. 10.5).

However, this simple selection method has to be complemented with efficient screening techniques and for many traits; the identification and the measurement of a particular trait is often the weakest operation (Martin, 1988). In practice, breeding lines are evaluated in a series of trials conducted in research stations and in farmers' fields. Undesirable genotypes are discarded as early as possible and the selection process concentrates on eliminating the poorest genotypes, rather than on selecting the best. It takes approximately 2 years from the crossing block until the harvest of the first clonal trial (Table 10.1). Consequently, if a crossing block is planted once a year, there are two recurrent-selection populations to be managed at the same time (Wilson, 1989; Lebot, 2010).

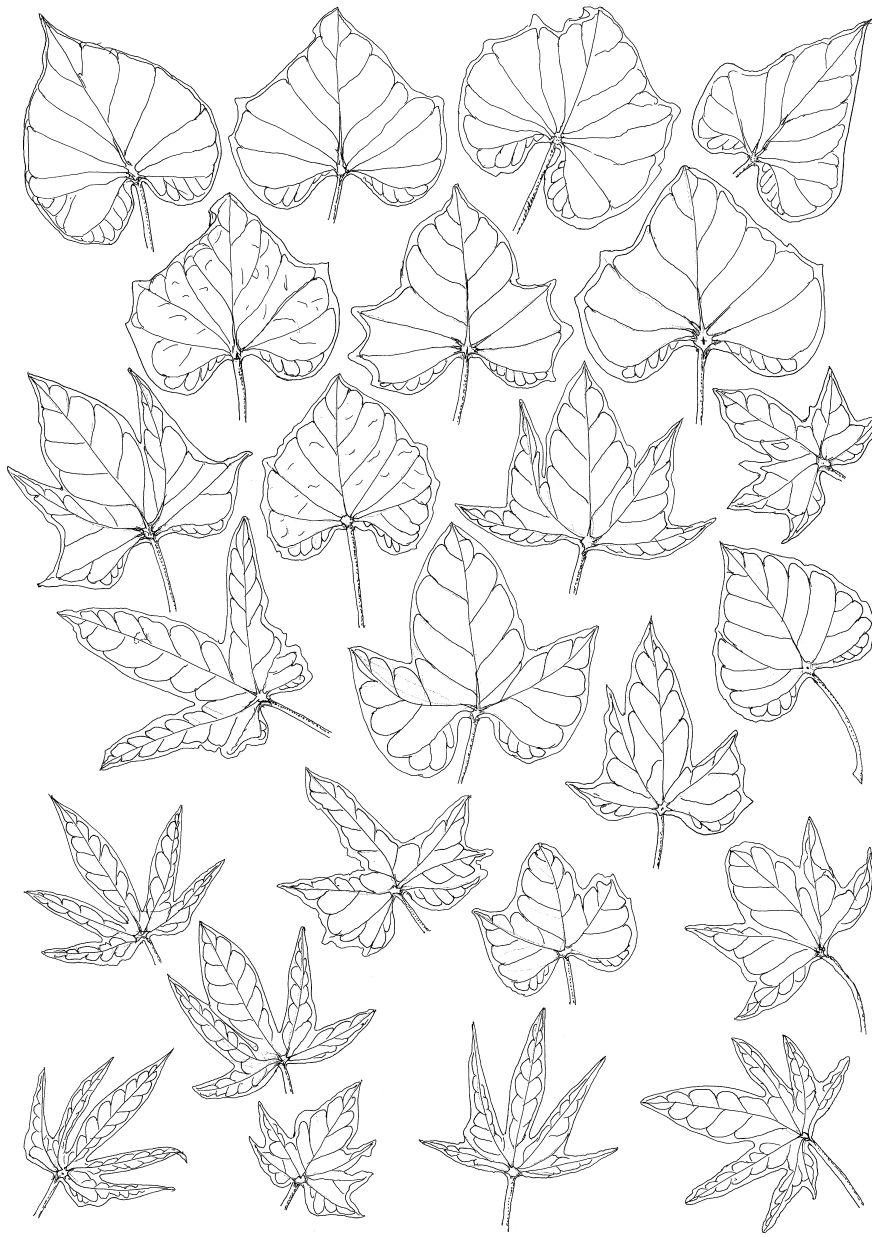

**Fig. 10.5.** Morphological variation found in polycross breeding lines (in Vanuatu).

Superior genotypes usually have an efficient photosynthetic surface and produce high yields of high quality in a relatively short time. The factors determining the photosynthetic surface are the length of the stem and the number of leaves per unit length of stem. Simple visual tools are developed to screen thousands of genotypes efficiently for such traits. Some bushy types, however, can develop with short stems an ample photosynthetic surface over a small area. Selection has to be cautious and to proceed step by step, combining important characters. The short shelf life of the sweet potato is being improved and a simple technique for assessing rates of deterioration is the measurement of weight loss during the first week of storage, a good indicator of the subsequent rates of deterioration (Rees *et al.*, 1998). Smallholders often prefer varieties with high survival rate of the cuttings after planting (often in drought conditions) and early vigour to suppress weeds. These traits are often associated with aggregative-type of canopies with short internodes and thick stems.

The chemical composition of the sweet potato root is being improved to satisfy particular needs. In Japan, *Shochu* alcohol production is one of the largest markets for processed sweet potatoes. 'Joy White', a cultivar released by the Kyushu National Agricultural Experiment Station in 1994, has a starch content of approximately 25% DM and its roots have low sugar content (approximately 2.7% DM). *Shochu* alcohol obtained from 'Joy White' is fruitier and has a lighter taste than the usual sweet potato alcohol. A new variety for use in the manufacture of starch, 'Konamizuki' (KM), has been bred and is attracting new demand among food processing manufacturers. The production of various mutants by RNAi (Ribonucleic acid interference)-mediated gene silencing has been achieved and several mutants related to starch pathways produced artificially by RNAi methods (Kitahara *et al.*, 2017).

The colorant industry is looking for natural red colour because consumers prefer natural food ingredients to artificial ones. New cultivars with high anthocyanin content and high yields are being developed. 'Ayamurasaki' for example, has elongated, fusiform and uniformly well-shaped roots with dark-purple skin and a deep purple flesh. Anthocyanins extracted from its roots are used for confectionery and in various foods as a colorant. A dry powder and a paste made from this variety are also used for breads, noodles and snack foods (Yamakawa, 1998; Yoshinaga, 1998). Anthocyanins, responsible for the bright purplish colour, are synthesized throughout the stage of storage root development, but not in a steady manner. It is possible to screen numerous genotypes but only after the ninth week of growth, when the percentage of peonidin (which is an index for anthocyanin composition in purple-fleshed sweet potato) becomes constant and when the storage roots reach a diameter over 20 mm (Yoshiniga *et al.*, 1999; Hu *et al.*, 2016).

The total carotenoid content of the flesh seems to be negatively correlated with DM and starch but positively correlated with colour, odour and taste (Tomlins *et al.*, 2012). Varieties with high DM and starch contents are low in sugars. The flavour of sweet potato is of utmost importance to consumers, but

**Table 10.1.** Characters evaluated in each trial of a sweet potato breeding programme.

| No. of genotypes in trial | Planting pattern | Characters evaluated |
|---|---|---|
| 2000 seedlings in seedling nursery | 50 × 50 cm, 1 seedling per genotype | Leaf scab score at harvest, vine length and thickness, storage root skin colour and flesh colour |
| 100 genotypes in three hills trial | 1 × 1 m, 3 plants per genotype (2 cuttings per mound) | Leaf scab score, early maturity, little-leaf score, virus score, vine length and thickness, storage root skin and flesh colour, yield (low, medium, high) and specific gravity measured in the field |
| 100 genotypes in first clonal trial | 1 × 1 m, 6 plants per genotype (2 cuttings per mound) | Leaf scab score, early maturity, little-leaf score, virus score, vine length and thickness, storage root skin and flesh colour, root shape, skin smoothness, skin cracking, number of storage roots per plant and individual size, yield (low, medium, high) and specific gravity measured in the field |
| 25 genotypes in second and third clonal trials | 1 × 1 m, 10 plants per genotype (2 cuttings per mound) | Leaf scab score, early maturity, little-leaf score, virus score, vine length and thickness, storage root skin and flesh colour, root shape, skin smoothness, skin cracking, number of storage roots per plant and individual size, marketable weight, edible weight per plant and specific gravity measured in the field |
| 7 genotypes in advanced trials | 1 × 1 m, 16 plants per genotype, 4 datum plants (2 cuttings per mound) | Same as IT (intermediate trial) plus tuber dry weight and eating quality |
| 2 genotypes in on-farm trials | Planting patterns determined by farmers. Number of replications and number of plants per replication determined by availability of cuttings. Trial is best located in the middle of the farmer's field | Average leaf scab score over the season, virus score, marketable weight and tuber numbers and eating quality, as judged by farmers and farmers' choice of which clone will be replanted |

Source: adapted from Wilson *et al*. (1989).

it is difficult to measure accurately, and this is an obstacle to reliable selection (Laurie *et al.*, 2012; Leksrisompong *et al.*, 2012). If flavour could be measured analytically, then the number of genotypes that could be screened accurately would be increased. A study conducted in Georgia, USA, indicates that it is possible to distinguish differences in aroma between genotypes using gas chromatography analysis. Compounds such as sugars and organic acids can also be quantified. The advantages are an accurate parent line and progeny selection (Kays *et al.*, 1998). However, the practicalities and economics of establishing such a system on a routine basis for breeders has yet to be demonstrated.

In Guadeloupe, French West Indies, consumers prefer the non-sweet varieties of sweet potato, and studies were conducted to obtain genotypes with low sugar content, high yield and high DM content. Eighteen introduced and local cultivars were characterized using high performance liquid chromatography (HPLC) and results showed that sucrose was the major sugar in all clones, with glucose and fructose contents being higher than maltose or raffinose (Mathurin *et al.*, 1998).

In the USA, breeders are also attempting to reduce sugar levels. The cultivar 'GA90-16', an open-pollinated seedling selection derived from a polycross nursery, has been released to farmers because of its lower levels of odour-active volatiles and endogenous sugars. In baking trials, it has a bland flavour compared to the intensely flavoured cv. 'Jewel'. However, when prepared as French fries, 'GA90-16' absorbs less fat than 'Jewel'. These are yellowish, dry tasting and devoid of the typical sweet potato flavour, while 'Jewel' French fries are, because of their high sugar content, very dark, oily and present a soft texture. (Kays *et al.*, 2001). Sugars are measured using HPLC but the protocols are cumbersome and time consuming and it is difficult to use this technique for routine, high-throughput screening of numerous hybrids.

Major compounds (starch, sugars, proteins, minerals) can be predicted routinely and accurately using near infra-red reflectance spectroscopy (NIRS), but NIRS calibrations for cellulose are not good enough (Lebot *et al.*, 2011b). This technique seems promising for breeders. On the other hand, for β-carotene, spectrophotometry overestimates the HPLC values for β-carotene content because of the presence of minor carotenoids. It is thought, however, that screening large numbers can be done using a cost-efficient spectrophotometer and that the expensive HPLC is necessary only for the accurate quantification of β-carotene (Kimura *et al.*, 2007).

Sweet potato breeding is not an expensive operation and can be achieved successfully when many crosses are conducted between parents adapted to local requirements. As a matter of fact, many landraces are hybrids appearing spontaneously in farmers' fields, and cloned for further evaluation. Consciously or not, farmers are contributing to the constant genetic improvement of the crop.

The most widespread varieties now cultivated result from conventional breeding programmes. For example, 'Xushu 18', the leading variety in China, is the result of a cross conducted in 1941 between the US-introduced 'Nancy

Hall' and the Japanese variety named 'Okinawa 100'. The next leading variety ('Nanshy 18') is also the result of a cross between the local 'Junzhuan 7' and the introduced 'America Red'. These varieties have elliptic root shape, orange flesh colour and moderate DM content (20%–26%). In Japan, the leading variety is 'Beniazuma' and it was selected from an offspring of varieties 'Kanto 85' and 'Kogeanesengan' released by the National Institute of Crop Science of Japan in 1981. It has a very sweet taste. 'Ayamurasaki' is rich in anthocyanins and DM (35%) and was released in 1995 for the colorant industry. The National Agricultural Research Institute (NARI) of Papua New Guinea has selected varieties for their tolerance to frost, drought, high yield and taste. All were produced through conventional (polycross) breeding. Finally, the American variety 'Beauregard' is a polycross selection released in 1987 by Louisiana State University (LSU) and now widely cultivated in New Zealand, Australia, Portugal, Spain and elsewhere around the world. It is sweet and low in DM but has an attractive appearance (shape and skin colour) and an orange flesh. 'Evangeline' and other new varieties with high sugars and low DM have been released by LSU to satisfy US market requirements (Carpena, 2009).

In Japan, where sweet potato breeding is ancient and well advanced, future priorities have been identified. To reduce production costs, improving seedling plant types that are suitable for transplanting, and cultivating using machinery are seen as critical. In addition, new cultivars with high direct planting suitability are expected for raw materials of starch and alcohol. To secure a stable supply it is necessary to improve storage ability. It is also planned to enhance health functionality through the improvement of eating quality and the increase in levels of anthocyanins, $\beta$-carotene and dietary fibres. The manufacturers of processed foods, *Shochu* spirits or starch are demanding improved varieties containing specific pigments or starches with new properties to meet new demands (Katayama *et al.*, 2017).

In Africa, the successful breeding programmes conducted by national agricultural research systems have focused their efforts on virus, weevil and nematode resistance; biomass; drought tolerance; DM; and, of course, farmers' and consumers' acceptability. The development of high-yielding orange flesh sweet potatoes (OFSP) is supported by the public sector, international aid projects and CIP (Grüneberg *et al.*, 2015).

Sweet potato can also be improved for its leaves, either for human consumption (as they are recognized, especially in Asian countries, as a very healthy food) or for animal feed (Islam, 2016).

## HERITABILITY OF MAJOR TRAITS

It has been determined that flesh colour, flesh oxidation, percentage dry weight, percentage crude starch, percentage crude protein, skin colour, resistance to root-knot nematode and vine length all have high heritabilities (Table 10.2).

**Table 10.2.** Narrow-sense heritability estimates for sweet potato.

| Trait | Heritability estimates (%) |
|---|---|
| Root weight | 25, 41, 44 |
| Growth cracking | 37, 51 |
| Flesh colour | 53, 66 |
| Flesh oxidation | 64 |
| Dry matter | 65 |
| Fibre | 47 |
| Skin colour | 81 |
| Sprouting | 37, 39 |
| Vine length | 60 |
| Leaf type | 59 |
| Flowers/inflorescence | 50 |
| Fusarium wilt resistance | 50, 86, 89 |
| Nematode egg mass index | 57, 69, 75 |
| Insect complex resistance | 45 |
| Flea beetle resistance | 40 |
| Weevil resistance | 84 |

Source: adapted from Jones (1986) and Martin (1988).

These heritability estimates depend on the experimental design and on the number of environments and replications, which vary among studies and experiments. They do, however, give a good idea of the improvement potential of each trait via conventional breeding.

In Bogor, Indonesia, heritability of storage roots is about 61.2% for the family and 58.6% for individual genotype response, agreeing with estimates in temperate countries, but it is not certain that this would be the case for other traits. For DM content, heritability is high enough to make rapid progress with phenotypic variation (Grüneberg *et al.*, 2015; Mwanga *et al.*, 2017).

Qualitative characters are distinguished easily one from one another (for example, storage root skin colour) and generally are controlled by only one or two sets of genes. Quantitative characters such as the shape and yield of the storage roots are indistinct and continuously grade into each other, involving many sets of genes. White flesh colour seems to be dominant over orange flesh. For such characters, progenies often resemble the parents and genetic improvement through recurrent selection is rapid. As for other root crop species, the total carotene content appears to be controlled by several genes, probably six that are additive.

Starch, along with carotene and protein, are the three essential characters in sweet potato breeding programmes for human consumption (Tomlins *et al.*, 2012; Truong *et al.*, 2014). The broad sense heritability of starch digestibility is very high and its improvement is theoretically feasible, but it necessitates facilities for routine analysis and screening of numerous genotypes. The costs

are so high that unless a simple screening tool is available, it does not seem practical to retain this trait in a conventional breeding programme (Zhang and Li, 2004). Apparently, the starch content of sweet potatoes is determined mainly by the additive effect of polygenes and, therefore, the accumulation of genes controlling high starch content is recommended. A few genes with simple dominance seem to control the inheritance of fibre size, while the total fibre content is controlled by several genes, suggesting that low-fibre improvement is quite feasible. Unfortunately, carotene content seems to be correlated negatively with DM, while starch content and DM are correlated positively: both are associated with eating quality. A genotype with only high-carotene content would probably have a low DM and high moisture, and this would be unpalatable for most consumers throughout the tropics. A starch content of about 68%–70% DM, a DM above 30% and sugars around 10% DM should be considered as important criteria (Lebot *et al.*, 2010).

In the USA or Japan, consumers prefer low DM and high sugars but, in many developing countries, consumers prefer high DM and low sugars. When a fresh sweet potato root is analysed, only sucrose, glucose and fructose are present; but, during cooking, starch is hydrolysed into maltose giving the sweet flavour to cooked roots and this represents a major constraint in analysing hybrids for their sweetness. In South Africa, studies have shown a significant correlation of maltose content with sensory sweet and sweet potato-like flavour. It is thought that maltose quantification can be used as a tool for early selection (Laurie *et al.*, 2012). A high performance thin layer chromatography (HP-TLC) protocol for the rapid quantitative determination of maltose and total sugars has been tested and gives reliable results on microwaved tubers. After analysis of 243 hybrids, mean maltose content within each group ranged from 7.6% for white-fleshed, to 8.5% in orange-fleshed and 12% in purple-fleshed. Total mean sugar content was 20.2, 22.1 and 26.8%, respectively, for white-, orange- and purple-fleshed hybrids (Lebot, 2017).

Selection for high DM content is very effective because there is tremendous variation for this trait in the germplasm, ranging from only 14% to more than 44%, and because the heritability of DM has been estimated at 75%–88% (Zhang and Li, 2004).

The Japanese approach for accumulating the genes for starch content is via inbreeding by selfing and sib cross. The development of inbred lines with high DM content and subsequently crossing them with elite cultivars is thought to be a practical approach. The first step is to develop inbred lines that are derived from different parents and the second step is the evaluation of the specific combining ability of each inbred line. Enhancement of the combining ability of various traits is an important step in the Japanese programme as it raises the efficiency of cultivar improvement. Apparently, inbreeding depression occurs in root yield but not in DM, and heterosis is observed through crosses of inbred lines in root yield rather than in DM content. The differences in the inbreeding depression and heterosis of agronomic traits in the progenies of self-compatible

genotypes suggest that each trait is controlled by different genes. DM content is probably controlled by additive gene effects, while root yield is controlled by dominant gene effects. Breeding lines with a starch content of up to 28%–30% of fresh weight have been developed (Komaki *et al.*, 1998; Katayama *et al.*, 2015).

In China, the majority of the cultivars released before the early 1990s had a DM content lower than 30%. Chinese breeders have introduced accessions from various sources, and especially from CIP, from which more than 100,000 botanical seeds and 55 advanced breeding lines have been introduced. The population mean is increasing for this trait through population improvement (Zhang and Li, 2004).

Considerable variation exists for crude protein content in sweet potato and Li (1982) has reported a range of 1.27%–10.07% dry weight among 300 different accessions in Taiwan, with most of them averaging around 4%–5%. A high broad sense heritability of 90% has been reported with significant genotype × location interaction but no genotype × year interaction (Collins *et al.*, 1987). Zhang and Li (2004) found that the narrow-sense heritability of family means for crude protein is 0.57, while narrow-sense heritability among individuals is only 0.15. Moreover, they recorded a negative genetic correlation between crude protein content and DM. They concluded that mass selection cannot be effective in increasing crude protein in sweet potato because the heritability based on individuals is too low.

In sub-Saharan Africa, some experiments have been conducted to identify the extent of genetic variability of Fe and Zn concentrations and to determine their heritabilities. The results showed high heritability for Fe (0.74), Zn (0.82) and DM concentrations (0.93) among half-sib families. In this case, mass selection could improve the nutritional value of sweet potato (Courtney, 2007).

Resistance to weevils (*Cylas* spp.) has been identified in several East African varieties and is thought to be produced by hydroxycinnamic acids that are present in the skin of the storage roots. A study quantified these metabolites and evaluated levels of insect colonization of the same progeny. There is a correlation between field and laboratory resistance to *Cylas* spp. and sweet potato root chemistry. However, the results showed that resistance was mediated by root chemicals in most but not all cases. It appears that ecological interaction of hydroxycinnamic acid esters with weevils confers resistance (Anyanga *et al.*, 2013, 2017). In Tanzania, it was observed that weevil resistance is controlled by a significant general combining ability (GCA) effect of the male parent used in controlled crosses. Heritability of major traits was measured for the total number of roots, root yield, DM, percentage infested roots number and weevil damage. Narrow-sense heritabilities were 0.24, 0.56, 0.84, 0.62 and 0.62, respectively, while broad sense heritabilities were 0.58, 0.72, 0.93, 0.78 and 0.77, respectively. These high heritabilities indicate that genetic gains can be obtained through conventional breeding and clonal selection of hybrids (Kagimbo *et al.*, 2019).

## GENOTYPE × ENVIRONMENT (G × E) INTERACTIONS

Because sweet potato is very sensitive to environmental changes, it is necessary to decentralize breeding programmes. Most programmes intensify recombination by polycross with usually 20–30 parents and attempt to produce a maximum of true botanical seeds (50,000–100,000) for field screening and evaluation in different environments. In East Africa, multi-local yield trials comparing newly selected clones to local cultivars were used to test yield stability in adverse environments. Some genotypes appear to be fairly yield stable but, for most of the others, G × E interactions increase with increasing elevation, for example. Selecting new cultivars in an environment with adverse conditions seems to be an efficient and practical way of identifying cultivars with good environmental adaptability (Janssens, 1984, 1988). In Ethiopia, a study conducted to determine root yield stability and the nature and magnitude of G × E interaction using six introduced and one farmers' cultivar, at four locations for 3 consecutive years, has also shown significant variation among genotypes (Tekalign, 2007).

Quality traits of interest to breeders, such as β-carotene content, are also influenced by the environment (Collins *et al.*, 1987; David *et al.*, 1998). A study conducted in Peru to investigate G × E interaction effects on commercial yield and β-carotene concentration in storage roots revealed that out of nine cultivars tested, none had had satisfactory stability. The lack of association between high yield and stable performance suggests that G × E interactions are important and there is a need to study the yield performance of selected genotypes in varying agroclimatic conditions. Interestingly, β-carotene content increased in almost all tested genotypes when grown at higher altitude (Manrique and Hermann, 2001).

Another study in Peru, comparing nine genotypes of diverse origins with local cultivars at seven locations using two N treatments (0 or 80 kg/ha) has, however, shown that the G × E interactions are smaller than the genetic variation in nutritional traits. The G × E interactions are larger, or nearly equal to, the genetic variation of yield traits. The contribution of N application to G × E appears not to be significant. A specifically adapted genotype was observed with considerable yield advantage over all widely adapted genotypes in low-yielding environments. Different locations varied in their selection ability for storage root yield. Apparently, low-yielding or marginal environments are not disadvantaged when breeding efforts are conducted in more favoured locations (Grüneberg *et al.*, 2005).

Various environmental factors such as growing season, total rainfall and location have been shown to affect the protein content of the sweet potato (Bouwkamp *et al.*, 1985; Bradbury *et al.*, 1985; Lin, 1989). Trypsin is a major digestive tract enzyme that hydrolyses proteins so they can be digested and assimilated. Different levels of trypsin inhibitor activity (TIA) in sweet potato have been reported but G × E interactions affect TIA significantly. When

environmental conditions change, TIA and crude protein content change as well (Zhang *et al.*, 1998).

Similar responses and significant G × E interactions are known to occur in Papua New Guinea (PNG), where sweet potato is the major food crop in the highlands. It is observed that a variety that performs well under wet conditions is likely to perform even better in places with a distinct dry season. In that country, subsistence farmers do not readily adopt improved varieties developed away from farming systems and local environments, and it is more appropriate to develop new cultivars in the different agroecological zones (Van Wijmeersch, 2001).

To satisfy varied regional needs for improved varieties and to take into consideration these significant G × E interactions, CIP has adopted an accelerated breeding scheme (ABS). In practice, unreplicated three-hill trials are established in more than one environment, providing exposure to key stresses such as drought, lower soil fertility or disease pressure. The use of three-hill trials allows the breeder to assess interplant variability, selecting for genotypes with uniform performance. The problem, however, is that some seedling plants can produce enough distal cuttings (six) for one three-hill trial but often not for more trials; consequently, it is necessary to propagate them before the multilocation evaluation. Local standard check varieties are also used for comparative evaluation. It is, however, necessary to make sure that the health status of these local checks is comparable to that of the seedling genotypes, since virus accumulation in clonal planting material is significant. ABS is very efficient for quality traits such as DM, starch, sugars and carotene contents (Grüneberg *et al.*, 2015; Mwanga *et al.*, 2017). ABS is also well suited for participatory evaluation, which is often necessary in countries with insufficient means to develop a full-scale breeding programme (Gibson *et al.*, 2011a, b).

In Uganda, a study where farmers' (5 cvs) and breeders' (11 cvs) varieties were evaluated for yield in 20 trials (during 2000–2001 for three seasons in four locations) has shown that farmers' varieties performed, on average, better than official breeder varieties. This illustrates the potential that local cultivars can have in regions where high diversity of sweet potato landraces exists (Abidin *et al.*, 2005). Again in Uganda, researchers and farmers have identified preferred introduced varieties through participatory evaluation and selected new cultivars from seedling populations. One released variety ('NASPOT 1') has been adopted by farmers, mostly for its high and early yield of large and mealy roots. Farmers also selected cultivars among the seedling populations for a wider range of attributes. Some of the attributes needed by farmers, such as suitability for sequential piecemeal harvesting or the tolerance to abiotic or biotic stresses such as drought or pest damage, were found to be difficult to predict by researchers during their on-station work (Gibson *et al.*, 2008; Gibson *et al.*, 2011b).

In Mozambique, storage root yield (t/ha) was found to be negatively affected by drought and genotype × year interaction. Harvest index stability

may be the most reliable trait to identify sweet potato clones with storage root yield stability. It was observed that at least two environments should be used in the early breeding stage to evaluate new hybrids (Andrade *et al.*, 2016). In Tanzania, GCA and specific combining ability (SCA) were found to be highly significant among full-sib families. There are significant GCA × sites and SCA × sites effects indicating environmental effects on gene action and expression (Ngailo *et al.*, 2019).

In PNG, combined analysis showed significant environmental effects on tuber yields, tuber number and gall mite; while harvest index, tuber DM and scab disease were influenced by genotype. However, new improved varieties generally outperformed local varieties in terms of yield and stability. The high degree of variation in tuber yields and related traits due to diverse environments and G × E interactions indicate that further breeding and selection for high yield and widely adaptable varieties is necessary (Wera *et al.*, 2018).

## USE OF RELATED SPECIES

Other *Ipomoea* spp. may contribute to the genetic improvement of the sweet potato by providing new genes, such as those for resistance to pests and diseases. Their usefulness is not straightforward as tremendous variation already exists for most traits within the *I. batatas* germplasm. Resistance to weevils (*Cylas* spp.), scab (*E. batatas*) and black rot (*Ceratocystis fimbriata*) have been found in *I. trifida*. Adaptation of the wild *Ipomoea* species to very different environments makes them attractive, but their use is often constrained by the absence of storage roots and the sexual barriers to crossability with *I. batatas* due to different ploidy levels (Khoury *et al.*, 2015). In Japan, interspecific hybridization has been used since the 1950s to improve sweet potato. Some traits of *I. trifida* are of interest to sweet potato breeders: drought tolerance, disease resistance and root storability. After interspecific hybridization and subsequent introgression, high starch cultivars have been developed (Shiotani *et al.*, 1991). Other related species might be useful to build up resistance to weevils as there is very little resistance in sweet potato. The characteristics of the *I. batatas* group and the related species assumed to be close relatives are presented in Table 10.3.

The A-group includes species that are self-compatible and cross-compatible with each other. In the X-group, there are two tetraploids which can be intercrossed with one another. Species of the X-group can cross with those of the A-group when they are pollen parents. The B-group is composed of di-, tetra- and hexaploids, which cannot intercross with species of the A- and X-groups. The crossability between two different *Ipomoea* species depends on the balance of chromosome numbers and also on the homology between the two genomes. The crossability with sweet potato is less effective with diploid and tetraploid *I. trifida* than between hexaploid *I. trifida* and hexaploid *I. batatas*. The efficiency of the $2n$ pollen was evaluated in polyploidization using $4x \times 4x$ ($2n$) crosses

**Table 10.3.** Sexual compatibility relationships in *Ipomoea batatas*, *Batatas* section.

| A-group<br>Self-compatible<br>*I. triloba* group | X-group<br>Self-incompatible | B-group<br>Self-incompatible<br>*I. batatas* group |
|---|---|---|
| *I. triloba* (2*x*) | *I. tiliacea* (4*x*) | *I. leucantha* (2*x*) |
| *I. lacunosa* (2*x*) | | *I. littoralis* (4*x*) |
| *I. ramoni* (2*x*) | *I. gracilis* (4*x*) | *I. trifida* (6*x*) |
| *I. trichocarpa* (2x) | | *I. batatas* (6x) |

but all progenies were 4*x*, which suggested the existence of barriers to crossability between 4*x* genotypes and their 2*n* pollen-producer counterparts (Hoa and Carpena, 1994; Becerra Lopez-Lavalle and Orjeda, 2002).

The most frequently used species are: *I. trifida* and *I. littoralis* for resistance to weevils, scab (*E. batatas*) and black rot disease (*Ceratocystis fimbriata*); *I. grandiflora* for nematodes and sweet potato virus disease (SPVD); and *I. triloba* for drought tolerance and resistance to root rot and other fungal disease. However, in practice their real contribution to sweet potato breeding remains somewhat limited (Khoury *et al.*, 2015; Mwanga *et al.*, 2017).

## USE OF MOLECULAR MARKERS

One of the earliest uses of DNA markers was that of restriction fragment length polymorphisms (RFLPs) to conduct a phylogenetic study of the *batatas* section. Random amplified polymorphic DNA (RAPD) and amplified fragment length polymorphism (AFLP) markers have also been used together to identify relationships among some species in the *batatas* group. Similarity measures and resulting dendrograms using RAPD and AFLP data are comparable. They reveal that the wild tetraploid species, *I. gracilis* and *I. tiliacea*, are distinct from *I. batatas*. The diploid *I. trifida* and the wild tetraploid accessions are genetically related to the cultivated sweet potato and are the possible progenitors of *I. batatas* (Jarret *et al.*, 1992).

Internal Transcribed Spacer (ITS) sequences and Simple Sequence Repeat (SSR) data did not support an allopolyploid origin for *I. batatas*, nor any contribution of *I. triloba* in the genome of domesticated sweet potato. *I. trifida* and *I. batatas* are closely related, but an autopolyploid origin of sweet potato has been suggested from the ancestor it shares with *I. trifida*. Two *I. batatas* chloroplast lineages were identified, but they are more divergent to each other than to *I. trifida*. It was thus proposed that cultivated *I. batatas* varieties have multiple origins, and evolved from at least two distinct autopolyploidization events in distinct wild populations of a single progenitor species.

Secondary contact between sweet potatoes domesticated in Central America and in South America, from differentiated wild *I. batatas* populations, would have

led to the introgression of chloroplast haplotypes of each lineage into nuclear backgrounds (Roullier *et al.* 2013b). Chloroplast and nuclear SSRs support the existence of two geographically restricted genepools: the north-western part of South America and the Caribbean and Central American region. This analysis suggests at least two independent domestications for sweet potato, in Central America and in the north-western part of South America. The exchanges of clones and sexual reproduction were both important processes in sweet potato diversification (Roullier *et al.*, 2011). In New Guinea, chloroplast and nuclear SSRs reveal lower diversification than the one found in tropical America. Sexual reproduction has, however, played a major role in the diversification process of sweet potato in New Guinea (Roullier *et al.*, 2013a).

Molecular marker research has focused on germplasm evaluation and characterization (Villordon and La Bonte, 1994, 1996; He *et al.*, 1995; Prakash *et al.*, 1996) and to map making (Ukoskit and Thompson, 1997; Ukoskit *et al.*, 1997). To promote the implementation of genetic analyses in the Japanese breeding programmes, a set of microsatellite markers has been developed which covers the entire genome. Seventy-five SSR loci showed length polymorphisms and, out of these polymorphic loci, 71% were associated with some genes (Hu *et al.*, 2004). Microsatellites have been used successfully to analyse the genetic diversity and genetic relationships among genotypes produced via polycross breeding (Hwang *et al.*, 2002). Also, the use of microsatellite co-dominant molecular markers demonstrates the feasibility of identifying paternity using a minimal number of loci (Buteler *et al.*, 2002). Microsatellite markers can disclose multiple alleles at a particular locus but are more expensive than others.

AFLPs have been used to detect markers suitable for the identification of plants possessing a resistant reaction to root-knot nematode (*Meloidogyne incognita*). Two $F_1$ populations were screened. The first population consisted of 48 half-sib genotypes developed at the LSU. The second population consisted of 54 full-sibs developed by CIP breeding programmes. The results for plant nematode resistance indicate a bimodal distribution among the genotypes for the LSU population and a normal distribution for the CIP population. Models for root-knot nematode resistance prediction achieved 89% (LSU) and 88% (CIP) efficiencies (Mcharo *et al.*, 2005). AFLP markers have also been found to be useful to identify genotypes susceptible or resistant to SPVD in Kenya (Miano *et al.*, 2008).

Genetic linkage mapping studies have been conducted, but the technique is not used in sweet potato breeding programmes. The markers used for these maps include RAPD (random amplified polymorphic DNA), AFLP (amplified fragment length polymorphism), ISSR (inter-simple sequence repeats), SSR (simple sequence repeat), SRAP (sequence related amplified polymorphism) and RTISP (retrotransposon insertion polymorphism). The quantitative traits loci (QTL) studies have focused on resistance to root-knot nematode, DM, starch and carotene content (Cervantes-Flores *et al.*, 2011). AFLP and SSR markers

have been used to identify no fewer than 27 different QTL for DM content (Zhao *et al.*, 2013). The complete chloroplast genome and gene expression atlas of cultivar 'Xushu 18' has been finalized using next generation sequencing (NGS) methods (Yan *et al.*, 2015). High-quality reference genomes of *I. trifida* and *I. triloba* have been developed by North Carolina State University, USA (Mwanga *et al.*, 2017). There are now great expectations from genomic selection (GS). GS can predict the performance of a genotype based on genomic data using the genomic estimated breeding values (GEBV). The approach aims at associating single nucleotide polymorphisms (SNP) with quantitative trait performance. It is, therefore, a statistical approach to produce predictive models, but the efficiency of these models has yet to be demonstrated for sweet potato breeding. It is expected that, once they are developed, these models will be useful for one country but not for others.

Although these results appear promising on paper, for the time being there is no practical use of molecular markers in sweet potato breeding programmes (e.g. for marker-assisted selection (MAS) at the field level) This is quite surprising, considering the global importance of the crop and the fact that sweet potato is also an economically important crop in developed countries (the USA, China and Japan). In these countries, conventional breeding is delivering genetic gains on a regular basis and programmes are progressing continuously. The return on investment for MAS is far from obvious.

Mutation breeding could be an interesting method of selecting cultivars of erect plant type; these are quite rare, despite their advantages over the spreading type, such as simplicity of cultivation and ability to adapt to limited space. However, large numbers of *vitro*-plantlets should be used for irradiation with gamma rays (Kuranouchi *et al.*, 2016).

## TRANSGENIC TECHNOLOGIES

Genetic transformation offers the promise of accelerating the genetic improvement of sweet potato for traits that are difficult to breed using conventional techniques. One of the major constraints in developing transgenic sweet potatoes is that transformation and regeneration are genotype dependent. Varieties that lack the novel trait (e.g. virus or weevil resistance) are still difficult to transform. Different protocols have been described for genetic transformation through direct gene transfer. Two different approaches are being used, one mediated by *A. tumefaciens* and the other by direct gene transfer using particle bombardment (Kreuze *et al.*, 2009).

The regeneration protocol mediated by *A. tumefaciens* uses two different plasmids, which are transferred to *A. tumefaciens* by electroporation. Trypsin inhibitors are potential candidates for the development of transgenic sweet potato with resistance to weevils (*Cylas* spp.) and genes coding for them have been selected (Newell *et al.*, 1995). Ten sweet potato transgenic lines of the cultivar

'Jewel', hosting a cowpea trypsin inhibitor, have been developed successfully by Axis Genetic Ltd (UK) and CIP. After propagation and isolated screenhouse trials, these lines have been evaluated in the field in Cuba and China for their resistance to *C. formicarius*.

In Japan, transgenic plants of cv. 'Kokei 14' have been obtained from embryogenic calluses using *A. tumefaciens*-mediated transformation. They were evaluated in the greenhouse and the plants grew normally with well-formed storage roots after 3 months. It was concluded that some agronomically important genes can be introduced easily with this system (Otani *et al.*, 2001). For example, starch composition can be altered by genetic transformation: out of 26 transgenic plants obtained, one plant showed the absence of amylose in the storage roots (Kimura *et al.*, 2001). Transgenic approaches for weevil resistance now focus on toxins from *Bacillus thuringensis* (Bt). Different proteins have been tested; several gene constructs have been developed and varieties have been transformed by *Agrobacterium*. However, it seems that the transgenic varieties with the Bt genes are not sufficiently resistant to the weevil (Rukarwa *et al.*, 2013). The *Agrobacterium*-mediated transformation method based on callus organogenesis has since been improved. Stable transgenic plants are obtained in 6–10 weeks after infection with *A. tumefaciens*. PCR (polymerase chain reaction) is used to confirm the stable integration of transgenes into the sweet potato genome (Luo *et al.*, 2006). In South Korea, a successful and reliable *Agrobacterium* transformation of the *bar* gene conferring herbicide resistance has been achieved, and the method seems to have the potential to develop new varieties with enhanced tolerance to the herbicide 'Basta' (Choi *et al.*, 2007).

In Japan, the coat protein gene of the sweet potato feathery mottle virus (SPFMV) was introduced by direct gene transfer using electroporation or particle bombardment. Calluses were bombarded with particles and regenerated plants were confirmed as hosting the transgenes using PCR analysis (Murata *et al.*, 1998). Transgenic lines were then obtained from independent calli and each line was vegetatively propagated and grafted onto morning glory (*I. nil*) that had been infected with the SPFMV. Three months after grafting, an ELISA (enzyme-linked immunosorbent assay) test showed that virus accumulation was suppressed in the transgenic lines as compared with normal ones. The transgenic lines were also shown to be highly resistant to primary and secondary infections by the virus. Consequently, particle bombardment appears to be a reliable technique to transfer foreign genes into the sweet potato genome (Okada *et al.*, 2001, 2002).

The enhancement of tolerance to various environmental stresses is also attractive and has been attempted. Sweet potato was transformed with spermidine synthase genes derived from *Cucurbita ficifolia*. The transgenic plants showed twice as high spermidine content as the wild type counterpart in both leaves and storage roots. These transgenic plants were tested for their tolerance to salt and drought. One of their most interesting traits was the increase

in the number of storage roots produced under both non-stress and stressful environments. It was also observed that the transgenic plants were less affected, producing a higher mass of storage roots and starches than normal plants under stress. The transgenic plants also showed increased tolerance to chilling- and to heat-mediated damage compared to the normal plants. It was concluded that sweet potato could be made more tolerant to environmental stresses through the introduction of the spermidine synthase genes. The transgenic plants were also found to be more tolerant to the herbicide Paraquat™ (Kasukabe *et al.*, 2006).

A study conducted to evaluate the nutritional quality of genetically modified sweet potato on the growth, lipid metabolism and protein metabolism of hamsters has shown that they contain insufficient protein to maintain normal animal growth. It was, however, observed that transgenic sweet potato had good-quality protein that supported the growth of hamsters better than did normal plants (Shreen and Pace, 2002). Improvement in the baking quality of sweet potato flour has also been attempted. Sweet potato flour is presently used as a mixture with wheat flour for producing bread, because sweet potato has no gluten. A glutenin gene of wheat has therefore been introduced into the variety 'Huachano' and 13 transformed plants were obtained: three expressed the glutenin in significant amounts (Kreuze *et al.*, 2009).

The long-standing debate around the safety of GMOs has stimulated researchers to investigate a natural infection of sweet potato by *A. tumefaciens*. It was observed that, among 291 accessions analysed, all contained one or more transfer DNA (T-DNA) sequences. These sequences suggest that an *Agrobacterium* infection occurred in evolutionary times. One T-DNA is present in all accessions, but not in the closely related wild relatives, suggesting the T-DNA provided a trait selected for during domestication. This finding illustrates natural plant–microbe interactions in a crop that has been eaten for millennia (Kyndt *et al.*, 2015).

There are no commercial GM varieties of sweet potato available yet. It is hoped that the enhancement of molecular data and DNA sequencing information will be very useful in improving genetic engineering (Kreuze *et al.*, 2009).

## GERMPLASM CONSERVATION

The maintenance of *ex situ* collections of sweet potato is laborious and losses are frequently suffered due to biotic and abiotic stresses. There are at least 36 germplasm collections known to maintain more than 29,000 accessions, including landraces, improved material and wild *Ipomoea* species. Only 9 collections are known to maintain more than 1,000 accessions each. The largest collection maintained by CIP in Lima, Peru, holds more than 7,000 accessions). The remaining 8 collections are distributed in South America, North America and East Africa; four in Asia and one in Melanesia (Papua New Guinea).All

collections hold landraces and improved materials, but only six maintain wild species. Most genebanks maintain collections in the field, followed by greenhouse and *in vitro* storage (Roca *et al.*, 2007).

A major task is to eliminate duplicates. Most collections encounter difficulties in plant health status and maintenance, documentation, regeneration and safety duplication. Regeneration is a critical genebank function and is linked to the issue of plant health. Accession regeneration is mostly carried out by root sprouts and vines in field collections. *In vitro* culture is used by 12 collections that have implemented this approach but regeneration capacity is too low to support the maintenance of all accessions, either *in vitro* on in the greenhouse.

Core collections are being developed using molecular markers. Morphological characterization is conducted routinely with standardized morphological descriptors, and the identification of duplicates within the Peruvian sweet potato germplasm collection has permitted its reduction from 1929 accessions to 909 (Mwanga *et al.*, 2017). A study conducted with 25 SSR markers to characterize and assess the diversity of a subset of the CIP germplasm (540 accessions) has shown that many genepools can be observed within *I. batatas* and that a considerable genetic distance exists among them (Grüneberg *et al.*, 2007). The large island of New Guinea (composed of the Indonesian province of Irian Jaya and of PNG) is the second largest centre of genetic diversity in the world. The number of varieties grown in New Guinea has been estimated at some 5000, of which about 1600 are maintained in *ex situ* collections.

Sweet potato accessions can exhibit very similar or almost identical morphotypes and be genetically distant, yet they can also present very different morphotypes, although they are clones of each other. New morphotypes can arise from two types of changes occurring in vegetative buds: the tissues may change, or only a part of a given tissue may change. The first type gives rise to a bud sport, which is an individual that arises from somatic mutation; all the tissues have a different genetic make-up from the parent, although very few genes are involved. The second type of change produces chimeras that correspond to tissues with genetic make-up different from those of adjacent tissues on the same plant. Sweet potato is a plant species particularly prone to the two types of mutations and it is not uncommon for germplasm collection curators to observe that some of their accessions may change over propagation cycles. High levels of ploidy usually increase the chances of fixing this type of mutation, and therefore one may observe a genetic drift in successive clonal generations. Despite these difficulties, tissue culturing is the best approach for preserving germplasm, and *in vitro* collections exist in CIP (Peru) of course, but also in American universities, in Asia (China, Japan, India, Vietnam, Indonesia, the Philippines, PNG) and in Africa. It is estimated that the maintenance cost is around US$2 per accession per year (Gaba and Singer, 2009).

CIP is distributing internationally elite cultivars *in vitro* or as seeds, and an important number of cultivars are now available for testing. The distribution of true botanical seeds has practical advantages compared to *in vitro* clones, as

it presents fewer quarantine problems and reduced distribution costs and risks. It also permits the rapid distribution of allelic diversity on a broad scale and its selection for adaptation to local conditions.

On-farm conservation strategy has been identified as a complementary but necessary approach to compensate for the losses inevitable in the *ex situ* collections. Since farmers tend to grow different cultivars together, this might represent a sound basis for developing an *in situ* strategy (Rao and Campilan, 2002). It is, however, difficult to assess accurately the impact of such a strategy and to design an appropriate system for on-farm conservation.

Although an impressive amount of research work has already been done, the research needs that scored highest in most developing countries are still related to germplasm conservation and plant improvement. They involve the control of viruses through genotype resistance, improvement in availability and quality of planting material and improved cultivars exhibiting high and stable yield potential. Additional priorities for sub-Saharan Africa include improved control of the sweet potato weevil and cultivars with high-carotene content; and, for China, other priority needs are the conservation and characterization of genetic resources, pre-breeding and cultivars with high starch yield (Fuglie, 2007).

# 11

# Developmental Physiology

## GROWTH CYCLE

The young seedling develops a taproot and a complete root system, as well as a complete foliage canopy, but it takes about 6 months in the lowland tropics to cover an area that a vegetatively propagated plant covers in only 3 months.

Once the stem cuttings have been planted, the growth and development of the sweet potato plant present four distinct phases:

**1.** An *initial phase*, characterized by rapid growth of the adventitious roots which arise from the underground stem cuttings, accompanied by a slow growth of the vines.
**2.** An *intermediate phase* of rapid vegetative growth of the vines, increasing the leaf area. This phase is also accompanied by an initial storage root development.
**3.** A *final phase* where the vegetative growth of the vines stops and rapid bulking of the storage roots occurs.
**4.** A *regeneration phase* where sprouts develop from the storage roots and give rise to new plants.

There are overlaps between these four phases. Their duration varies greatly, depending on cultivar and environmental conditions. In tropical warm lowlands, the initial phase occurs during the first 40 days after planting (DAP), the intermediate phase occurs from 40 to 70 DAP and the final phase from 70 to 120 DAP. During the initial phase of growth, the usage of carbohydrates is dominant; during the intermediate phase, usage is less dominant until their storage becomes dominant; and, in the final phase, their storage is dominant over usage. During the regeneration phase, their usage is again dominant. There are no clear indicators to determine maturity in sweet potato and the leaves do not senesce (Fig. 11.1).

The leaf area index (LAI) increases from the 2nd week after planting (WAP) in the initial phase, reaches a plateau between 6 and 16 WAP and declines at the end of the growth period owing to leaf shading and reduced light intensity in the lowermost leaves (Ravi and Saravanan, 2012).

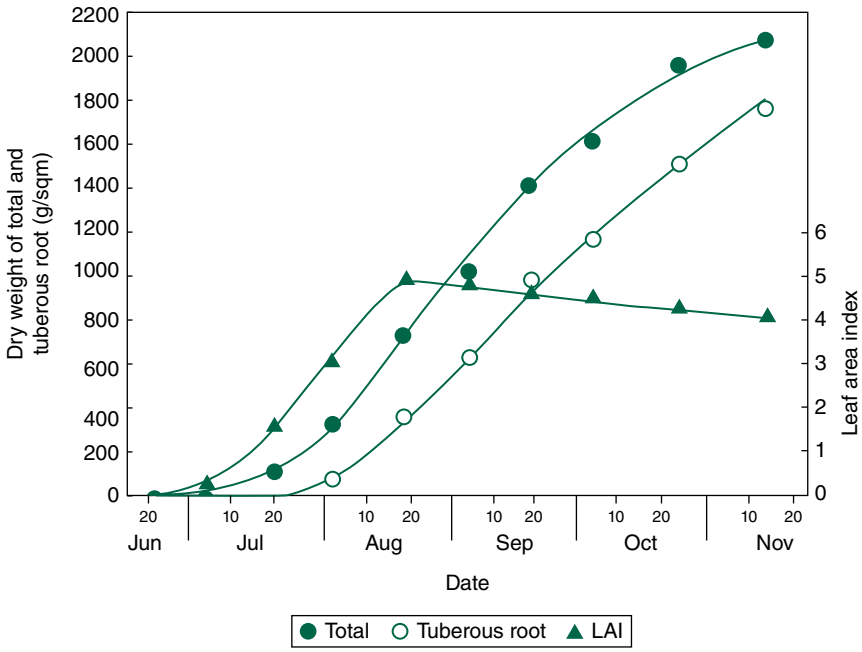


**Fig. 11.1.** The first three phases of growth of the sweet potato plant (source: Edmond and Ammerman, 1971).

The relative contribution of the source potential (the leaves where the assimilates are produced) and the sink capacity (the storage roots where they are accumulated) varies during the day during the sweet potato growth cycle, and depending on environmental conditions. It is therefore, difficult to generalize a clear relationship between source and sink. The relative contribution of source and sink towards storage root growth is not constant through the whole growth cycle.

## The initial phase

In this phase, there is slow growth of the vines and rapid growth of the young roots. Three types of roots arise from a stem cutting, a plug transplant or a piece of storage root: primary fibrous, pencil and storage (fleshy) roots. From these three types of root, lateral roots may develop. The young adventitious roots can be either thin or thick roots. Usually, thin roots arise from the internodal areas and thick roots from the nodes of the underground stem. Thick roots differ from thin roots in their size and the faster growth of their apical meristems. Depending on soil texture and growing conditions, these roots may penetrate to a depth of 2 m, or even more. This deep penetration allows survival during

droughts by the root system absorbing water from deeper soil layers. If the environment is favourable, the young thick roots develop into storage roots.

Anatomically, the feeding roots of the sweet potato are typical of dicotyledons, having an outer epidermis and then a cortex, endodermis and pericycle. A four-pointed primary xylem is located at the centre of the root. A few sweet potato roots have xylem with five or six points instead of four, and these will develop later into storage roots. Most of them develop from the initial fibrous root system produced by the stem cuttings but, if the plants are hilled-up, some of the thick roots that are produced at the nodes of the stems will also produce storage roots. There is a rapid increase in the number of pigmented and non-pigmented roots between 1 and 4 WAP.

The storage root tissues of the plant develop from meristematic activity of the vascular cambium and the anomalous cambium. The process that leads to the formation of storage roots occurs at two major locations in the root. The vascular cambium located between the xylem and the phloem produces secondary phloem on its outside layer and secondary xylem and a great volume of storage parenchyma on the inside. While the storage tissues are being laid down in the roots, the stalk connecting them to the rest of the plant is also subject to some modification, which includes an extensive amount of secondary growth of phloem. This increase in phloem will allow the translocation of photosynthates necessary for the bulking of the storage roots. During this initial phase, the plant is consuming all the carbohydrates it produces.

## The intermediate phase

This phase corresponds to the initiation of storage root development, a fast growth of vines and a large increase in leaf area. Genotypes are erect-bushy, intermediate or spreading types with long internodes. Branching is genotype dependent and branches vary greatly in number and length. At the end of this stage, the vines are fully developed and present a large photosynthetic and transpiring leaf area. The absorbing roots are also fully developed and present a thoroughly ramifying root system penetrating deep into the soil. During the period between 30 and 80 DAP, there is a significant mean increase in the number of thick roots and a decline in the total root number. The period between 50 and 80 DAP is critical for the production of pencil and string roots.

## The final phase

This phase is one of rapid bulking of the storage roots, reduced growth of the vines and their senescence. In contrast with the growth of vines and absorbing roots, the development of storage roots requires the formation of relatively few cells, while depositing large volumes of starch grains and carotene in the

storage tissues. At this stage, the sweet potato plant is storing all the carbohydrates it produces. When the storage roots are developing, the sucrose produced in the leaves is translocated to the storage roots, where it is changed into glucose, and this glucose is then transformed into starch, which is stored finally in the storage root tissues (Edmond and Ammerman, 1971). The storage root can undergo periods of arrested growth due to unfavourable conditions and continue to grow as soon as these conditions improve. In temperate countries such as the USA, where the growth cycle is slower and longer, approximately 92%–100% of the final length of the storage root is reached 120 DAP, but only 49%–77% of the final diameter is reached at that time (Wilson, 1982). Dry matter (DM) content always increases over time. The total sugar concentration (fructose + glucose + sucrose) also increases linearly over time and sucrose is the predominant sugar (Lewthwaite *et al.*, 2000).

Storage root formation seems to involve different processes including induction of anomalous cambial cell formation, cell division and starch accumulation, and is affected by external factors such as water, temperature and nutrients. Their interactions determine whether an adventitious root will develop into a fibrous root, a storage root or a pencil root (Firon *et al.*, 2009). Comparison made between *I. batatas* and its presumed non-tuberizing ancestor, *I. trifida*, suggests that endogeneous abscisic acid (ABA) is involved in the development of the storage root by stimulating cell division. ABA content may be related to the activity of the vascular and anomalous cambia and promotes cell differentiation and thickening of storage root (Ravi and Saravanan, 2012).

## The regeneration phase

The senescence of the foliage cannot be used as an indicator of the time to harvest, and sweet potato maturity is difficult to assess precisely. If the storage roots are not harvested when mature, the plant can regenerate itself. The regeneration phase can start as early as 100 DAP, depending on genotype and environment.

Very early in the storage root ontogeny, adventitious buds are produced on the thin and thick roots, either singly or in groups of four. These buds are distinguished easily from lateral root primordial buds. New vegetative buds can develop at the surface of the storage roots and regenerate the plant (Fig. 11.2). As these buds develop, they require a regular supply of glucose, which comes from the starch that has been stored in the storage roots. These sprouts develop from the vascular cambium zone of the storage root. Larger sprouts are produced from larger storage root pieces, suggesting that carbohydrate mobilization plays an important role in sprout vigour and growth. Adventitious buds produced on storage roots can be stimulated into shoots with high levels of N supply. While they are still attached to the periderm of the storage root, the sprouts will draw food reserves from it, at least up to the eight-leaf stage, and

**Fig. 11.2.** At the beginning of the regeneration phase, vegetative buds develop on the surface of the sweet potato storage root. They can be used in nurseries to produce cuttings (photo: V. Lebot).

sprouts will continue to use reserves of carbohydrates as long as they remain attached to the storage root.

## PHOTOPERIODISM

Sweet potato is a heliophilous (sun-loving) plant species that grows best when light intensity is high, and this is why it often performs poorly when intercropped under perennials. Sweet potato plants can grow under low light intensity (e.g. in nurseries) if they are still attached to the storage root and probably would not grow correctly without the aid of storage root nutrients. Sweet potato leaves show a maximum net photosynthetic rate between 10:00 and 11:00 followed by stomatal closure and a significant decrease in net photosynthetic rate at 12:00. Under constant environmental conditions, sweet potato net photosynthetic rate remains high during the morning and decreases towards the end of the afternoon (Ravi and Saravanan, 2012).

Day length affects flowering and the plant's storage roots directly. In the tropics, flowering is promoted by a day length of 11 h and is inhibited by a day length of longer than 13.5 h. In temperate countries, above 30° latitude north or south, no flowering occurs during the long and warm summer days favourable to its cultivation. Increased day length has been assumed to be the factor responsible for higher yields in northern latitudes of temperate countries (i.e. Japan and the USA), but some experiments have shown reduced yield with a day length of 18 h (McDavid and Alamu, 1980).

However, Bonsi *et al*. (1990) conducted some experiments in environmental growth chambers to clarify the issue and studied the response of three genotypes to two different photoperiods (Table 11.1).

Continuous light seems to result in an increased number and weight of storage roots and an increased dry weight of fibrous roots and total foliage. High light intensity also seems to promote the production of a higher number of storage roots, as well as an increase in dry weight of fibrous roots and total foliage, confirming that sweet potatoes grown under shady conditions or low light produce poor yields.

Experiments conducted in glasshouses have confirmed that long light and short dark periods during 24 h promote the development of foliage rather than storage roots. On the other hand, short light and long dark periods promote the development of storage roots rather than foliage. Field experiments also show clearly that the formation and development of storage roots is promoted by short days, while long days favour foliage development. This is not genotype dependent and, in the lowland tropics, sweet potato yields more during the short days of the cool season than during the long and hot days of the summer season (Lebot, 1986). A long photoperiod (18 h) decreases the number of branches while increasing the branch length. A short photoperiod (8 h) increases the branch number and decreases the branch length (Ravi and Saravanan, 2012).

Normal growth and development of the storage roots can occur only in the absence of light and, if the storage roots are exposed to light, they will not store nutrients in their flesh. Exposure to light stops enlargement, decreases starch content and increases fibre content, but this is reversed easily by restoring the roots to darkness (Onwueme and Charles, 1994). However, light use efficiency is genotype dependent and it has been shown that leaf trait assessment at early stages could be used as a starting point for the screening of genotypes (Ramírez *et al*., 2017).

**Table 11.1.** Yield components of three genotypes cultivated in growth chambers under different photoperiods.

| Cultivar | Photoperiod light/dark (h) | Storage roots, number | Storage roots, fresh weight (g) | Fibrous roots, dry weight (g) | Total foliage, dry weight (g) |
|---|---|---|---|---|---|
| Georgia Jet | 12/12 | 1.0 | 11.0 | 4.3 | 25.8 |
| | 24/00 | 5.3 | 202.8 | 7.5 | 31.6 |
| TI 155 | 12/12 | 0.3 | 7.5 | 206 | 14.2 |
| | 24/00 | 2.6 | 132.6 | 7.0 | 24.6 |
| Georgia 120 | 12/12 | 0.3 | 4.0 | 3.0 | 17.0 |
| | 24/00 | 2.6 | 116.0 | 10.3 | 47.3 |

Source: adapted from Bonsi *et al*. (1990).

## TEMPERATURE

The sweet potato is essentially a warm weather crop which grows best at temperatures above 24°C, while temperatures below 10°C seriously retard its growth. The plant is damaged by frost and, in temperate countries, this restricts its distribution to areas where frost does not occur during at least 4–6 months (i.e. North Carolina and Louisiana in the USA; North Island in New Zealand).

Sweet potato plants which are subjected to an air temperature of 20°C during the period of darkness alternated with a temperature of 29°C during a light period of 16 h produce early maturing and higher yields than plants subjected to a constant temperature of 29°C. The temperature of the soil also directly affects the development of storage roots. For rooted single-leaf cuttings, for example, optimum storage root development occurs when the soil temperature reaches 25°C, whereas temperatures of 15°C or 35°C inhibit their development. The sweet potato produces the greatest increase in storage root weight when it is grown over a constant soil temperature of 30°C, combined with an air temperature of 25°C during the night.

Prolonged exposure of very young plants to 10°C can cause death. In the field, however, it is not uncommon for sweet potatoes in the USA, New Zealand or Japan to be exposed to night temperatures of approximately 10°C or less without apparent damage, and this suggests that plant age and duration of exposure are important as well.

Crop growth rate (CGR), net assimilation rate (NAR) and LAI have been determined for sweet potato in Japan in an attempt to understand DM production under field conditions in relation to temperature and solar radiation. After planting, the LAI increases rapidly until 60 DAP, then decreases gradually but remains above 4.0 throughout the second half of the crop cycle (from June to November in Japan). Mean air temperature and solar radiation are considered to be the main climatic factors affecting CGR in temperate countries. Experiments conducted in Kyushu, Japan, indicate that, during the first half of the cycle, DM production depends on LAI and that LAI values are closely related to ambient air temperature (Agata, 1982). During the second half of the cycle, DM production and storage root growth rate depend on NAR, and NAR values are closely related to solar radiation. The growth rate of the storage roots is influenced strongly by solar radiation through NAR and CGR when LAI is above the optimum value (Table 11.2).

## NUTRITION

The amount of nutrients exported depends on the yield of the crop and if both foliage and storage roots are exported. For a given cultivar, spectacular increases in yield can result from a low increase in essential nutrients. The approximate nutrient removal for a storage root yield of 12 t/ha (average yield)

**Table 11.2.** Correlation coefficients of crop growth rate (CGR), leaf area index (LAI) and net assimilation rate (NAR).

| | First half of crop cycle | | Second half of crop cycle | |
|---|---|---|---|---|
| Items | Mean air temperature | Mean solar radiation | Mean air temperature | Mean solar radiation |
| CGR | 0.96* | 0.85* | 0.66** | 1.0** |
| LAI | 0.88* | 0.76* | 0.98** | 0.71* |
| NAR | 0.75* | 0.92* | 0.62** | 1.0** |

*Significant at 5% level, **significant at 1% level (source: adapted from Agata, 1982).

**Table 11.3.** Nutrient removal for an average yield (12 t/ha) and a high yield (50 t/ha).

| | Nutrient removal (kg/ha) by crop with root yield of: | | | |
|---|---|---|---|---|
| | 12 t/ha | | 50 t/ha | |
| Nutrient | Roots only | Foliage & roots* | Roots only | Foliage & roots |
| N | 26 | 52 | 110 | 215 |
| P | 6 | 9 | 25 | 38 |
| K | 60 | 90 | 250 | 376 |
| Ca | 3.6 | 16 | 15 | 65 |
| Mg | 3 | 6.5 | 12.5 | 27 |
| S | 1.8 | 4.3 | 7.5 | 18 |
| Cl | 10 | 18 | 43 | 75 |
| Fe | 0.06 | 0.16 | 0.25 | 0.67 |
| B | 0.02 | 0.07 | 0.1 | 0.31 |
| Mn | 0.02 | 0.18 | 0.1 | 0.73 |
| Zn | 0.04 | 0.06 | 0.15 | 0.26 |
| Cu | 0.02 | 0.04 | 0.08 | 0.16 |
| Mo | 0.004 | 0.006 | 0.015 | 0.023 |

*Assuming 70% moisture in the storage roots and 86% in the foliage, and a foliage/root ratio of 0.6. Source: adapted from O'Sullivan *et al*. (1997).

and 50 t/ha (high yield), when only the storage roots are removed and when both foliage and roots are removed from the field, are presented in Table 11.3 (O'Sullivan *et al*., 1997).

When N, P, K, S, Mg, Ca and Fe are below critical levels, there are spectacular symptoms of deficiencies. Storage root formation can occur in N-deficient plants, despite restricted foliage growth. However, a high supply of N favours foliage development, which competes for carbohydrate supply (Harper and Walker, 1985). It is now accepted that K is required for good development of the storage root and a high supply of N would result in an adverse effect in storage root development when K is low.

Since the foliage grows most during the first half of the growth cycle and the storage roots develop during the second half, the foliage contains the greater quantities of N, P and K during this first half of the growth cycle and the storage roots contain greater quantities during the second half. The uptake of K is generally twice that of N and five times that of P.

K appears to play a critical role in sweet potato storage root starch synthesis. The $K_2O$/N ratio is critical for increased water content, respiration rate and storage root growth, leading to fast translocation of photosynthates from the leaves to the roots. A high $K_2O$/N ratio in the storage root induces higher water content and this ultimately increases the respiratory rate. High K supply and the $K_2O$/N ratio in the storage roots are thought to be associated with increased protein production, resulting in enhanced storage root growth (Kays *et al.*, 2005).

Light, dry and compact soil, waterlogged soil, high levels of N supply, gibberellins and long days are known to promote lignification and to inhibit the development of the storage root. Dark conditions, high K supply, well-aerated soil conditions, low temperatures, short days and kinetins have been shown to encourage their development (Wilson, 1982).

## WATER DEFICIT AND STRESS

Sweet potato cannot tolerate dry conditions at planting. The amount of rainfall needed is site-specific and varies greatly with evaporation, cultivar response and number of days to maturity. The storage root initiation period is the most sensitive to water deficit stress and it impacts directly the number of storage roots. Under typical conditions, sweet potato requires about 500 mm water for 16–20 weeks of growth.

Decreasing water-use efficiency under N stress is thought to be due to lower total plant DM production rather than to an increase in total water transpiration per plant. A pot experiment was conducted in a tropical mid-elevation environment (861 m altitude) to evaluate sweet potato genotypes of different origins for traits such as transpirational water-use efficiency (weight of roots produced per unit amount of water), growth and N-use efficiency as affected by different levels of N fertilization. The results regarding the response of cultivars with gathering-type canopies were revealing. Genotypes with small canopies were associated with a consistently positive response in their final storage root DM yields to increasing N supply, and with efficient allocation of DM and N in their storage roots. Genotypes with high canopy NARs had a high proportion of leaves exposed to the sun and high chlorophyll content in their leaves. N stress provoked increased transpiration per unit leaf area and decreased water-use efficiency. As these results were obtained in pots and controlled conditions, it would be interesting to see if similar responses would be obtained in field conditions (Kelm *et al.*, 2001).

Adequate water supply through rainfall or irrigation is essential for the optimum development of the storage roots, but excess water results in poor aeration. Because the storage root is displacing its volume equivalent of soil by compressing the soil next to it, it is assumed that the physical resistance of the soil can also decrease storage root development. Over-irrigation reduces storage root yield in areas with high rainfall and temporary drought stress appears to stimulate root development whenever vegetative growth is stopped for a short duration. The marketable root yield is influenced significantly by different irrigation levels. A reduction in the number of marketable size roots is responsible for lower root yields and is accompanied by an increase in root DM content (Ekanayake *et al.*, 1990).

The effects of time of irrigation on sweet potato total foliage weight, storage yield, number and size has been investigated in Taiwan. It appears that irrigation applied at a later growth stage gives better foliage growth and the trend is similar for storage root yield. Suppression of leaf growth by moisture stress has also been observed to favour the development of flower buds. The formation of sweet potato roots is stimulated when drought stress occurs some time during the growth cycle. It has been observed that if the sweet potato is irrigated when 40% of the total available water in the soil is depleted, it will produce the highest yields. The first irrigation has to be withheld until 60 DAP in order to provide the translocation of more photosynthates and the development of storage roots. The density of the soil should also be considered. In Taiwan, loose soils – or soils with low density – enhance vegetative growth and lessen storage root development. Soils with high densities reduce both storage root yields and foliage development. The optimum density of the soil is approximately 1.5 g/cc (Sajjapongse and Roan, 1982) (Table 11.4).

**Table 11.4.** Effect of time of irrigation on foliage and root yield of sweet potato in Taiwan.

| Time of irrigation DAP | Foliage weight t/ha | Storage root yield t/ha | Number of roots per plant | Root size, g/root |
|---|---|---|---|---|
| No irrigation | 3.8 | 13.4 | 3.8 | 116.8 |
| 30 | 4.4 | 14.2 | 4.1 | 112.9 |
| 60 | 5.2 | 18.8 | 4.3 | 152.3 |
| 90 | 5.8 | 18.6 | 4.2 | 152.1 |
| 120 | 6.8 | 19.9 | 4.3 | 148.7 |
| 30, 60 | 5.3 | 18.1 | 3.9 | 164.7 |
| 30, 90 | 5.6 | 17.0 | 4.8 | 120.4 |
| 60, 120 | 6.9 | 19.6 | 4.4 | 147.2 |
| 90, 120 | 6.5 | 17.6 | 3.9 | 154.4 |
| 30, 60, 90, 120 | 6.5 | 19.2 | 4.3 | 143.2 |

Source: adapted from Sajjapongse and Roan (1982). DAP, days after planting.

When sweet potatoes are grown in waterlogged conditions or in a culture solution, they fail to produce storage roots. In field conditions, yields may be improved remarkably by ridging. It appears that low storage root yield under field conditions with excess moisture is due to inadequate oxygen within the root zone. Low soil oxygen is probably more detrimental when occurring late in the growth cycle, when the storage roots have already been formed and have reached their full length just before enlarging.

In Vanuatu, Melanesia, sweet potato production is affected by high rainfall, and high soil moisture during the wet season slows down storage root development. In wet weather, leaf growth is vigorous but no roots are produced. The ideal situation is to obtain sufficient rainfall during the period of early growth and sunny weather during the period of storage root bulking and growth (Lebot, 1986).

When sweet potato plants are subjected to water stress, total chlorophyll content of the leaves decreases. Cultivars tolerant to water stress have lower chlorophyll content and higher adenosine triphosphate (ATP) content in leaves than susceptible cultivars (Ravi and Saravanan, 2012). Sweet potato cultivars show a large reduction in canopy cover under water deficit and also experience a significant reduction in yield. The yield reduction can be directly linked to low LAI values under water deficit conditions. Large decreases in stem length are observed when sweet potato plants are deprived of soil water. Water stress impacts the photosynthetic process; it also affects stomatal movement, light absorption and the biochemical pathways for $CO_2$ fixation. It is known that stomatal conductance varies with leaf irradiance, leaf temperature, atmospheric water vapour pressure deficit and $CO_2$ concentration. Yield is largely impacted by the retarded growth as a result of the drought conditions and the optimum yield depends directly on canopy cover, stem length and stomatal conductance. Measurement of LAI and stem length can be used as drought screening tools to evaluate drought-tolerant genotypes (Laurie *et al.*, 2015).

## CLIMATE CHANGE ADAPTATION

For sweet potato, just like for other root and tuber crops, genetic variation is the source of the adaptive variation necessary to adapt to climatic change. Some genotypes present particular traits which improve their adaptive potential. The physical components of the yield are the number and the mean size of the storage roots at harvest, which depend on the foliage characteristics, the patterns of storage root growth and their mean weight and shape.

The increase in root weight depends on leaf photosynthesis. The transport of assimilates from the leaves to the root stalk is a process influenced by storage root growth, as storage root cells must be formed and expand before they can store assimilates. The final yield depends on the rate of increase and the length of the growing period. It seems that in Japan, yields of 120 t/ha can be obtained

in 8 months in Kyushu (north) and 80 t/ha in 6 months in Okinawa (south) (Agata, 1982). In Vanuatu, yields of 60–80 t/ha can be obtained in 5 months with local cultivars and no fertilizers (Lebot, 1986).

The development process of the storage roots results from characteristics such as their number and length, and the function of the root stalk and shape. All these characteristics vary significantly between cultivars and are under genetic control. When different genotypes are studied for the partitioning of leaf, vine and root tissues, significant variation is observed. The proportions of leaf to stem dry weights are cultivar specific and are constant throughout the harvest period (Lebot, 1986; Lewthwaite and Triggs, 2000a).

One of the most striking morphological traits of the sweet potato is its variety of foliage. Several attempts to demonstrate relationships between yield and particular morphological or physiological characteristics of the foliage have failed. However, some varieties with small canopies, short stem length and small leaves can produce higher yields than those with long stems with numerous broad leaves. Some experiments have been conducted to understand the complexity of the matter. Staking can result in LAI increase of a low-yielding variety and this is thought to be due to the vertical leaf display. It is also assumed that the low light intensity in shaded leaves of unstaked plants may also contribute to yield reduction (Wilson, 1982).

In Japan, an experiment was carried out to conduct a quantitative analysis of two different branching patterns of two cultivars ('Shiroyutaka' and 'Beniazuma'). 'Shiroyutaka' has a gathering type of canopy architecture and 'Beniazuma' has a dispersing type. Branching ability is very high in 'Shiroyutaka' (gathering type) but the elongation of each branch is relatively limited, giving a bushy appearance to the plant. Characteristics opposite to these are seen in 'Beniazuma' (dispersing type). This work has shown that total DM production is higher in 'Shiroyutaka' than in 'Beniazuma' through the growth period. It is also observed that CGR in 'Shiroyutaka' is higher than in 'Beniazuma', especially at the middle growth period. The high CGR in 'Shiroyutaka' is thought to be due to its large NAR, instead of its LAI. It is, therefore, suggested that the canopy type might affect the NAR of each cultivar (Sasaki *et al.*, 2005). Particular types of canopies may, therefore, strengthen sweet potato adaptative potential to climate changes.

Two models of prediction have been tested for sweet potato but had limited field validation under current climate conditions; therefore, these models are not ready for climate change impact assessments. It is expected that these sweet potato models may be developed successfully. They, however, need to be calibrated with modern cultivars across different agro-climatic zones, and tested and improved with crop physiology measurements, growth, partitioning and water and N uptake. The variable would need to be recorded under different management and environmental conditions and tested with field experiments. Such complex studies have not been conducted yet for sweet potato and will require coordinated international initiatives (Raymundo *et al.*, 2014).

A few experiments have, however, been conducted in controlled conditions. Elevated concentrations of $CO_2$ in the atmosphere stimulate sweet potato growth. It has been shown that the production of roots from stem cuttings of the variety 'Georgia Jet' was more pronounced when these concentrations reached 675 ppm (Bhattacharya and Strain, 1985).

In Hawaii, sweet potato plants were grown to maturity with various $CO_2$ concentrations (353, 763, 1109 and 1515 ppm) and conventional and organic fertilizers were compared. Increases in average above-ground dry biomass were observed at 763 ppm, 1109 ppm and 1515 ppm and average storage root dry biomass increased at 763 ppm, 1109 ppm and 1515 ppm for both conventional and organic treatments, respectively. It was observed that sweet potato may be better at utilizing very high atmospheric $CO_2$ concentrations compared to non-root-crop species. Using sweet potato as an example, it was suggested that storage root fertilization under very high $CO_2$ concentrations could dramatically supplement crop production in developing countries, provided that the response found for sweet potato represents a generalized root-crop response. However, the performance of chemical over organically (i.e. manure-based) fertilized plants suggests that optimal nutrient availability will be crucial for support of enhanced crop production at elevated $CO_2$ (Czeck, 2014).

Sweet potato is clearly under-researched. A study aiming at prioritizing crop-specific research for long-term adaptation to climate change attempted to identify crops that are deemed to be most relevant. Sweet potato (along with potato and wheat) was shown to present the largest overall research deficits compared to the nutrients sweet potato is presently currently contributing to the food system. Sweet potato was found to present the largest research deficits in regions where its suitability is likely to increase with climate change. Although its cultivation is anticipated – through modelling – to expand on all continents, sweet potato has extremely high regional and global research deficits (Manners and van Etten, 2018) but represents a promising species to strengthen smallholders' capacity to adapt to climatic change.

# 12

# Agronomy

Sweet potato is a smallholder crop grown on marginal land with limited inputs. Average yields in many developing countries are lower than average yields in temperate countries, which are in turn well below the potential of the crop. Therefore, rapid improvements in productivity can be achieved easily with suitable cultivation techniques. Sites with high sunlight, an average temperature of 25°C or more, receiving a well-distributed annual rainfall of 1000–2000 mm have the highest yield potential. Yield is also dependent on the cultivar planted, the number of plants per unit area, the length of the growing season, the management of biotic and abiotic stresses and the cultural practices used during the crop cycle.

## SEED SYSTEMS AND PROPAGULE SELECTION

Most producers in the USA and Europe (Portugal, Spain, Italy, France) use virus-tested tissue culture materials to complement their own on-farm seed system with certified virus-free mother plants. These new seed systems have a significant positive impact on the yield and quality of the sweet potatoes. Average yield losses due to viral diseases in China are estimated at over 20% (Zhang *et al.*, 2009). However, responses to viral infection are cultivar dependent. A study aiming at comparing virus-tested tissue-cultured and field-derived plants from 14 cultivars concluded that 'Beauregard' showed the greatest gain with a 148% increase in total storage root yield when grown from tissue-cultured plants, while 'Wanum' showed the greatest loss, decreasing in yield by 23% under the same conditions (Okpul *et al.*, 2011). However, in Uganda, the cultivars 'Beauregard' and 'Ejumula' had highest disease incidence and severity in trials started with virus-free planting material, replanted in five succeeding trials with cuttings from the previous trial. It is observed that degeneration is very fast but that it is difficult to supply farmers with virus-free planting material every year (Adikini *et al.*, 2015; Gibson and Kreuze, 2015).

Tissue culture of sweet potatoes has received much attention and applications are numerous in sanitization and rapid propagation of selected genotypes. Meristem culture is often coupled with thermotherapy for sanitation. Several protocols have been developed and have shown their efficiency for *in vitro* propagation (Jarret *et al.*, 1984; Liu and Cantliff, 1984; Sonnino and Mini, 1993). Different micropropagation methods have been elaborated including photoautotrophic micropropagation; somatic embryogenesis for synthetic seed mass production; and bioreactors for mass propagation of nodes in liquid culture (Gaba and Singer, 2009). Sweet potato is unusual in that shoot regeneration may also occur from adventitious roots produced in culture. Significant differences in callus characteristics are apparent in the early establishment of cell cultures. Some of these differences are due to the protocols but genotypes are the most important sources of variation (Templeton-Somers and Collins, 1988) (Fig. 12.1).

In Zimbabwe, it has been shown that different cultivars react differently to micropropagation. The productivity of four micropropagated cultivars was compared to traditional cuttings for survival, vine length and root yield. It appeared that survival percentages for all the cultivars do not improve significantly with micropropagation and there are no significant differences in vine length between micropropagated and farm-retained planting materials 10 weeks after planting (WAP). However, the mean tuber weight differs significantly and this could imply differences in susceptibility to virus infection. It was concluded that the use of micropropagated planting material may result in increased yields for certain varieties, but most farmers do not have ready access to micropropagated sweet potato material (Matimati *et al.*, 2005).

**Fig. 12.1.** Sweet potato virus-indexed plantlets in plastic boxes containing approximately 100 plants prepared for shipment (photo: Y. Lamagnere, Vitropic SA).

An efficient protocol for the production of meristem culture, graft transmission and virus indexing for management of viral pathogens in sweet potato has been developed. The plantlets are first grown *in vitro* from the apical meristematic dome with one to two leaf primordia. Mericlones are then grafted on virus-sensitive *Ipomoea setosa* to detect potential symptoms, but in most cases no viral disease symptoms are seen on *I. setosa* leaves. This indicates that no viruses are translocated from meristem-derived scions to the virus-sensitive root stock (*I. satosa*). More than 80% of mericlones recovered from meristems 0.3–0.5 mm in size are tested as virus-free with this technique. Finally, during field exposure, only a low percentage of healthy plants were found infected with viruses when grown in a net house. This low-cost technique of producing virus-tested planting material could increase yields through efficient removal of pathogens (Alam *et al.*, 2013).

In Queensland, Australia, a seed system has been developed successfully for commercial sweet potato growers.) Pathogen-tested (PT) plants regrown from tissue culture are placed in pots in a safe screen-house and tested on *I. setosa* and with ELISA. The PT plants that pass these tests are propagated in a screen-house to keep them free from insects. When the PT plants are mature enough, cuttings are planted in field plots isolated from other sweet potatoes to make sure that they are not contaminated by insects. After 120–130 days the storage roots are harvested, cured for 4–5 days, washed and dipped in fungicide and sold to growers as a source of healthy material. The growers use these PT sweet potatoes to establish their own nurseries and develop their source of PT cuttings (Dennien *et al.*, 2013) (Fig. 12.2).

In Japan, a temperate country, the production of healthy propagules has to be done at a certain time of the year, rapidly and in sufficient volumes. For propagule production, a number of shoots are harvested from stock mother plants and they are prepared in single-node or multi-node cuttings for successive regeneration. A first approach is to micropropagate, under artificial light, leafy node and shoot cuttings which are about 2 cm in length, using a medium in multicell plug plastic trays. During a 2-week period, these microcuttings develop their roots and then produce shoot growth with 4–6 unfolded leaves. When these leafy node and stem cuttings are about 15–30 cm in length, they can be used as propagules. A second approach is done in an insect-proof greenhouse under natural light. The production rate has been shown to be greater when single-node leafy cuttings are used instead of multi-node leafy cuttings. Pathogen- and pest-free plug transplants can be produced in great numbers with minimum space and at low cost under artificial light and on a commercial basis in Japan. In fact, the photosynthetic abilities of young plants grown from tissue culture and under hydroponics with artificial light are as high as those grown in a greenhouse under natural light (Kozai *et al.*, 1998).

Single-node leafy cuttings can be used to produce low-cost, pathogen-free transplants but necessitate great care and high labour inputs. The yield and growth of plants obtained from transplants with four to six unfolded leaves

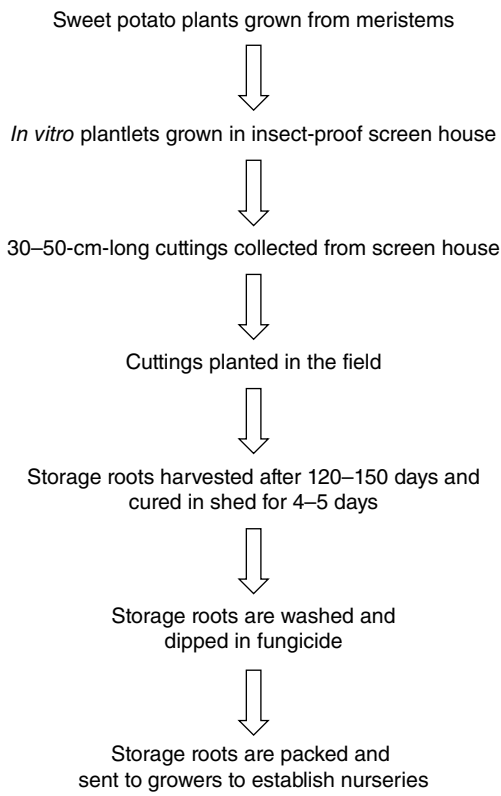


**Fig. 12.2.** Queensland, Australia, seed system developed for commercial growers, using virus-free *in vitro* plantlets (source: Dennien *et al*., 2013).

(about 15 cm shoot length) produced in plastic 55- or 35-ml multicell plug trays, similar to those used for vegetable production, have been compared with unrooted conventional cuttings (terminal vine cuttings about 30 cm long with seven to eight unfolded leaves). Overall, it was found that the growth and yield from plug transplants were significantly higher than those from conventional cuttings. Plug transplants with intact roots produced greater growth and yield, regardless of plug volume, than did plug transplants without roots. It appears that plug transplants produced with artificial light result in a higher yield of storage roots after a complete cycle in the field than those produced with traditional stem cuttings. These plug transplants have a survival rate close to 100% and a rapid and uniform growth because they already have a developed root system before their field transplantation, unlike traditional stem cuttings (Saifu Islam *et al*., 2002).

Sweet potato has an unusually high rate of somatic mutation, even as great as 20% in the cultivar 'Jewel' in the USA. The incidence of these mutations is higher in the storage roots than in the foliage, and propagation by stem cuttings rather than from storage roots appears to reduce the rate of mutation. The most frequent mutation affects the colour of the root skin and

flesh. Mutations may appear either as bud sports or as chimeras. It is too early, however, to assess the incidence of single-node cutting propagation on the rate of mutation. However, single-node plug transplants are a clearly promising technique for the rapid propagation of planting material. There are still several steps which require simplification for the technique to be used easily by commercial growers.

In the USA, where planting must be seasonal, farmers have to preserve their own or purchase seed stock before the yearly establishment of seedbeds (also called hotbeds). Selected storage roots are laid on the ground for sprouting. These are usually small sweet potatoes that are not sold for the market. In North Carolina, the most practical bed type is the field bed covered with clear plastic. The seed stock is usually bedded by the end of March and cuttings are ready for planting by early May. Good drainage is necessary to prevent rotting of the bedded roots. The width of the beds is often decided by the characteristics of individual machinery. Narrow beds of 1 m width are preferred because they can be covered with soil mechanically and, in some cases, a plastic cover is also placed mechanically on the beds. Each bedded seed root can produce up to 15 plants and quite often as many as six sprouts may grow on the same root at the same time. Transplants can be cut by hand from the seedbeds or with mechanical plant cutters; they are harvested from the seedbeds 6–8 weeks after bedding and then transplanted into sweet potato fields. The best plants are 20–30 cm long and have eight or more leaves (Smith *et al.*, 2009).

In East Africa, where several virus diseases are major constraints, it is necessary to develop new seed systems to provide growers with virus-indexed propagation material. A new protocol has been developed. Sweet potato mother plants prepared from meristems are tested for viruses, and the resulting plants are kept in insect-free greenhouses or in insect-protected screen-houses. The PT planting material can be distributed to growers who can further propagate the plants and plant them in the next season's fields. If this type of system were rigorously implemented, it is thought that the present yields would increase significantly (Loebenstein, 2016). There are, however, practical constraints for the establishment of such system, especially the cost of screen-houses.

In East Africa, and in order to ensure availability of planting materials when the rains start, dry season conservation is necessary and this requires some planning, as well as nursery preparation. Nurseries are protected from wandering livestock, which are attracted by the green tops. Some nurseries can be established in the field, in a swampy area, under the shade of a tree where moisture is preserved, or in places where water is readily available. Swamp nurseries are raised beds made in swampy areas where the soil is moist throughout the dry season. A nursery bed is prepared with loose soil mixed with compost or organic manure to favour vegetative growth. Healthy storage roots from selected plants are buried in beds established away from other sweet potato crops. When the vines are long enough (30–50 cm), they are cut at their base and planted directly into the new field (Stathers *et al.*, 2005).

In nurseries, rapid propagation is by mini vine cuttings having one to three nodes; the whole vine can be used, including young and older parts. Sharp knives and secateurs are used to produce these mini cuttings. They are then planted at very high density (10 × 20 cm), upright and with at least one node in the soil. They should be planted deep enough so that they do not become exposed after intense watering. The beds are watered twice a day to keep the surface moist and, after 3–4 weeks, the first cuttings are long enough to be harvested. The stem cuttings are cut 5 cm above the soil level, leaving some nodes to ensure subsequent axillary shoot growth from the buds and new stem cutting production 4 weeks later.

Healthy cuttings can be selected visually by identifying vigorous mother plants that are free of pests and diseases. It is also possible to select cuttings only from those plants giving the highest yields (positive selection), and these cuttings are likely to come from plants free of viruses. Vine cuttings taken from young plants (2–3 months) tend to produce higher yields than vine cuttings taken from old plants (4–5 months). This difference occurs because old plants are putting most of their energy into their storage root development and the tips of their vines are growing slowly. The vine tips of young plants grow vigorously and rapidly. If many cuttings are taken from a young plant, yield will be reduced, but if only one or two cuttings are taken from each young plant, there is no effect on final yield (Stathers *et al.*, 2005).

Stem cuttings from the tips of the vine are the best planting material. Cuttings from the middle and base can be used but they will produce lower yields, and cuttings from the base often carry weevil pupae, larvae and eggs. Vine cuttings can be kept for a maximum of 7 days but, in order to preserve the food reserves of the stem, most of the leaves should be removed, leaving very few at the tip. Once they have been tied in bundles, with their bases wrapped in a wet sack or cloth, they should be kept in a cool, moist and shady place. During the storage period, roots will develop at their base and the cuttings will have to be transplanted with great care so that they are not damaged.

Cuttings infected with leaf scab disease (*Elsinoe batatas*) or with weevil (*Cylas* spp.) pupae and eggs can be treated. Soaking cuttings in fungicide can help control leaf scab (15 min in a solution of mancozeb 80% wettable powder (WP), 3 g/l water). If vine cuttings are infected with leaf scab, free tuber sprouts can be used to produce healthy ones. The recently harvested storage roots are soaked for 5–20 min in a solution comprising 20% household bleach containing sodium hypochlorite, to destroy the spores on the outside of the roots. These are then established in an isolated nursery so that leaf scab does not spread. For weevils, the cuttings are soaked in insecticide solution (diazinon EC (Emulsifiable Concentrate), 3.5 ml/l water) just after cutting for at least 20 min so that the insecticide can penetrate the vine.

Long cuttings tend to produce higher yields than shorter ones. Generally, cuttings 30–40 cm long are recommended. In many countries, however,

smallholders use cuttings of approximately 60 cm long. If the internodes are short, shorter cuttings can be used, while longer cuttings will be used for varieties with long internodes.

Good cuttings can be collected from an established crop. In fact, 'topping' increases yield and the starch content of the roots because it minimizes competition for photosynthates between shoots and roots. Storage roots will attract the photosynthates, instead of them going to the shoots and buds. The limitation of vegetative growth enhances the starch concentration in the roots; but late topping at 3–4 months, after the storage roots have started to develop, is recommended. Topping can be carried out at bi-weekly intervals, depending on cultivars. It is appropriate to collect vegetative tops for livestock feed at this time.

## SOIL PREPARATION

Good land preparation always enhances fast sprouting and crop establishment and reduces weed competition. Soils contaminated with diseases, nematodes or weevils should be avoided and 4-year rotations are recommended to reduce damage from scurf and fusarium wilt. Sweet potato should not be replanted on the same plot. Furthermore, new sweet potato fields should not be planted next to old or existing fields. The use of a barrier crop between plots, or leaving a gap of approximately 100 m between plots, prevents pest and disease populations from moving from an old to a new crop. When land is scarce, it is better to remove storage roots and vines from the old fields and burn them, or feed them to livestock. In the tropics, sweet potato is rarely planted at the beginning of the cropping cycle. Forest or fallow land might not be suitable if their soils are rich in organic matter as this will promote rough, cracked, over-sized roots and vegetative growth but not storage root development.

Sweet potato grows on almost any soil but performs best on deep and moderately fertile soils. Preferred soils are sandy loams that are level or slightly sloped and well drained. Heavy clay soils produce irregularly sized and shaped storage roots. Light soils are preferred as, in many countries, land is prepared by hand. Ploughing and hoeing are necessary to turn over the soil, control weeds and produce the ridges or hills on which the stem cuttings will be planted. Mounds are common on flat land, whereas ridges along the slope contours are used on sloping land. The height of the mound or ridge is important as it ensures good drainage and makes harvesting easier. Sweet potato plants established on the flat are laborious to harvest. The heights and sizes of the mounds and ridges vary greatly, depending on location and the farmer. Ploughing the land with a tractor or bullock plough, and the practice of no-till using appropriate herbicides such as glyphosate, are techniques commonly used throughout the tropics.

## PLANT DENSITIES AND CROP ESTABLISHMENT

Sweet potato is planted as soon as there is sufficient moisture in the soil to secure root development. Planting is done by inserting the basal portion of the stem cutting into the soil. The insertion is sometimes done with the aid of a small forked stick, but in most cases it is done by hand. It is made in such a way that the cuttings are almost horizontal, with their basal extremity located fairly shallowly in the soil. If it lies too deep, root yield may be reduced. The aim is to establish almost two-thirds of the stem cutting length under the soil. In some countries, farmers produce a loop with the cuttings before burying them by hand to make sure that a great number of nodes are actually in contact with the soil. Once the cuttings are planted, they are usually hilled-up.

Cultivars with dispersing-type canopies and trailing stems are planted at wider spacings than cultivars with gathering-type canopies. In traditional cropping systems, dispersing-type cultivars can be left after harvesting the main crop to allow farmers to harvest a secondary crop from the vines rooting in contact with the soil. These storage roots are of smaller dimensions but are a valued food source.

Usually, two cuttings are established per planting hole on ridges or per mound. In some traditional systems of Papua New Guinea (PNG) where big mounds are used, up to 12 cuttings can be planted on a mound. Farmers always experiment to discover the optimum number of vine cuttings per mound for their different varieties. Depending on the type of weeding planned, spacing can vary from 50 cm to 1 m apart on the line, and lines can be established either in pairs (50 cm between the lines) or singly (1 m between the lines).

Sweet potato genotypes are able to compensate rapidly for variations in planting density and, as plant population per hectare increases, the number of storage roots per plant decreases, the mean weight per root decreases and the final yield per plant tends to decrease as well. The average size of the sweet potatoes produced is controlled more by spacing within the row than by the row width. A uniform stand of evenly spaced plants is important and the plants on each side of an empty space will usually produce 'jumbos' at the same time that properly spaced plants are producing normal sizes. Replanted plants to replace missing ones will, however, produce storage roots that are much smaller than are acceptable. Fast and complete establishment of the clonal population is, therefore, essential for the harvest of a homogeneous crop.

The effect of two different planting densities (35 × 100 cm and 70 × 100 cm) on the growth of two cultivars showed differences in leaf area (LA) per $m^2$ (LA/$m^2$). The LA/$m^2$ increases progressively up to 100 days after planting (DAP), and then declines slightly until 150 DAP. Increase in plant density reduces the number of branches per plant, indicating the high adaptation of branch formation in response to changes in plant spacing and density per unit of area. Some genotypes can produce higher total and marketable yields per hectare under high planting density, while others will produce higher total and

marketable yields per plant and per area under low planting density (Hamid and Sasaki, 2001).

In temperate countries, drag and precision-type transplanters are used to plant the crop. Precision equipment spaces the plants uniformly but it is often difficult to adjust when planting is done in light, soft or dry soil. Workers on seats mounted on a tool bar independent of the planting mechanism can minimize this problem and adjust plant spacing. Some processing-type cultivars developed at the Kyushu National Agricultural Station in Japan can be grown from seed tubers and still produce reasonable yields. The direct planting of small seed tubers (25–100 g) reduces costs and labour requirements compared to the use of rooted vine cuttings. Seed tubers cut into halves are planted horizontally or vertically. Those planted with the epidermis upwards produce higher yield than those planted with the epidermis downwards. The planting machine is self-propelled, semi-automatic and consists of a feeder and planting beak mounted on a two-wheel drive chassis. The feeder has eight cups which revolve intermittently and seed tubers are fed into the cups by hand. The planting speed is restricted by human efficiency (Hosokawa *et al.*, 1998).

In Saintes Marie de la Mer, southern France, an automatic tomato planter pulled behind a tractor has been adapted to sweet potato planting on sandy soils. The mix of the substrate used to root the cuttings has to be prepared with great care. It has to be compact enough to resist the mechanical transplanting manoeuvres but loose enough to allow the good development of a vigorous root system (Fig. 12.3).

The whole system is operated by only two persons, the driver of the tractor and a technician who is feeding the multicell trays of sweet potato plantlets (two-node cuttings) into the automatic vegetable transplanter. This type of planting system also allows the establishment of the drip irrigation system necessary to secure the growth of the young plants during the dry Mediterranean summer (Fig. 12.4).

**Fig. 12.3.** Plug transplants are produced in plastic multicell plug trays with an appropriate substrate to allow handling and root development (photo: Ph. Vernier).


**Fig. 12.4.** Mechanized planting on sandy alluvial soil in southern France. An automatic vegetable transplanter is pulled behind a tractor and fed with multicell plastic trays (photo: Ph. Vernier).

In temperate countries, when the soil temperatures are too low, black plastic mulch can be used to heat the soil and improve growth. In a study conducted in Québec, Canada, it was shown that average root weight, yield per plant and number of roots per plant increased with wider spacing under plastic mulch. It was observed that the yields continued to increase even when plants were growing under the cooler conditions of late September and early October. The results were, however, genotype dependent and 'Georgia Jet' had higher total and marketable yields than 'Beauregard' (Wees *et al.*, 2016).

## INTERCROPPING

Sweet potato is always grown in pure stands. However, when population pressure on land is high, gathering-type cultivars may be intercropped with beans and maize and, to a lesser extent, with cassava. When sweet potato is used as a cover crop to control weeds, dispersing types are preferred. Intercropping is easier to implement when sweet potato is planted on ridges, with the intercrop (e.g. maize) established between the ridges. In this case, light seems to be more important than nutrients in its effects on fresh storage root yield (Moreno, 1982). In Uganda, double rows of maize and four rows of sweet potatoes result in good yields in both crops. Furthermore, this combination produces a considerable volume of biomass per year and, in some areas, it can be cultivated twice a year, depending on rainfall (Stathers *et al.*, 2005).

In humid climates, when the soil is moist, roots will grow from the nodes of the stem in contact with it. If this occurs too soon in the crop cycle, nutrients supplied to these roots will result in a reduction of marketable yield. This can be prevented by lifting the vines so that the roots growing on the stem nodes are cut off. Intercropping sweet potatoes restricts hilling-up mounds or ridges by moving extra soil up on to the sides. This technique is valuable in reducing weevil damage when the soil is dry. It is particularly important to add more soil around the base of the plant to reduce the potential points of entry for weevils and to prevent attacks by rats when the storage roots are mature.

Maize and beans is the most widely cultivated crop combination among smallholders in Central America. The intercrop of sweet potato is considered a valuable alternative to make better use of fertilizers and other inputs applied to common beans. Sweet potatoes planted at 0.4 × 0.5 m can be intercropped in alternate rows up to 30 DAP with beans (*Phaseolus vulgaris*) planted at 0.2 × 0.5 m. This crop combination is grown only once and the field is left fallow during the rest of the year. At 60 and 90 DAP, the foliage biomass of sweet potatoes is not significantly different from the biomass of a monocrop. A reduction in storage root numbers does occur and is thought to be due to competition for nutrients during the early stages of the development of the intercropped sweet potato. However, no significant difference in the intercepted radiation is recorded between the monocrop and the intercropped sweet potato (Moreno, 1982).

Cassava has a slow initial growth and covers the ground usually between 90 and 120 DAP. Some cassava genotypes also have their foliage reduced considerably by leaf loss after 200–240 DAP and it is, therefore, possible to plant sweet potatoes in the interspaces before the harvest of cassava. Nutrients rather than light seem to be the main limiting factor for intercropping sweet potato and cassava. Erect types of cassava cultivars provide sufficient light, and cultivars that have their LA reduced at the end of their cycle allow a sweet potato crop to be harvested simultaneously. The proper management of Mg and K is the most critical aspect of maintaining this system (Moreno, 1982).

In certain areas of the West Indies, sweet potato is intercropped during the establishment phase of a perennial crop such as banana.

## WEEDING

Vines grow slowly during the initial phase, so it is essential to make sure that the land is weed-free until the crop is well established. Weeds can cause remarkable losses because they compete with sweet potato for light, water and nutrients. They may also harbour pests and diseases. Proper cultivation, field selection, rotations and timely applications can reduce the volume of herbicides used. The easiest is to ensure that weeds and their root systems are removed or buried deeply during land preparation. Herbicides can also be applied

most effectively before the stem cuttings are planted. Once plants are established, weeding should be conducted before they cover the soil and that is approximately before 30 DAP, depending on the spacing. Weeding frequency is reduced if the sweet potatoes are planted on ridges. Weeds are often left in the field between ridges or mounds as green mulch.

Some weeds may be controlled by the 'flush' control technique. After the field is prepared for planting, including pre-plant fertilization, sprinkle irrigation of the field promotes the germination of weed seeds near the soil surface. The field is then treated with a contact herbicide (e.g. Gramoxone™) to kill the initial growth. This may be repeated a second time. The sweet potatoes may then be planted after either 15 or 30 days, depending on the number of growths which were promoted to kill the germinating weeds. Fields should be kept weed-free during the first 4–8 weeks, after which the vines will cover the field completely. Weeds are also kept in check with cultivation performed by disc hillers during the hilling operation. A traditional practice is to dig ridges or mounds 2–3 weeks prior to planting, then to spray any weeds that emerge the day before planting vines. This ensures the control of perennial weeds for the first 6 weeks or so after planting.

The sweet potato crop, once established, requires little field management, apart from hilling-up weed control. Currently, weeds are minimized by hand weeding, inter-row cultivation and the application of Paraquat™ (100 g a.i./ha) over the crop. Alternative herbicide treatments have been examined in New Zealand and it was observed that hand weeding produced the highest marketable yield (26.7 t/ha), significantly more than all other treatments apart from acetochlor (2.4 kg a.i./ha), which produced 21.8 t/ha. Weed numbers were reduced significantly to 3.5% with acetochlor and to 16.2% with Paraquat™, compared to the unweeded plots. There was a strong negative relationship between early weed count and final total root yield (Lewthwaite and Triggs, 2000b).

## FERTILIZATION AND NUTRIENT DISORDERS

Sweet potato thrives best on sandy loam soils. Heavy clay soils often produce low yields and low-quality storage roots of irregular shapes because their formation is hampered by the sticky soils. Light sandy soils can, however, favour weevil infestation when the soil is washed down by rains and the roots are exposed.

Repeated cultivation of sweet potatoes on the same land increases the population of pathogens. The aim of a rotation is to control these, to restore the organic matter and fertility level of the soil and to reduce soil erosion to a minimum. Most of the nutrients absorbed by sweet potatoes are removed from the field when the crop is harvested. Depending on the nutrient reserves and deficiencies of the soil, this removal may be incurred only once before the yields

of the subsequent crops express nutrient deficiencies. For sweet potato, a comprehensive and illustrated description of nutritional disorders occurring in the field is available (O'Sullivan *et al.*, 1997). The adequate concentration ranges for sweet potato are shown in Table 12.1.

Cultivars may differ in their expression of visible symptoms of nutrient deficiencies. Visible symptoms often take the form of spectacular chlorosis due to reduction of the chlorophyll pigment in the leaves. Chlorosis can be interveinal when the tissues present a different colour than the lamina and when they are uniform. Chemical analysis of the plant tissues is used for assessing soil characteristics. The seventh and ninth youngest leaves are considered the most appropriate for this analysis. The blades are removed without the petiole and are dried between 60 and 70°C over 48 h (O'Sullivan *et al.*, 1997).

N deficiency can cause reduction in growth but is not easily recognized in the field. The symptoms are a uniform light green chlorosis of the leaves and a slow vegetative growth. Often, there is increased anthocyanin pigmentation of the young leaves, though P and S deficiencies also result in similar symptoms. In cultivars with young pigmented leaves, the symptom is a deepened purple colour. A critical concentration of 4% N has been determined on the basis of vine growth in solution culture (Table 12.1) and it agrees closely with the critical concentration in field-grown plants. Soil N measurements are difficult to interpret. A rough indication is that a concentration below 0.1% (Kjeldahl method) is considered to be very low and concentrations ranging from 0.5 to 1.0% N as suitable for good growth.

The recommendation for N fertilizers is between 30 and 90 kg N/ha. N supply can be provided by growing a leguminous crop (groundnut or beans)

**Table 12.1.** Critical nutrient concentrations for deficiency and toxicity.

| Nutrient | Critical concentration for deficiency | Adequate range | Critical concentration for toxicity |
|---|---|---|---|
| Nitrogen (%) | 4.0 | 4.2–5.0 | |
| Phosphorus (%) | 0.2 | 0.26–0.45 | |
| Potassium (%) | 2.6 | 2.8–6.0 | |
| Calcium (%) | 0.8 | 0.9–1.2 | |
| Magnesium (%) | 0.1 | 0.2–0.4 | |
| Sulfur (%) | 0.3 | 0.4–0.5 | |
| Chlorine (%) | – | – | 0.9–1.5 |
| Iron (mg/kg) | 33 | 45–80 | |
| Boron (mg/kg) | 40 | 50–200 | 220–350 |
| Manganese (mg/kg) | 19 | 26–500 | 1600 |
| Zinc (mg/kg) | 11 | 30–60 | 70–85 |
| Copper (mg/kg) | 4–5 | 5–14 | 15.5 |
| Molybdenum (mg/kg) | 0.2 | 0.5–7 | |

Source: adapted from O'Sullivan *et al*. (1997).

in rotation with sweet potato if the residues remain in the field. Low rates of N increase yields but higher rates can cause a yield decline by stimulating an exuberant foliage. N supply has a strong influence on the distribution of dry matter (DM), affecting root growth relative to top growth. Applications of N also increase the protein content of the storage roots, while sweet potato plants which are N deficient have a low protein concentration in their roots (Purcell *et al.*, 1982). Fallowing seems the safest way to obtain steady sweet potato yields; with extra inputs through inorganic fertilizer or poultry litter, storage root yields may be increased or decreased greatly if there is an excess of N (Hartemink *et al.*, 2001).

P deficiency can reduce growth by 50%. Low P is associated with a darker and bluish-green colour of the foliage. On the older leaves, stunting may occur. The chlorotic area appears orange or red and necrotic lesions develop, spreading the necroses as irregular patches until the leaf lamina is entirely brown and dry. Some genotypes may exhibit a purple pigmentation on the upper surface of the youngest leaves, especially on their veins, symptoms similar to those of N deficiency. However, in the case of P deficiency, there is no general chlorosis of the plant (O'Sullivan *et al.*, 1997).

P deficiency can be corrected easily by broadcast, side (band) or spot application of soluble P, such as triple superphosphate, ammonium phosphate or mixed fertilizers including N, P and K. Rock phosphate is cheap and efficient on acidic soils, but should be incorporated into the soil. On some P-fixing soils, very high rates (up to more than 100 kg P/ha) may be needed to correct the deficiency during the first year of application. The decomposition of organic matter can supply P to sweet potatoes and it has been shown that the response of the crop to organic matter is, in fact, the result of an increased P availability (Floyd *et al.*, 1988).

K deficiency is frequent and sweet potato has a high requirement for K as the storage root content is high. A crop of 20 t/ha removes approximately 100 kg K/ha, and much more if both foliage and roots are removed from the field. K deficiency tends to have a greater effect than N and P deficiencies on root yield rather than on foliage growth. In the field, symptoms develop when bulking of the storage roots takes place 2–3 months after planting. The oldest leaves turn yellow, while the youngest ones appear normal. Plants which are K deficient tend to produce small and thin storage roots of poor quality and, in orange-fleshed cultivars, the tubers have lowered carotene content. An application of between 80 and 200 kg K/ha is generally recommended. Mulches are bulky and therefore more laborious to apply, but their efficiency may be higher (Floyd *et al.*, 1988). If sweet potatoes are planted on ridges, a split application of K just before planting and 30 DAP is often used.

In China, the fertilizer level that gives the highest yield is 300 kg $K_2SO_4$/ha. The yield increase as a result of K application is due mainly to the increase in the root/top ratio, which leads to a greater amount of photosynthate translocation into the storage roots, producing their increase in size and weight. But

most of the quality parameters also improve with K application: root DM (%), Brix (%), carotene content and anthocyanin content (George *et al.*, 2002).

Mg deficiency can be the consequence of either a low content of Mg in the soil or an oversupply of K and Ca, which inhibit the crop's Mg uptake (O'Sullivan *et al.*, 1997). Deficient plants present a very pale overall colour. The chlorosis appears first on the older leaves and then spreads to the younger ones and may be accompanied by curling of the leaf margins and a drooping of the lamina. It is possible to correct Mg deficiency by incorporating 20–50 kg Mg/ha in the form of lime or magnesium oxide into acid soils or by applying magnesium sulfate (10–40 kg Mg/ha). The latter is often preferred for correcting the deficiency in an already established crop. Magnesium sulfate can also be applied as a foliar spray if the foliage is already covering the ground.

Ca deficiency symptoms are the development of necrotic tissues on young leaves. The addition of lime (40% Ca) provides the needed Ca and raises the soil pH. Agricultural lime should be applied to soils with adequate moisture and incorporated to a depth of 15 cm with a disc or rototiller 4–8 weeks before planting. Single and triple superphosphate contain 23% and 16% of Ca, respectively, and are good sources (O'Sullivan *et al.*, 1997).

Applications that are made above the required levels may result in excessive foliage growth at the expense of storage root growth, nutrient leaching into aquifers and an undesirable accumulation of salts in the soil. Sweet potato is grown extensively on highly leached acid soils and is adapted to soils of low to moderate fertility. On these soils, poor yields are most likely to be due to Al toxicity or, to a lesser extent, Ca deficiency. Mn toxicity or deficiencies in Mg, P or Mo are other potential limiting factors, but these elements play a less important role than do Al or Ca (Lla'ava, 2001).

Nutrient deficiencies in acid soils are a major problem and these soils occupy approximately 40%–60% of the total land area of the tropics. Preliminary experiments have been conducted to identify sweet potato cultivars with a tolerance to acid soils, low Mg availability and low P availability. There is considerable genetic variation in acid soil tolerance and it is unrelated to yield potential at the experiment site (O'Sullivan *et al.*, 2001).

## HARVESTING

Sweet potato roots are ready for harvest between 3 and 8 months after planting, much sooner than other root crops. In the tropics, most cultivars are harvested between 4 and 5 months after planting. The plant does not mature and will continue to grow as long as it has green leaves. The storage roots may reach their regeneration phase and initiate the growth of new shoots if nothing is done. The time to harvest can be assessed by sampling and digging a couple of plants. Cultivars differ in the length of the growing season required to produce optimum yields. Plant spacing also has an effect: the closer the spacing, the

longer it takes for the sweet potato to reach the desired size. Within the tropics, most varieties are harvested as soon as the roots reach marketable size. Most consumers prefer roots of 200–300 g with no damage but, within each plant, there is significant variation between roots and these need to be calibrated before marketing (Fig. 12.5).

Unmarketable 'jumbos' (1–3 kg) may continue their development if the plants are left in the field longer than desirable, but they usually crack and have a poor appearance. Sweet potato weevil outbreaks or rat damage may also increase crop losses if plants are left in the field. If the crop is harvested too late, the storage roots may become fibrous.

In many countries, sweet potato is grown mainly for home consumption and staggered harvesting is the usual practice. A few large roots are harvested and taken home for cooking, while the others are left on the plants to be dug later. The soil is heaped up over the remaining roots to allow them to continue their development; the heaping of earth will also protect them from light-induced greening and will reduce weevil access. Harvesting is usually done with great care to avoid injuring the roots. When sweet potatoes are uprooted on sunny days, they must be taken out of the fields within 2–3 h to avoid sunburn.

In mechanized cropping systems, a rotary or flail-type mower is used first to mow the vines at their base. The vines are then either removed or rolled into rows before harvesting. The roots are spaded out by hand or ploughed out with

**Fig. 12.5.** Each harvested plant presents roots of different sizes and weight and these have to be calibrated to satisfy market needs (photo: V. Lebot).

a double mouldboard plough, or with a modified potato harvester. The potato digger with its rod conveyor chain does an excellent job of lifting the roots to the surface but can cause considerable skinning in light, dry soils because the soil sifts through the conveyor very rapidly. In the USA, some potato diggers have been adapted to separate the vines from the roots, which are transferred to bulk bins, and considerable skinning may also occur in this case. Roots fall to the ground at the end of the digger, where they are selected, placed in crates and transported to the packing shed, where they are washed. Fleshy root damage is minimized when harvesting is done in dry soil (Smith *et al.*, 2009).

Sweet potatoes are then separated into different grades. Ideally, workers should have gloves to prevent damage from fingernail nicks. Each worker can have a sizing board to help grade roots for length and diameter. Packing minimizes deterioration of the roots within the container and cushions against impact and compression. During packing in the field, great care is taken to minimize damage that could result from bruises due to stacking or overfilling containers, or vibration bruises due to the roots moving against each other. Packages should be neither loose nor overfilled and should provide good aeration. In temperate countries, where most of the harvest will be stored for months, curing is an important operation. The purpose of curing is to allow rapid healing of cuts, bruises and skinned areas on storage roots, thereby preventing future infections. The rapid healing of wounds is dependent on maintaining the correct temperature, high relative humidity and aeration. Curing roots at 30°C and 80%–90% humidity for 4–7 days promotes the rapid formation of a toughened periderm. However, these curing conditions also favour respiratory activity and, consequently, DM loss. Therefore, curing should not be extended longer than the minimum necessary. Just after curing, the roots should be stored at 15–16°C and 80%–90% relative humidity.

# 13

# Pests and Diseases

Sweet potatoes are often damaged – and sometimes destroyed – by various pests and diseases, which are major limiting factors in their production. The most important diseases are caused by root pathogens capable of spreading systemically through the plant and, generally, it is not possible to restore the health of an infested plant. Planting materials, whether roots or stems, provide a perfect vehicle for pathogens and the most effective control is prevention.

## PESTS

Different pests feed and damage different parts of the sweet potato and have variable effects on final yields (Table 13.1).

Globally, sweet potato weevil (SPW) is the most important pest, and different species prevail in different geographic areas. The South American species, *Euscepes postfasciatus* (Coleoptera: Curculionidae), occurs in South America and a few other places. The Asian species, *Cylas formicarius* (Coleoptera: Brentidae) is now extensively pantropical. The African species, *C. puncticollis* and *C. brunneus*, are restricted to sub-Saharan Africa. SPWs are beetles with a four-stage life cycle (egg, larva, pupa and adult) and the duration of each stage is temperature dependent, the warmer the faster. It is, therefore, expected that the weevils will represent a main constraint with global warming (Fig. 13.1).

The female weevil lays eggs in holes that she has chewed in the vines or easily accessible roots. The storage root is the preferred site for laying eggs but, at the beginning of the growth cycle when the plants have not yet developed their storage roots, adults feed on the foliage and lay eggs on the vines. The larvae then pupate in the stem. Eggs hatch after 3–7 days and the larvae, which are curved and white, tunnel through the vine and root while feeding over 10–20 days before pupating. The development of the weevil, from the egg to the adult, takes approximately 30 days. When the vines are attacked by a large number of larvae, they become thickened and cracked. The damage can reduce the size and number of storage roots and the plants may die as a result

**Table 13.1.** Major pests of the sweet potato.

| Species | Common names | Damage | | |
|---|---|---|---|---|
| | | Roots | Stems | Foliage |
| *Cylas formicarius* | Sweet potato weevil (SPW) | × | × | |
| *C. brunneus* | SPW | × | × | |
| *C. puncticollis* | SPW | × | × | |
| *Euscepes postfasciatus* | SPW | × | × | |
| *Blosyrus* spp. | Rough SPW | × | × | |
| *Alcidodes dentipes* | Striped SPW | × | × | |
| *A. erroneus* | Striped SPW | × | × | |
| *Graphognatus* spp. | White-fringed beetles | | × | |
| *Omphisa anastomasalis* | Vine borer | | × | × |
| *Megastes grandalis* | Vine borer | | × | |
| *Diabrotica* spp. | | | | × |
| *Brachmia* spp. | | | | × |
| *Ochyrotica fasciata* | | | | × |
| *Cosmopterix* spp. | | | | × |
| *Bemisia tabaci* | Sweet potato whitefly | | | × |
| *Conoderus amplicollis* | Gulf wireworm | | × | |
| *C. fulli* | Southern potato wireworm | | × | |
| *C. scissus* | Wireworm | | × | |
| *C. rudis* | Wireworm | | × | |
| *Chaetocnema confinis* | Fleabeetles | | | × |
| *Acraea acerata* | Sweet potato butterfly | | | × |
| *Agrius convolvuli* | Sweet potato hornworm | | | × |

Source: adapted from Sorensen (2009)

**Fig. 13.1.** The sweet potato weevil (*Cylas formicarius*) larvae are tunnelling through the root causing serious damage and economic losses (photo: V. Lebot).

of stem damage. Low levels of infestation reduce storage root quality as the plants produce a bitter toxin, a terpenoid, in response to *Cylas* spp. feeding. Weevils are more dangerous in dry conditions because the adults can reach the roots through the cracks in the soil. The most effective way to control this weevil is removal and destruction of infested vines and root residues, removal of volunteer plants and alternative hosts and crop rotation with non-host

species. These measures have to be combined with several others during cultivation, such as hilling-up the plants to prevent soil cracks and applying sufficient irrigation.

Chemical control is not highly effective because weevils are protected by their development within roots and stems. In some countries, stem cuttings are dipped in pesticides before planting and this treatment can delay infestation for several months, but pesticides are expensive and toxic. The vines are dipped in an insecticide with 0.01%–0.05% active ingredients for at least 30 min and most organophosphorus or carbamate insecticides (acephate, carbaryl, dimetheoate) or all insecticides listed for post-planting are suitable. Once the plants are established, it is possible to treat them with fenthion (0.1% active ingredient, a.i.) using a knapsack sprayer, starting 2 weeks after planting (WAP) and repeating the application every couple of weeks until 2 weeks from harvest (Macfarlane and Jackson, 1989).

Despite intensive efforts to develop resistant cultivars, little has been achieved so far and attention is now turning to escaping weevil damage through deeper formation of storage roots and early maturing varieties which are less exposed to weevil infestation. Because weevils digest their food with the help of certain proteinases, it may be possible to block their digestion by incorporating proteinase-inhibitor genes into the sweet potato genome using transformation and regeneration protocols (Hue and Low, 2015).

The SPW female produces sex pheromones which attract males for mating. Sex pheromones of *C. formicarius* have been synthesized and are produced commercially in Asian countries as baits for traps that are placed in the fields above the foliage and covered to protect them from the sun and rain. The males are attracted, fall into the traps and are collected easily and removed from the field. In Taiwan, the use of pheromone-baited traps is estimated to save one to three applications of insecticide. A successful formulation for a sex pheromone lure has been developed; experimental results indicate that the use of pheromone-baited traps placed at a density of 4 traps/0.1 ha reduces damage to storage roots by 57%–65%. Use of such traps in combination with the pre-planting application of chlorpyrifos granules at 2.25 kg a.i./ha reduces damage to roots by 62%–75%. The effect is comparable with two applications of chlorpyrifos (80%–85%), one applied just before planting and the other when hilling-up (Hwang, 2000).

In Cuba and the Dominican Republic it has been demonstrated that the use of numerous traps is efficient in reducing weevil populations. If no traps are used, males attracted to a lure of sex pheromones are killed by spraying insecticides or a suspension of the fungus *Beauveria bassiana*. This fungus plays an important role in controlling weevils and farmers spray the fungus spore suspension around pheromone traps instead of using insecticides. Although it is quite clear that soil moisture is important for fungus survival, researchers still need to study the conditions that favour the effectiveness of the fungus in the field.

A light emitting diode (LED) colour ray has been used to determine the most effective light colour for capturing *E. postfasciatus*. Preference tests were conducted using four colours of LED ray (blue, green, yellow and red) at fixed light quanta in the laboratory. The weevils were found to prefer the green LED and subsequently the effectiveness of a green LED trap was compared with that of a sweet potato root trap in a field. The green LED trap was shown to be useful for monitoring the number of weevils (Nakamoto and Kuba, 2004). Table 13.2 summarizes some cultural practices for weevil control.

The rough SPW (*Blosyrus* spp.) can be a serious pest in East Africa. The larvae damage roots by digging grooves in the skin surface. This damage resembles that caused by millipedes or white grubs, and can reduce market value drastically. Furthermore, the deep peeling necessary to remove the damage can result in yield losses but, unlike damage caused by *Cylas* spp., it seems that no terpenoids are produced as a result of the attack. The use of clean material, sanitation, timely planting and crop rotation contribute to its control (Stathers *et al*., 2005).

**Table 13.2.** Cultural practices for weevil control.

| Cultural practices | Geographic areas where used | Results |
|---|---|---|
| Hilling-up | East Africa, Taiwan, Philippines, Indonesia, Oceania, Vietnam, India, Cuba, South America | Works well but should be implemented before the dry season and before the adults reach the roots and lay their eggs |
| Early harvesting | East Africa, Vietnam, Cuba, Philippines, South America | Harvesting 2 weeks earlier can reduce losses from more than 30% to less than 5% |
| Mulching | East Africa, Taiwan, India, South America | Use of rice straw mulches can reduce weevil damage. The soil surface should be covered soon after planting and the cover maintained until harvest |
| Intercropping | Philippines, India | More than 100 intercrops have been tested and the best results were obtained with coriander |
| Routine irrigation | Philippines, Taiwan, America, Vietnam, Indonesia | Prevents soil cracking and is therefore effective for farmers with reliable water supply |
| Field sanitation | Taiwan, Philippines | Is efficient when practised in a large ecosystem area or community. Infested roots must be buried deep in the ground (> 15 cm) |
| Flooding the field | Indonesia | Flooding of the field for more than 48 h can kill the larvae present in the roots |

Source: adapted from Stathers *et al*. (2005).

The striped SPW (*Alcidodes dentipes* and *A. erroneus*) is about 1.5 cm long and has remarkable stripes along the wings. The larvae are very similar to the SPW larvae when they are young but are much larger when they age. They feed inside the vines and, after pupation, the adults eat their way out. The larvae bore into the stems and sometimes into the storage roots. Cultural practices similar to those used for *Cylas* spp. are effective (Stathers *et al.*, 2005).

Other Coleoptera species, including larvae of *Diabrotica* spp. (Coleoptera: Chrysomelidae), cause extensive damage in the form of shallow holes on the outside of the storage root and some cause mining on the inside. A bioassay technique has been developed to evaluate sweet potato germplasm by using adults of the banded cucumber beetle (*D. balteata*) and spotted cucumber beetle (*D. undecimpunctata howardi*). A single beetle is placed on a piece of sweet potato storage root skin, which is embedded periderm side up in a Petri dish. The longevity of the beetles ranges from 12 days on a resistant cultivar to 123 days on a susceptible cultivar. This bioassay appears consistent with field results, indicating that it could be useful for evaluating resistance to *Diabrotica* spp. in sweet potato genotypes (Jackson and Bohac, 2007).

The vine borer, *Omphisa anastomasalis*, is the second most important insect pest after the SPW. The larvae of vine borers feed inside the vines. Heavy vine borer feeding results in reduced root growth, by up to 50%. The larval stages normally last 30–35 days and the larvae begin to bore down the vines as soon as they hatch. They usually pupate in the vine for a period of 2 weeks. Insecticide sprays are ineffective because the borers are inside the stems. Possible controls include hilling-up and the removal of alternate weedy *Ipomoea* hosts.

Lepidoptera species have been identified as foliar pests. Their larvae feed on the foliage, causing irregular-shaped cavities. *Brachmia* sp. (Gelechiidae), *Ochyrotica fasciata* (Pterophoridae) and *Cosmopterix* sp. (Cosmopterizidae) are responsible for severe damage from larval feeding, leading to complete defoliation.

The sweet potato whitefly, *Bemisia tabaci*, can be controlled using pyriproxyfen, but resistance to it may occur rapidly. Some results suggest that growers may be able to prolong the usefulness of pyriproxyfen by applying lower toxin concentrations (Crowder *et al.*, 2006).

The gulf wireworm (*Conoderus amplicollis*) is a yellow worm about 3 cm long, which feeds on the fleshy sweet potato roots. The larvae make small, irregular, ragged holes in the skin and burrow less than 0.5 cm into the fleshy roots. Their feeding gives the roots an unmarketable appearance and allows the entry and spread of pathogens. Damage is normally greater under dry conditions. Wireworms may remain in the field for several years since the larvae may take over 1 year to mature to adults. Wireworms are controlled with insecticides (Sorensen, 2009).

*Chaetocnema confinis*, or fleabeetle, is a black beetle, 0.1–0.2 cm long, which jumps in all directions when disturbed. The fleabeetle larvae feed on roots, leaving shallow tunnels below the periderm. The small tunnels

enlarge as the storage roots grow and cracks develop. The fleabeetles appear to move frequently from one feeding area to another and weeds may accentuate infestations.

The sweet potato butterfly (*Acraea acerata*) is found in all production areas of East Africa. The larvae eat the entire leaf, except for the midribs, and a severe attack may result in complete defoliation. Outbreaks are sporadic and usually occur at the beginning of the dry season. Consequently, severe attacks can be avoided by early planting and harvesting.

The sweet potato hornworm (*Agrius convolvuli*) can cause heavy defoliation, which usually takes place when the crop is still young. A single larva can defoliate a plant on its own and a large population can defoliate a complete field overnight. The larvae feed on the leaf blades, producing irregular holes. Turning over the soil exposes the pupae to predators. Manual removal of small larvae can prevent the increase of a large population in small plots (Stathers *et al.*, 2005).

## NEMATODES

Root-knot nematodes represent a significant problem in sweet potato, causing reduction in yield and quality of the storage roots. When susceptible cultivars are infested with nematodes, they wilt, appear stunted and their infested fleshy roots crack and show growth deformities. Storage roots of root-knot nematode-infested plants also develop galls. Several genera of nematodes have been associated with sweet potato in the field, but only root-knot nematodes (*Meloidogyne* spp.) and reniform nematodes (*Rotylenchulus* spp.) can cause significant damage (Overstreet, 2009).

Several *Meloidogyne* species infest sweet potato, including *M. arenaria*, *M. hapla*, *M. incognita* and *M. javanica* (Clark *et al.*, 2013). The diagnostic symptom is a round, spindle-shaped swelling on roots. Such galls occur on the infected fibrous roots and are often about 1–2 mm in diameter, but their size varies significantly between cultivars and sometimes they are too small to be observed visually. Additional symptoms are a reduction in vine growth, yellowing, wilting of foliage and abnormal production of flowers, indicating stress. Root-knot nematode damage can be severe in soils and under conditions of moderate drought. If the soil moisture is maintained at an adequate level during the growing season, the nematodes may have less effect on crop yield.

Clean or weed fallow prevent feeding. The use of resistant cover crops, for example green panic (*Panicum maximum* var. *trichoglume*), siratro (*Phaseolus artropurpureus*) or mucuna (*Mucuna pruriens*), is efficient. The selection of nematode-free propagating material is essential in reducing the population. Nematicide treatment in beds or nurseries can be effective. Several techniques are reliable, including fumigation of the soil with dichloropropene-dichloropropane or methyl bromide, incorporation into the soil of nematicides such as

ethoprop or fenamiphos and the use of systemic nematicides such as oxamyl. Carbofuran, a granular systemic nematicide, can be used before or at planting or in established crops, but is expensive for large fields.

Reniform nematode (*Rotylenchulus* spp.) control is much more difficult than for root-knot nematodes. Fields with severe infestation should be avoided. The use of a fallow period may be useful in reducing the population but its length is critical since reniform nematodes are able to survive many adversities. Hot water treatment is laborious and has not been adopted by farmers because it tends to reduce planting material vigour. The treatment of the soil with nematicides is more important than for root-knot nematodes as there are fewer alternative measures. These treatments are effective in reducing the population level by 80%–90%, but they are expensive. Nematicides such as dichloropropene and methyl bromide are effective but can be applied economically to small fields only (Overstreet, 2009; Clark *et al.*, 2013).

Many other nematode species can potentially affect sweet potato, but they have been poorly investigated. As the crop expands geographically, new nematode species are identified as pathogens. Stubby-root nematodes (*Paratrichodorus* spp.) have been identified in South Africa and the yam nematodes (*Pratylenchus* spp. and *Scutellonema bradys*) are affecting sweet potato in the yam belt of West Africa.

Nursery beds should, of course, be free of nematodes and infected plant materials should not be used. Unfortunately, root-knot nematodes survive in storage roots. Crop rotation is one of the most efficient preventive measures against nematodes. Soil solarization is another useful cultural technique used to reduce nematode damage. The ground is covered with transparent plastic film which is allowed to remain in place for several weeks. This technique is also efficient to reduce weeds and especially the *Cyperus rotundus* population. The most convenient approach is the use of resistant cultivars but, since races of nematodes can break resistance, it is important to combine different techniques (Clark *et al.*, 2013; Overstreet, 2009).

## BACTERIA

Four major diseases are caused by bacteria and each has a very restricted geographic distribution.

The soil rot known as 'pox' is caused by *Streptomyces ipomoea* and is very common in temperate areas of the USA and Japan. The symptoms include deformed roots, surface pits and scabby cavities, as well as black spots on the crevices. The lesions are normally smaller than 2 cm in size and usually less than 5 mm deep. Affected plants appear stunted and may die before the end of the growing season. Unfortunately, *S. ipomoea* is soilborne and can persist in the soil for years in the absence of sweet potato. The pathogen does not penetrate the periderm of healthy storage roots directly, but enters the fibrous roots of the plant by penetrating the wall of the epidermal cells. The development

of the pathogen is favoured by dry soil. Control measures include the use of resistant cultivars and soil fumigation. Rotations with other crops may reduce crop losses from soil rot in sweet potato. Because dry soil conditions favour disease growth, watering throughout the growing season is recommended (Clark *et al.*, 2013).

Bacterial stem and root rot caused by *Dickeya dadantii* (syn. *Erwinia chrysanthemi*) may appear in the field, in nurseries and during storage. The pathogen is widespread in warm climates and it has an extensive host range. Foliar symptoms are black, necrotic, water-soaked lesions. Lesions in the root develop more commonly in storage, with a characteristic black margin surrounding the lesions. In the USA, the cultivar 'Beauregard' is very susceptible to root rot but 'Centennial' and 'Porto Rico' are less susceptible than others. Controls include minimizing wounding of the roots, selection of propagating material from disease-free fields and the use of cultivars with tolerance to the disease (Clark *et al.*, 2013).

Bacterial wilt of sweet potato is caused by at least four different bacteria: *Pseudomonas batatae*, *Xanthomonas batatas*, *Bacillinium kwangsinensis* and *P. solanacearum*. The symptoms appear at any stage of the growth cycle. The base of the sprouts becomes water-soaked and turns yellowish to dark brown. Infected plants fail to develop roots. The use of resistant cultivars, the use only of disease-free storage roots for propagation in nurseries, crop rotation with a flooded crop such as paddy rice and establishing the crop during a cooler period of the year are necessary control measures.

Sweet potato little leaf disease is characterized by an excessive proliferation of young shoots and from leaf axils. Dwarfing of subsequent growth is caused by a mycoplasma-like organism (MLO). This disease occurs throughout the Pacific Islands and is a serious constraint in Melanesia (Papua New Guinea (PNG), the Solomon Islands and Vanuatu). Severe outbreaks of the disease occur with low rainfall and a distinct dry season. The first symptom is a yellowing of the veins, and progressively smaller leaves are formed until they are about one-eighth of the size of healthy leaves. The diseased stems are short and multibranched, with a gradual shortening of internodes, which gives the plant a bushy appearance. If the plants survive until harvest, only pencil-like storage roots will be found amid the mass of an extremely branched root system (Fig. 13.2).

The sweet potato black-spotted leafhopper, *Orosius lotophagorum ryukyuensis*, spreads the disease in Melanesia. A similar leafhopper, *Nesophrosyne* (*Orosius*) *ryukyuensis*, is spreading the disease in Japan. The leafhoppers suck in the MLO when they feed on the sap of diseased plants and then transmit the MLO to healthy plants. Sweet potato planting material may be infected with MLO but appear healthy because there is a long time (approximately 50–100 days) between infection and the development of symptoms. The use of cuttings with latent infection is the commonest way of spreading the disease. Yields are reduced by 30%–90% when there are disease outbreaks, especially during the dry season (Jackson *et al.*, 1984).

**Fig. 13.2.** The sweet potato little leaf disease is caused by a mycoplasma-like organism and causes the dwarfing of the plant and the production of smaller leaves (photo: V. Lebot).

Efficient elimination from phytoplasma and production of pathogen-tested (PT) plant stocks can be achieved with cryotherapy of tissue-cultured plantlets. The technique can be simultaneously for long-term storage of plant germplasm and for production of PT plants (Wang and Valkonen, 2008). However, in field conditions, the destruction of diseased plants (rogueing) offers a reliable and economical method of controlling little leaf disease. Several wild species of *Ipomoea* are hosts of the MLO, and they should also be rogued in areas where the disease is severe, and near nurseries where certified healthy stocks are maintained. Although the use of insecticides has not been investigated thoroughly, they may be efficient in nurseries to maintain healthy planting material and any of the following are likely to control leafhoppers: malathion (50%, 2 ml/l), acephate (75%, 0.75 gm/l), dimethoate (30%, 3 ml/l) or carbaryl (80%, 3 gm/l). To be effective, chemical control should be combined with intensive rogueing of infected plants. So far, no cultivars have shown any form of resistance to this serious disease. In severely affected areas, farmers are selecting volunteer plants on a regular basis and these spontaneous seedlings offer a good source of healthy planting material.

## FUNGI

Fungi cause infected sweet potato plant parts to die and rot. They occur on the leaves, stems and storage roots, and produce blackened areas which are

often circular because of the spread of the infection. There are various symptoms, which include the appearance of spots on healthy tissue; powdery areas; or filaments. Various pathogens are implicated and infect predominantly the roots or foliage (Table 13.3).

Leaf scab is the most serious foliar disease and is widespread throughout the humid tropics. It is caused by *E. batatas* (sometimes known under the name *Sphaceloma batatas*). The symptoms are prominent on the younger parts of the vine as distorted leaves and petioles with rusty brown lesions. The vines take on a stunted and 'scabby' appearance. Characteristic symptoms are small, scabby areas and small, oval lesions, especially along the midrib and veins of leaves. The lesions eventually become corky, resulting in shrinkage and complete leaf deformation (Fig. 13.3a). Yield losses from leaf scab can reach up to 60% in Melanesia (PNG, the Solomon Islands and Vanuatu). This fungus does not infect the storage roots.

Scab can be spread by splashing rain and by using infected cuttings for planting. Production is affected seriously if the fungus infects the crop during

**Table 13.3.** Major fungal diseases affecting sweet potato.

| | | Damage | | |
|---|---|---|---|---|
| Species | Common names | Stems | Foliage | Roots |
| *Elsinoe batatas* | Scab | × | × | |
| *Alternaria* spp. | Alternaria leaf spot | × | × | |
| *Cercospora bataticola* | Cercospora leaf spot | | × | |
| *C. ipomoeae* | Cercospora leaf spot | | × | |
| *Phyllosticta batatas* | Phyllosticta leaf blight | | × | |
| *Septoria bataticola* | Septoria leaf spot | | × | |
| *Coleosporium ipomoeae* | Red rust | | × | |
| *Albugo ipomoeae-pandurateae* | White rust | | × | |
| *Phomopsis ipomoea-batatas* | Phomopsis leaf spot | | × | |
| *Sclerotium rolfsii* | Sclerotial blight, circular spot | | × | × |
| *Fuligo violacea* | Slime moulds | | | × |
| *Physarum plumbeum* | Slime moulds | | | × |
| *Ceratocystis fimbriata* | Black rot | | | × |
| *Sclerotium bataticola* | Charcoal rot | | | × |
| *Rhizopus nigricans* | Bread mould | | | × |
| *Plenodomus destruens* | Foot rot | | | × |
| *Fusarium oxysporum* sp. *batatas* | Fusarium wilt or surface rot | | | × |
| *Fusarium solani* sp. *batatas* | Fusarium fibrous root rot | | | × |
| *Pythium* spp. | Mottle necrosis | | | × |
| *Monilochaetes infuscans* | Scurf | | | × |
| *Helicobasidium mompa* | Violet root rot | | | × |

Source: adapted from Clark *et al*. (2013).

[a]

**Fig. 13.3a.** Scab (*Elsinoe batatas*) symptoms on sweet potato leaves (photo: V. Lebot).

the growing stage. Recommended controls include crop rotation, as the fungus survives in debris; the use of clean planting material (cuttings produced from storage roots treated with a 10%–20% chlorox solution for 20 min); and the use of resistant or tolerant cultivars (Fig. 13.b). Breeding cultivars for resistance to scab is very efficient and several programmes have produced resistant genotypes, especially in the South Pacific (Tonga, Vanuatu and PNG) (Lebot, 2010).

Several fungicides can be used to control the disease. Just before planting, stem cuttings can be dipped for 15 min in a suspension of mancozeb 80% wettable powder (3 g/l). To control the spread of the disease, as soon as the symptoms appear, the foliage should be sprayed with mancozeb with a knapsack sprayer (3 kg in 1000 l water/ha) or with a motorized mist blower (3 kg in 250 l water/ha) and the treatment should be repeated every couple of weeks during the outbreak of the disease (Jackson and McKenzie, 1991).

Alternaria leaf spot is a widespread disease, which involves several species of *Alternaria* and causes characteristic brown lesions on older leaves. Very humid and cool weather (e.g. on the plateaus of Ethiopia or Uganda) is favourable for lesion enlargement, whereas drier weather reduces its incidence. The death of vines can occur and the ground under affected vines is covered with blackened stem and leaf debris, which are sources of inoculum. Infected material should be removed and burnt. Phomopsis leaf spot occurs in the same geographical region and causes irregularly shaped lesions on the upper and lower surfaces of the leaves. The same control measures apply to prevent the spread of this fungus (Clark *et al.*, 2013).

Cercospora leaf spot is present in the warm humid tropics of Asia, South America and Africa. The lesions caused by the fungi *S. bataticola* and *C. ipomoeae* may be circular or angular and are delimited by veins. There are no reports of control measures but selection of tolerant cultivars is the most practical approach.

[b]

**Fig. 13.3b.** Hybrids being field evaluated for their tolerance to scab (*E. batatas*) exhibit symptoms (front) and resistance (back) of their leaf canopies (photo: V. Lebot).

Phyllosticta leaf blight is present in the Caribbean region and in the southern USA and is favoured by humid climates. Septoria leaf spot also occurs in the same region and this disease is similar to Phyllosticta leaf spot but with smaller lesions. Red rust (*Coleosporium ipomoeae*) and white rust (*Albugo ipomoeae-pandurateae*) are both of minor importance and most cultivars have high levels of resistance, although susceptible seedlings are often observed and discarded in breeding programmes.

Scletorial blight caused by *Scletorium rolfsii* may be very destructive; it occurs almost exclusively in beds established for plant production and is therefore

a problem in temperate countries only. The symptoms are a sudden wilting of the sprouts, followed by their death. Disease development stops when the plants are established in the field. The control measures include the selection of an area that has not grown sweet potatoes for at least 3 or 4 years. The use of a fungicide such as dichloronitroaniline can reduce the incidence of scletorial blight.

*F. oxysporum* sp. *batatas* can be a serious pest in sweet potato. Fields are commonly infected through contaminated cuttings. Once in the field, the fungus penetrates healthy plants through open wounds. Yield losses may be up to 50% and are more likely in warm weather and in dry soils. Plants normally die within a few days of visible symptoms appearing. There are resistant or tolerant cultivars in the USA, including 'Jewel', 'Redgold', 'Nemagold' and 'Centennial'. In addition to resistance, other controls include crop rotation, selection of seed roots from disease-free fields and regular fungicide treatments (Clark *et al.*, 2013).

Black rot is caused by the fungus *C. fimbriata* and the symptoms include leaf yellowing of young plants; underground sections of the stem showing black areas; and circular, greyish lesions developing on the fleshy roots and causing a bitter taste. The fungal spores reproduce rapidly and are spread easily by mites or weevils during storage or transport to market, resulting in severe postharvest losses. This pathogen persists in the soil for 1–2 years in affected roots that have been left after harvest. Recommended controls include the use of disease-free propagating material, fungicide treatment, 3- or 4-year rotations, adequate curing of roots and the sanitization of any tool that may come in contact with the roots.

Charcoal rot causes some losses during storage in tropical and subtropical countries. As the disease progresses, the pathogen crosses the vascular cambium of the storage root and the pith rots progressively. Like most storage pathogens, *S. bataticola* requires a wound to enter the storage root. Proper curing after harvest reduces the incidence of this disease.

The fungus *Rhizopus nigricans* (*R. stolonifer*) causes an important postharvest disease. Affected roots develop a grey, fuzzy mould, turn soft and later turn dry and hard. The fungus enters the roots through wounds. Recommended measures include careful postharvest handling of the roots to prevent wounds, curing to heal any wounds and disinfection of the packing shed and equipment. Spores are carried by wind and flies.

Foot rot (*Plenodomus destruens*) and surface rot (*F. oxysporum* sp. *batatas*) are of minor significance overall but may be very destructive in some fields or storage facilities. Root rot (*F. solani* sp. *batatas*) causes decay of the fibrous feeder root system. It has been reported in China and resistant cultivars have been developed. Scurf caused by *Monilochaetes infuscans* is primarily cosmetic damage as dark brown spots develop on the skin of the storage roots (Clark *et al.*, 2013).

Many other fungi species can affect sweet potato and a recent review conducted in PNG recorded no fewer than 73 different species of pathogens, from *Alternaria* spp. to *Verticillium* spp. Cultural techniques are diverse and have a

great influence on disease development and spread. In the future, it is likely that intensive cultivation of sweet potato, land shortage, increasing population pressure and improved transportation will contribute to an increase in fungal disease spread and severity (Kokoa, 2001).

## VIRUSES

A survey conducted throughout the developing countries to assess the research needs identified as priorities by local scientists revealed that the control of viruses through varietal resistance, quality planting material and crop management was ranked first (Fuglie, 2007).

Viruses affecting sweet potato can be perpetuated and transmitted between cropping cycles by the stem cuttings used as planting material. These viruses are transmitted from one plant to another by sap-sucking insects such as aphids and whiteflies. The sweet potato feathery mottle virus (SPFMV) and the related sweet potato virus 2 (SPV2) are transmitted mostly by aphids. The sweet potato virus G (SPVG) and the sweet potato mild virus (SPMV) are transmitted mostly by whiteflies, and especially by *B. tabaci*. These viruses may cause only mild symptoms but it has been observed that symptomless plants may still have a considerable reduction in yield.

SPFMV is a potyvirus that causes 'internal cork', is found in many countries and many different strains have been identified. The symptoms are influenced by genotype, environment and the strain involved. The symptoms are mainly on older leaves and consist of the classic chlorotic and feather patterns associated with the leaf midrib. Cultivars have been developed in the USA and have shown high tolerance to 'internal cork'. For control, it is necessary to use stem cuttings from disease-free fields (Clark *et al.*, 2013).

The sweet potato chlorotic stunt virus (SPCSV) can cause some dwarfing of the plants and purpling or yellowing of the leaves. When the SPCSV (a crinivirus) and the SPFMV both infect a plant, they interact synergistically to cause the sweet potato virus disease (SPVD), a serious constraint to food productivity and security in East Africa. The symptoms include stunting of the plant and small malformed leaves with chlorotic mottle or vein clearing. Plants affected by SPVD usually produce small storage roots and a severe reduction in yield (Stathers *et al.*, 2005; Loebenstein, 2016).

The most convenient means of controlling SPVD is to plant cultivars that have resistance to virus diseases. The genetic basis of the resistance to these viruses has been investigated in Uganda and Peru. Molecular marker (AFLP and RAPD) studies yielded two genetic markers associated with resistance to SPCSV and SPFMV. It is thought that, in the presence of both of these viruses, additional genes mediate oligogenic or multigenic horizontal effects in the sweet potato progenies. Breeders are now integrating this information in their schemes combining different sources of resistance (Mwanga *et al.*, 2017).

SPVD occurs at all localities around Lake Victoria, in Uganda and Tanzania. All the fields are planted with local cultivars and the most important control practices are the planting of cuttings derived from only symptomless parents and the destruction of diseased plants. SPVD-resistant cultivars seem to be available but are perceived by farmers as having poor and late yields. Farmers observe, however, that their greatest need is the availability of new genotypes. Most farmers do not know when one of these seeds falls on the ground and germinates, giving a new plant (and new variety, because every seed is genetically different), farmers tend to ignore them, which is a pity as they could select new varieties from them and/or select plants with no viral load (as seedlings are virus free). The neglect of seedlings by these farmers is likely to hinder the development of more acceptable, SPVD-resistant cultivars and is probably contributing to the establishment of SPVD as a long-term disease problem (Gibson and Kreuze, 2015). In Melanesian countries, on the other hand, farmers traditionally adopt volunteer plants resulting from the spontaneous germination of the numerous seeds produced in plots where different varieties are associated and it is likely that this approach has a positive impact on the health status of their plants.

Other viruses affect sweet potato in East Africa. The most prevalent viruses are SPFMV, sweet potato mild mottle virus (SPMMV), SPCSV and sweet potato chlorotic fleck virus (SPCFV). There is limited genetic variability among East African isolates for SPFMV and SPCSV but high variability for SPMMV. Co-infections of SPCSV with SPFMV and/or SPMMV have been found to be responsible for over 90% of field-diseased plants, showing that these three are the most important viruses. Severe symptoms including chlorosis, wrinkling and leaf strapping caused by the combined infection of SPMMV and SPCSV are observed. These symptoms can be differentiated from those caused by SPVD, characterized by a severe stunting of the plant, distortion and either a chlorotic mottle or vein clearing of the leaves.

The name 'sweet potato severe mosaic disease' (SPSMD) has been proposed for the disease combining SPMMV and SPCSV infections. A comparative analysis of the interaction between the phloem-limited SPCSV and either SPFMV or SPMMV reveals more severe symptoms and higher root yield reduction as compared to singly infected plants. The immunohistochemical localization of SPMMV suggests that it may be exploiting mesophyll and epidermal cells and that there are interactions between SPFMV and SPMMV. These findings show the role of SPCSV in increasing the virulence of SPFMV and SPMMV. Efforts to control SPCSV seem to be the next step towards management strategies for sweet potato viral diseases in East Africa (Loebenstein, 2016).

In the future, it may be possible to test material in nurseries routinely before using it for field propagation. Real-time polymerase chain reaction (PCR) has been shown to be a more sensitive and specific detection method for these viruses compared to conventional PCR or ELISA assays (Dennien *et al.*, 2013).

## INTEGRATED PEST AND DISEASE MANAGEMENT

Integrated pest management (IPM) programmes have a promising future, especially for SPW control (Hue and Low, 2015). They involve biological and parabiological management approaches well adapted to low-input cropping systems. The management of *C. formicarius* focuses on using non-infested stem cuttings as planting material and increasing the action of enemies, such as predatory ants, and the fungus *Beauveria bassiana* (also known as *Bacillus bassiana*) which lives in the soil and can infect and kill adults.

A successful IPM programme has been conducted in Cuba. Sweet potato is an important staple food but the potential to increase production is limited by damage from the SPW, which causes up to 45% yield reduction. Farmers faced losses of 40%–50% of total yield and used to spray their fields 10–12 times a season. With the elimination of subsidized pesticides, the Centro Internacional de la Papa, Peru (International Potato Center, CIP) and INIVIT (Instituto Nacional de Investigaciones de Viandas Tropicales (Cuba)), have implemented an IPM strategy involving the use of pheromone traps to eliminate male weevils. The naturally occurring insect-killing fungus, *Beauveria bassiana*, has also proved very effective against the larvae, pupae and weevil adults. A smallholder-level industry for producing the fungus has been established and this effective low-cost technology has been adopted by farmers. The use of ants against weevils is another component of the IPM strategy adopted in Cuba. Two species of predatory ants, *Pheidole megacephala* and *Tetramorium guineense*, are common inhabitants of banana plantations. CIP and INIVIT have devised a simple system using rolled banana leaves to transport the ants from their natural reservoir to the sweet potato fields, where they prey on weevils. It has been shown that setting up colonies in the field 30 days after planting (DAP) can keep weevil infestations at low levels (3%–5%) (Lagnaoui *et al*., 2000).

In the Dominican Republic, estimates indicated average yield losses of 39% from weevil infestation and a 40% decrease in gross income for farmers. In the early 1990s a CIP pilot project involved crop rotation, deep ploughing, timely weeding and the use of sex pheromone traps. For farmers, pheromone traps are an attractive option because of their effectiveness and low cost. Initial acceptance of these traps was successful and 15% of all fields in the Dominican Republic were protected by the traps. On average, farmers who practised IPM produced higher yields. Without the traps, crop yield reduction was approximately 1.8 t/ha; and, with the pheromones, the damage was 0.7 t/ha.

In Okinawa, Japan, *E. postfasciatus* and *C. formicarius* are important constraints. Four strains of *B. bassiana* were isolated from farmers' fields and one was found to infect the two SPW species aggressively. A sex pheromone trap was designed, containing a small bottle with 0.5 g fungus; males were attracted, infected and allowed to escape. Later, it was observed that females were infected while mating. Overall, the advantages of this IPM system were a high contamination rate at low cost (Yasuda, 1998).

# 14

# Postharvest Quality and Marketing

## CHEMICAL COMPOSITION

All parts of the sweet potato plant can be utilized as valuable foods and they contain a variety of chemical compounds. The leaves are high in proteins and rich in soluble dietary fibre and the stems have insoluble dietary fibre. Leaves are high in mineral (particularly Fe), polyphenol and vitamin content (such as carotene and vitamins B2, C and E) in comparison with other vegetables (Ishida *et al.*, 2000; Padmaja, 2009) (Table 14.1).

On average, the dry matter (DM) of most cultivar storage roots is 30%, but this trait also varies according to cultivation practices. To be comparable, different varieties have to be planted at the same time in the same growing conditions and harvested together, but significant variations also occur during the life of the plant. The average values in the composition of DM content are presented in Table 14.2.

Approximately 80%–90% of the DM of storage roots is composed of carbohydrates consisting of starch, sugars and lesser amounts of pectins, hemicelluloses and cellulose. This composition influences quality factors such as taste, texture, firmness and mouthfeel. Starch is the most important component and, in countries such as China, it is extracted at home and village levels. Starches isolated from three Chinese cultivars have been shown to differ in granule size and particle size distribution but the amylose contents are similar (19.3%–20.0%). The pasting behaviour, swelling pattern and synergetic properties also vary. The quality of the starch noodle made from cultivar 'Sushu8' starch has been evaluated by both instrumental and sensory analysis and has been found comparable to that made from mung bean starch, a frequently used source for noodle production. It was found that the small size (< 20 μm) granule fractions of 'Sushu8' were more suitable for starch noodle making (Chen, 2003).

Variability in sugars among cultivars is very high and has been recorded as low as 5.6% in a local cultivar of the Philippines and up to 38.3% of DM in American cultivars. Although they have not been investigated thoroughly, the hundreds of cultivars found in Papua New Guinea (PNG) and the islands

 

**Table 14.1.** Chemical composition of sweet potato roots and leaves in the Pacific.

| | Storage roots (165 samples from 5 countries) | | Leaves (one sample from Hawaii) |
|---|---|---|---|
| | Means | Ranges | |
| Moisture % | 71.1 | 61.2–89 | 87.8 |
| Energy (kJ/100 g) | 438 | 125–635 | 151 |
| Protein % | 1.43 | 0.46–2.93 | 4.0 |
| Starch % | 20.1 | 5.3–28.4 | |
| Sugars % | 2.38 | 0.38–5.64 | |
| Dietary fibres % | 1.64 | 0.49–4.71 | |
| Crude fibres % | | | 1.2 |
| Lipid, fat % | 0.17 | 0.06–0.48 | 0.3 |
| Ash % | 0.74 | 0.31–1.06 | 1.3 |
| Oxalate (mg/100 g) | 89 | | |
| Calcium oxalate (mg/100 g) | 32 | | |
| *Minerals (mg/100 g):* | | | |
| Calcium, Ca | 29 | 7.5–74.5 | 37 |
| Phosphorus, P | 51 | 41.0–70.0 | 94 |
| Magnesium, Mg | 26 | 18.4–35.7 | 62 |
| Sodium, Na | 52 | 13.8–84.0 | 9 |
| Potassium, K | 260 | 129–382 | 530 |
| Sulfur, S | 13 | | |
| Iron, Fe | 0.49 | 0.16–0.94 | 1.0 |
| Copper, Cu | 0.17 | 0.08–0.28 | |
| Zinc, Zn | 0.59 | 0.27–1.89 | |
| Manganese, Mn | 0.11 | 0.05–0.26 | |
| Aluminium, Al | 0.82 | 0.24–1.14 | |
| Boron, B | 0.10 | 0.07–0.14 | |
| *Vitamins (mg/100 g):* | | | |
| Vitamin A (retinol + β-caro/6) | 0.01 | 0.008–0.014 | 0.18 |
| Thiamin | 0.09 | 0.073–0.099 | 0.16 |
| Riboflavin | 0.03 | 0.025–0.041 | 0.37 |
| Niacin | 0.60 | 0.38–0.77 | 1.14 |
| Pot. Nic. Acid = trp/60 | 0.32 | | |
| Vitamin C | 24 | | 11 |
| Vitamin D | 0 | | |
| *Limiting amino acids* | | | |
| First | Lys 70 | | |
| Second | Leu 80 | | |
| Trypsin inhibitor (TIU/g) | 13.4 | | |

Source: adapted from Bradbury and Holloway (1988).

**Table 14.2.** Average composition of sweet potato storage root dry matter.

| Component | % in dry matter | |
|---|---|---|
| | Mean values | Ranges |
| Starch | 70 | 30–85 |
| Total sugars | 10 | 5–38 |
| Total protein (N × 6.25) | 5 | 1.2–10 |
| Lipids | 1 | 1–2.5 |
| Ash | 3 | 0.6–4.5 |
| Total fibre (non-starch polysaccharides and lignin) | 10 | ? |
| Vitamins, organic acids and other components | < 1 | ? |

Source: adapted from Woolfe (1992).

of Melanesia are also low in sugars, allowing important daily consumption. When a raw sweet potato root is analysed, only sucrose, glucose and fructose are present. However, during the cooking process, starch is hydrolysed into maltose by enzymes (α-amylase and β-amylase). There are differences between varieties for the level of starch conversion into maltose. Some varieties which are not sweet when raw do not stay non-sweet after cooking, owing to maltose. Other varieties are not sweeter after cooking because of their very low β-amylase. When sweet potato varieties are assessed for sensory characteristics and consumer acceptability, relationships between maltose content with starch and DM contents are observed. Maltose content has a positive correlation with sweet flavour and sweet potato-like flavour (Laurie *et al.*, 2012). A comparison of four commercial varieties with 243 hybrids revealed that mean maltose content varied from 10.3% to 15.6% fresh weight and total sugars from 17.8% to 27.8%. Maltose and total sugar content were highly correlated, maltose being the dominant sugar in cooked sweet potatoes (Lebot, 2017).

Not enough research has been conducted on the volatile flavours of sweet potatoes. The American cultivars have a strong, sweet aroma; whereas, throughout the tropics, cultivars with a gentle aroma similar to roasted chestnuts are often preferred (Kays *et al.*, 1998).

Among the non-starch polysaccharides, hemicelluloses and cellulose, which are found in the cells walls, are grouped together as dietary fibre and play an important role in the nutritional value of sweet potato. They have an important function in the diet and give protection against colon cancers, vascular diseases and diabetes. They also probably play a role in the firmness of canned storage roots and, therefore, genotypes with high values are more appropriate for the canning industry (Woolfe, 1992).

The total protein content of the sweet potato is on average 5% on a dry weight basis and 1.5% on a fresh weight basis. There is evidence from work conducted in the USA and Taiwan that total protein is not distributed evenly throughout the root. There are higher concentrations in the proximal rather

than in the distal end, and higher concentrations in the outer layer of the flesh, which unfortunately is often removed when peeling.

The red, purple or blue types of pigments found in various parts of the sweet potato are due to acylated anthocyanins. The major ones, cyanidin and peonidin, are a natural source of stable pigments for the food industry. No fewer than 13 different anthocyanins have been identified in three US varieties (Truong *et al.*, 2012), 12 anthocyanins in 25 Vanuatu varieties (Champagne *et al.*, 2011) and up to 16 anthocyanins in one single Chinese purple-fleshed variety (Jiao *et al.*, 2012). In Japan, the purple-fleshed sweet potato cultivar 'Ayamurasaki' contains a high anthocyanin content and its extract has been shown to exhibit multiple physiological functions in the laboratory, such as radical-scavenging, antimutagenic and an ameliorative effect on carbon tetrachloride-induced liver injury and decreased blood glucose levels in rats. In addition, their role in restoring the liver functions and blood pressure levels in volunteers with impaired hepatic function or hypertension has also been confirmed. This cultivar is now recommended as a superior source for the production of foods with health benefits (antioxidants) and some foods and beverages already make use of the characteristics of anthocyanin pigments (Suda *et al.*, 2003).

Sweet potato anthocyanins are stable after heat treatment (Xu *et al.*, 2015) (Fig. 14.1). Their antioxidant effects are variety dependent and the total anthocyanin (TA) content of different varieties has been used as an indicator of the antioxidant activity of their extracts (Kubow *et al.*, 2016). Improvement programmes are now interested in purple-fleshed sweet potatoes (Truong *et al.*,

**Fig. 14.1.** Sweet potato anthocyanins are stable after cooking and purple-fleshed varieties are increasingly attractive to consumers because of their antioxidant properties (photo: V. Lebot).

2012; Todd *et al.*, 2015). However, the antioxidant activity of root extracts results from both anthocyanins and hydroxycinnamic acids. Several phenolic acids have been isolated including chlorogenic acid (CGA) and dicaffeoylquinic acids (CQAs). It appears that methanolic extracts of purple-fleshed varieties present high antioxidant properties because they present high total CQA content and because these have higher radical-scavenging activities than anthocyanins.

Variation in phenolic compounds, and their correlation with the antioxidant activity of extracts, show great differences between plant parts and the curing and storage processes, but the most significant effects are variety dependent. An analysis conducted on 295 varieties and hybrids (100 white-fleshed, 64 orange-fleshed and 131 purple-fleshed accessions) found that purple-fleshed accessions presented the highest mean CQA content. The most active free radical scavengers (antioxidants) were found to be the four CQAs (CGA, 3,4-, 4,5- and 3,5-diCQA) while the anthocyanins were found to be less active. The total antioxidant capacity of the sweet potato methanolic extracts is mostly linked to total CQA content (Lebot *et al.*, 2016).

Carotenoid pigments are responsible for the yellow and orange flesh colours (Fig. 14.2). Orange-fleshed roots contain higher total carotenoids and β-carotene content than white- and cream-fleshed cultivars. Trans- and β-carotene predominate. The analysis of 30 varieties reported β-carotene content maxima around 12.8 mg/100 g fresh weight (Champagne *et al.*, 2010). Differences in


**Fig. 14.2.** Carotene- and dry matter-rich sweet potato varieties are appreciated by consumers in the tropics when they present low sugar content (photo: V. Lebot).

content between studies can be explained by the different genotypes and environment, as well as by the extraction and analytical procedures. The effect of the age of the root is significant and, 80 days after planting (DAP), the yield and amount of provitamin A in the storage roots of orange-fleshed varieties are high enough to provide an adequate dietary intake. However, it has been shown that boiling the roots for 30 min causes a reduction in total carotenoids (K'osambo *et al.*, 1998). In Kenya, where vitamin A deficiency is common, orange-fleshed sweet potatoes were introduced and their consumption was promoted, along with other vitamin A-rich foods. The yields of orange-fleshed sweet potatoes were at least twice those of local white-fleshed sweet potatoes and their DM content exceeded 25% (Mwanga *et al.*, 2017).

The three most abundant acids found in sweet potato cultivars are citric, malic and succinic acids. The small quantities of soluble oxalates are similar to those in other root crops but the calcium oxalate content is very low and one-tenth of what is found in aroids, for example. The lipid content of sweet potato storage roots is also very low and nutritionally insignificant.

Sweet potato French fries are gaining in popularity around the world. The sensory texture attributes of French fries vary widely and are significantly correlated with chemical components such as the DM, starch and total sugar contents of raw sweet potatoes. Just as for the Irish potato (*Solanum tuberosum*), some varieties are adapted to processing into French fries while others are not suitable. DM and starch content in raw sweet potatoes are correlated with overall hardness, sensory surface roughness and crispness. Total sugar content is positively correlated with sensory smoothness and moistness, and negatively correlated with overall hardness (Sato *et al.*, 2018).

It seems quite generally recognized that consumption of sweet potatoes can cause flatulence. It is assumed that about 85% of the hydrogen gas produced results from the ingestion of starch and the remaining 15% from dietary fibre.

In contrast to the extensive work conducted on the roots, there is insufficient information on the chemical composition of the greens (Table 14.1). The DM of tops contains higher quantities of proteins and minerals than the roots. There is considerable variation between cultivars for DM and protein contents, and breeding for livestock feed is presently improving the chemical composition of the tops. Sweet potato leaves are rich in CQAs and have antioxidant properties. Lutein is also present to the extent of 29.5 mg/100g fresh weight (Padmaja, 2009).

## PHYSIOLOGICAL DISORDERS IN FRESHLY STORED ROOTS

Cultivars with low DM have a higher respiration rate and therefore a shorter shelf life. Sweet potato roots may remain dormant for a very short duration and roots usually sprout very quickly after harvest if there is an adequate

temperature and relative humidity. Roots frequently sprout if the soil moisture is high and the harvest delayed. There are differences between the dormancy periods among cultivars. The respiration of the storage root contributes to weight loss and alteration of internal and external aspects. Respiration is higher just after harvest and is reduced during curing and storage. Damaged sweet potatoes have an increased rate of respiration compared to non-damaged ones. There is starch degradation during sprouting, and sprouting after harvest is attributed directly to temperatures that are too high (Ravi and Aked, 1996; Ravi and Saravanan, 2012).

Hardcore is a disorder in which roots remain hard after cooking and are unpalatable. It is attributed directly to temperatures that are too low. Symptoms of chilling injury in storage also include flavour changes and flesh that remains hard after cooking. Cold temperatures modify pectic substances so that the tissues remain rigid when cooked. Hardcore develops in storage roots exposed to 1.5°C for 1 day or to 10°C for at least 3 days, but cured roots are less sensitive to chilling and recover better from injury. Several factors have been shown to increase the occurrence of hardcore, including the cultivar, chilling temperatures and length of subsequent exposure to non-chilling temperatures. In Japan or the USA, if chilling occurs in the field during harvest or during transport, rotting may occur in sweet potato roots much later during storage. When roots are held in a warm, low-humidity environment for an extended period, they may develop a white, dry, spongy internal tissue. This internal breakdown of the flesh is referred to as pithiness. Proper control of curing and a good storage environment, coupled with the selection of adequate cultivars with a good shelf life, can minimize internal breakdown (Clark *et al.*, 2013).

## MARKETING AND QUALITY STANDARDS

From a marketing point of view, there are two groups of cultivars. There are those intended for processing (traditional or industrial), which are often very high in DM and have a white flesh; and those for the fresh roots market. In this latter group are the 'moist' North American types of cultivars with low DM content and high sugar and carotene contents, and those with much higher DM content and low sugars for daily consumption in developing countries. The quality standards are not the same for the two groups.

Depending on countries' requirements for fresh roots, there are different grades based mainly on the average length, width and individual weight of the roots. In all grades, the qualitative requirements are firm, smooth, clean roots, free from disease, insects and cracks. In temperate countries, roots also should be free of chill injuries and internal breakdown.

The practical operations involved in the preparation of fresh roots for the market involve washing and disinfecting, polishing, waxing, inhibiting sprouting and curing immediately after packing. Washing and disinfecting consist

of treating the surface of the roots with a chemical to prevent the entrance of pathogens. Much of the bruising and skinning that takes place in preparing sweet potatoes for the market can be avoided by putting them in buckets of water containing 50 ppm chlorine rather than onto hard surfaces. Polishing consists of removing dirt from the surface of the roots and brightening the natural colour of the skin. This is done by hand, either with bare hands or by rubbing a soft cloth on the surface. The application of a thin layer of wax on the surface of the roots is done immediately after the roots are washed, and special machinery has been developed for this purpose. The layer of wax is supposed to reduce the rate of transpiration, thus reducing losses in carbohydrates.

In general, sprouts on roots destined for the fresh market are extremely undesirable (Smith *et al.*, 2009). In the tropics, sprouting occurs frequently as a result of prolonged storage in conditions of high temperatures and humidity, and sprouts are generally broken off as soon as they appear. Their removal exposes the roots to attack by pathogens. However, more research is necessary to identify efficient sprout inhibitors of economical and practical use.

Knowing that most roots are usually cooked (boiled or baked), several other characteristics are also important. The quality of roots after cooking is a complex combination of colour, flavour, mouthfeel, texture and fibre content. The way quality is perceived is often very variable between cultures and countries (Fig. 14.3). The cooking time and carbohydrate transformation associated with cooking quality are mostly genotype dependent. Sweetness varies significantly


**Fig. 14.3.** Carotene-rich (left) and anthocyanin-rich (right) varieties for sale in Australian supermarkets (photo: V. Lebot).

between cultivars and is the dominant sensory attribute characterizing flavour (Laurie *et al.*, 2012). Cultivars can be grouped into categories based on the concentration and relative sweetness of individual sugars, expressed as sucrose equivalents per 100 g DM and ranging from very high to very low. It appears that all categories are present in most countries (Kays *et al.*, 2005).

In Italy, qualitative traits of different sweet potato cultivars were evaluated and four cooking methods were compared. High antioxidant activity was found in fried potatoes, and microwaving did not report any significant qualitative variation. It appears that ancient and new cultivars can be cultivated in temperate climate conditions and show interesting qualitative properties, especially as a result of the presence of antioxidant compounds, giving new opportunities for consumers and producers in Europe (Nicoletto *et al.*, 2017).

## STORAGE METHODS

Storage at high temperatures may result in excessive and rapid quality changes. The development of pithiness or internal cavities may occur in the roots and their severity differs with cultivars. A reduction in starch content with a corresponding increase in total sugars occurs as early as the second week of storage. High weight loss and sprouting are accompanied by a considerable decrease in moisture and a consequent increase in DM content. Investigation has been undertaken into changes during storage in carbohydrate level, digestibility, α-amylase, trypsin inhibitor activity and pasting properties of the roots of cultivars differing in DM content. Most genotypes show a slight decrease in starch content during the first 180 days of storage. The decline in starch content is accompanied by α-amylase activity in the first 60 days of storage. Storage also reduces flour-pasting viscosities with up to 30% decline in peak viscosity (Zhang *et al.*, 2002).

Ideally, sweet potatoes should be stored at temperatures of 13–15°C with 80%–90% relative humidity. In Japan or in the USA, where roots are stored for many months, this is achieved in specially designed storage houses where these requirements are controlled properly. Cured roots store better than uncured ones. Sweet potatoes can be cured and stored in bulk bins. Curing treatments in production areas where this is practised include storage at 30°C and 90%–98% relative humidity for 4–7 days with good ventilation, and then storage at 13–14°C with ventilation (Smith *et al.*, 2009). The benefits of curing include increased sugar content and flavour, suberization of periderm tissue to protect the roots against bruises and disease attack, and improvement of shelf life by reducing respiration and water loss. Sweet potato roots lose about 3%–6% of their weight during the curing process. Storage roots will not store well if wet soil conditions are prevalent just prior to harvest, if they are chilled below 10°C for a period of over 5 days after harvest or if they are not cured properly. Significant changes in the carbohydrate fractions of cured and non-cured

sweet potatoes occur after cooking. Baked cured roots have higher levels of total sugars and dextrins and less starch than non-cured roots baked just after harvest (Ravi and Akad, 1996; Padmaja, 2009).

Because sweet potatoes are difficult to store, farmers tend to avoid storage and harvest them only when needed, leaving them in the ground sometimes for months after attaining an adequate size. There are significant variations between genotypes, but most of them are prone to insect or rodent attacks when stored in the ground for too long. Most cultivars are tender and their quality deteriorates rapidly soon after harvest, because they lose water and weight during storage, and this subsequently alters the texture and taste. Some diseases can cause severe losses from rotting and off-flavours during storage, and weevil and other pest attacks can cause great damage.

It is, however, possible to store fresh roots and this allows farmers to harvest as soon as the roots are mature so that the field is available for other crops, or for a managed fallow. The proper storage of fresh roots enables village communities to eat fresh potatoes for a longer period after harvest. In some cases, the stored roots can be sold later in the season when fresh roots are not available and therefore generate income during the off-season. Successful storage depends on the careful selection of only good quality roots free of pests or diseases, their preservation in especially designed stores and the regular control of their status at frequent intervals (Stathers *et al.*, 2005).

Pit stores (holes dug in the ground) have long been used by farmers around the world, from Polynesia to India and Africa. There is a variety of sizes and shapes. These pits are dug in dry ground not subject to flooding. They are lined with dry grasses or ferns, which act as a cushion and protect the roots from damage, while absorbing humidity. The quality of the roots selected for storage is critical. The roots are placed carefully and the pit is then sealed with more dry grasses and covered with soil up to ground level. A ventilation system is put in place and, finally, a shed erected over the pit to protect it from the sun and rain.

Clamp stores are made on a raised mound of earth above ground level. The base of the clamp is covered with dry grass for cushioning and absorbing excessive moisture. The roots are then piled carefully and covered with more grass and soil to seal the clamp to prevent the roots from drying out and pests from entering. The mound is then covered with a roof to protect it from the sun and rain, allowing some space in between for good ventilation. Roots can be stored for up to 5 months in pits and clamps as long as there is proper routine maintenance every 2 weeks or so to avoid root rotting, rodent and insect damage (Stathers *et al.*, 2005). It is always better to make several small pits or clamps rather than a single large one because the entire content must be removed when the pit or clamp is opened. If a roofed structure cannot be built, the storage unit should be constructed in a shaded area.

Village storage structures made of coconut leaves and bamboo have been tried in the Philippines. Their slatted walling provides the stored roots with

diffused light, which partly suppresses sprouting. These are much cooler than the surrounding environment. High relative humidity is maintained by placing water in bamboo troughs, and sweet potatoes can be stored in these conditions for up to 3 months without much loss in quality.

## TRADITIONAL PROCESSING TECHNIQUES

Sweet potato is traditionally processed into dried chips and flour to preserve the product. Drying and processing into flour aims to increase shelf life, increasing the nutritive value per unit of weight, creating income opportunities and diversifying the range of uses. Traditionally, both roots and vines are also used for livestock feeding, and simple processing techniques are applied to improve the quality of the feed.

Sun drying is the simplest dehydration technique used by smallholders. The roots are washed, peeled and sliced and exposed directly to the sun. This technique has several drawbacks, including dependency on climatic conditions, high labour requirement, difficulty in maintaining hygienic conditions and lack of control over enzymatic oxidation. Different cultivars have different properties and farmers experiment and test several varieties before selecting the best one for processing, which is often not the one they prefer to consume fresh.

In practice, the various steps involved in the process are:

**1.** Selecting healthy roots.
**2.** Cleaning and peeling: usually with a simple kitchen knife.
**3.** Washing: often in drum washers (200 l) with brushes fixed on a horizontal axle and allowing 40 kg of roots to be washed in 10 min using 30 l clean water.
**4.** Slicing: once cleaned, the roots are pre-dried for 10 min and a mechanical slicer cuts the roots in uniform slices approximately 0.5 cm thick.
**5.** Soaking: the slices are soaked in water for 90 min (parboiling for 5 min or more reduces future insect infestation of the dried chips).
**6.** Drying: the slices are sun dried on raised trays for approximately 6 h in good conditions, depending on the rate of turning of the chips as they dry.
**7.** Grinding: the dried chips are milled into flour.
**8.** Storing: dried chips and/or flour are stored in bags protected from pests and sunlight.

In China, farmers fulfil simple processing such as slicing and field-dried chips after harvest and then sell directly to middlemen or processors for fine processing done in factories. Dried chips are used for the production of starch, which accounts for approximately 70% of the product. Organic products made from dried chips include ethanol, monosodium glutamate, citric acid, lactic acid and amino acids. Ethanol is the most important product and about 2.7–2.8 kg of dried chips are necessary to produce 1 l of ethanol fuel (Zhang *et al.*, 2009).

In East Africa, metal storage bins made from smooth or corrugated galvanized metal sheets are traditionally used to store dried products. They are placed on platforms to allow the air to circulate under the base and to prevent ground moisture causing corrosion. A roof provides shade and reduces overheating. These bins provide good protection against insects and rodents but can be used for well-dried products only (Stathers *et al.*, 2005).

In Uganda, farmers process the roots into dry chips, which constitute a very important off-season staple. The dried chips are dipped in water, boiled and salted. They can be eaten mixed with millet or sorghum, or ground into flour for making the local bread known as *atap*. However, even when dried properly, these chips succumb to insect infestation (*Araecerus fasciculatus*) after 2 months of storage in bags. Salting sliced sweet potato chips prior to drying seems to be a promising approach to control damage by *A. fasciculatus*, and an application rate of salt at 2%–3% (w/w) is recommended. Apparently, at this level, the culinary quality of the dried chips is not affected significantly, but it is necessary to re-dry the chips periodically because the salt tends to increase their moisture content (Agona *et al.*, 1998).

The effect of drying on the carotene content has been studied and the losses in flour made from dried chips varied between 16% and 34%. Hot-air cross-flow drying retains more provitamin A than sun drying. The shape of the sweet potato chips (chip or crimped slice) has an impact on the provitamin A retention during sun drying and it has been shown that crimped slices retained more provitamin A. Flour from orange-fleshed sweet potato is, therefore, a significant source of provitamin A (Bechoff *et al.*, 2009). The effects of storage temperature, water activity and oxygen level on the degradation of carotenoids and formation of volatile compounds during storage of dried chips were also evaluated. It is suggested that carotenoid degradation in dried sweet potato was by autoxidation (Bechoff *et al.*, 2010a).

In Uganda, it appears that the losses of total carotenoids during drying are generally low (15% or less). Total carotenoid retention in orange-fleshed sweet potato is not dependent on the type of dryer (solar or sun) but is variety dependent. High percentage losses of total carotenoids are also correlated with high moisture content and high carotenoid content in fresh sweet potato roots. However, it has been observed that, after 4 months' storage at room temperature, losses of total carotenoids in dried sweet potato chips can reach 70%. Again, the choice of the right variety contributes to reduce losses of carotenoids during drying (Bechoff *et al.*, 2010b).

Starch production is one of the major uses of sweet potato. In areas where the climatic conditions do not allow proper sun drying of the roots, simple techniques are used by farmers (Woolfe, 1992; Zhang *et al.*, 2009). In China:

**1.** Roots are cut by hand.
**2.** They are crushed by machine and sieved to remove waste such as peel and fibre.

3. Starch is left to settle in a tank and supernatant removed.
4. Water is added and the starch is settled and sieved once more.
5. Wet starch is transferred to jute bags to drip-dry for 1 day.
6. Starch is air-dried outside at ambient temperatures.

In some cases, an acid paste formed during the starch preparation by the action of lactic acid bacteria is added to the slurry to enhance coagulation and separation of starch, fibre and proteins. The starch settles, leaving the other components suspended above. The supernatant is then removed. In Japan, starch extraction is kept alkaline by the addition of lime to raise the pH to 8 and this enhances yield and improves colour. Centrifuges are used increasingly in place of settling tanks.

In China and Vietnam, sweet potato starch noodles are a popular food and are made mainly by smallholders. Fresh roots first are processed into starch, which is stored in open sheds. The smallholder process used for producing noodles is as follows (Woolfe, 1992; Padmaja, 2009):

1. The dried starch is put into large, round vessels.
2. Water at 80°C is added to gelatinize the starch.
3. Sulfite is added and stirring is done by hand or mechanically.
4. Native starch is added to make a 5% dough.
5. Stirring is done by hand or mechanically.
6. The mixture is put into a cylinder (30 × 40 cm) with holes in the bottom.
7. The material is pressed through the holes and the strings fall into hot water.
8. The strings are kept separated using sticks.
9. The strings are transferred to cold water.
10. The strings are dried indoors, then outside and noodles are obtained.

There are some local adaptations or improvements of the process but the basic principle is the same (Collado and Corke, 1997).

Fried chips are homemade in many tropical countries and are available in small, snack quantities in local markets. When cultivars rich in carotenes and/or anthocyanins are used, the resulting chips are of bright colours and are very attractive to children and adults alike. They may be salted, spicy or left natural, according to local tastes. Sweet potato chips are marketed and distributed on a large scale in the USA.

The postharvest life of storage roots can also be extended by fermenting them into silage or by sun drying them into chips for livestock feed. The roots are grated manually or mechanically into 1 × 1 cm or 5 × 5 cm 'chips'. The cutting into regular pieces facilitates air circulation and drying. The chips are then spread in a 3 cm layer and turned regularly. Hot-air drying is possible but expensive, as the final product needs to reach 12%–13% moisture content to store properly.

Traditionally, sweet potato leaves can be used for feeding pigs in fresh, dry and ensiled forms. In China, a very high proportion of the total annual

production is used for this purpose and, in some areas, fresh vines and leaves are harvested for pig feed three to four times during a growing season. Good silage is brownish green in colour and has a pleasant fruity smell that is attractive to animals. The breeding of cultivars with high biomass, DM and protein contents may lower the price and raise sweet potato feed energy and protein levels closer to those of cereals, but more research is needed. A number of cultivars have been evaluated in central Vietnam with respect to the biomass yield of the leaves, stems and roots under different harvesting intervals and defoliation techniques, with the aim of selecting the best for forage production. The biomass yields of leaves, stems and roots vary according to cultivar, season and defoliation technique. The best options in terms of leaf and stem production is to cut at intervals of 20 days with a defoliation of 50% of the total stems, since greater defoliation can reduce root production. Sweet potato leaves have a crude protein content of 25%–30% in DM, which is markedly higher than in the stems. The leaves can be preserved as feed for pigs by ensiling with either sweet potato root meal or sugarcane molasses as additives. They are high in protein content compared to other protein-rich forages, and lysine is the first limiting amino acid (An, 2004).

In the Red River Delta area near Hanoi, Vietnam, on-farm trials have been carried out to see if using fermented vines could reduce women's labour, processing costs and improve pig growth efficiency. Different mixtures of sweet potato vines, maize and cassava meals, rice bran, sun-dried chicken manure and salt were fermented and the results were compared for their nutritional values. Sweet potato vines fermented with chicken manure had higher crude protein, DM and ash contents than the other mixtures. None of the preparations contained aflatoxin or *Salmonella*; and *Escherichia coli*, although present in the original samples, disappeared after 14–21 days of fermentation. Pigs fed with the preparation containing chicken manure achieved higher growth rates than those fed with fresh sweet potato vines, and this mixture was considerably cheaper. However, while sweet potato vine fermentation addresses storage problems and increases pig growth, some farmers are concerned about balancing the feed when the volumes to be mixed together are important (Peters *et al.*, 2002).

## INDUSTRIAL PROCESSING

The production of quality dried products involves the following pre-processing operations:

**1.** Grading: inspection of health status, damage, cracks and size.
**2.** Cleaning: removal of soil by rod chains and water sprays or dry brushing.
**3.** Pre-heating: immersion in hot water (30 min at 70°C for dehydrated flakes, 30 min at 52°C or 8 min at 63°C for canning).

**4.** Peeling: hand paring with abrasive rollers, or steam peeling and washing.
**5.** Trimming: removal of surface blemishes and fibrous ends (root tips).

Sweet potatoes processed in this way are then dried and reduced to flakes, which can be reconstituted into mashed sweet potato or incorporated into various products. The dehydration process starts with pre-processed roots and reduces them into slices, dices, cuts or strips, before blanching and drying them through a tunnel. Another process first reduces them to a purée, which is subjected to enzyme treatment and then drum dried and turned into flakes ready for packaging. The steam-heated revolving drums dry the purée to a thin film with only 2%–3% moisture. The film is then dried into flakes of 0.2–0.6 cm and these are packed into films purged with an atmosphere containing less than 2% $O_2$ on closing (Woolfe, 1992).

In the USA, a considerable quantity of sweet potatoes is canned, but canning is too expensive for most developing countries. Sweet potato is canned whole, in halves or chunks, either in syrup or under vacuum without liquid. Flash sterilization followed by aseptic packaging increases storability and quality. Numerous other similar products exist, such as jams, juices, candies, sauces, catsup (sweet potato ketchup), paste, mash and purée, and are commercialized, mostly in the USA and Japan.

In many countries, industrial starch extraction is followed by conversion to a range of syrups and other derivatives that can be used as a replacement for expensive imported sucrose. Glucose syrup is produced from sweet potato starch by bacterial amylase but has only 70% of the sweetness of sucrose. Maltose is also produced from sweet potato by the action of bacterial amylase. In Asia, mostly in China, there are several industrial processing plants producing glucose and fructose syrups from sweet potato using dried chips, which are converted into starch (Woolfe, 1992). Citric acid, a flavour enhancer and preservative, is also produced from sweet potato starch in China and Japan. The process involves breakdown of the starch into sugars before they are fermented by moulds such as *Aspergillus niger*. Another important flavour enhancer in Asia, monosodium glutamate, is also produced from sweet potato starch degraded first into sugars, which are then converted to glutamic acid by microorganisms such as *Brevibacterium glutamicum* and finally into the monosodium salt.

Chinese sweet potato alcohol processing plants use mainly dried chips as raw material and this enables them to operate all-year-round. Some of these plants process not less than 140,000 t dried chips into 50,000 t alcohol every year. In Japan, the production of *Shochu* involves fermentation in modern automated factories. Unpeeled sweet potatoes are trimmed by hand and unwanted parts are removed, before washing, steaming and crushing into a mash. A heavy inoculum of *A. niger* or *A. kawachii* provides the enzymes that hydrolyse starch into sugars. During fermentation of the mash, simultaneous conversion of starch to sugars and fermentation of sugars to alcohol takes place using the

yeast *Saccharomyces cerevisiae*. The mash is then pumped, alcohol is steam distilled off and different batches can be blended so that a homogeneous product is obtained and adjusted to 20%–20% (v/v) and bottled (Woolfe, 1992).

Interest in bioethanol production has also stimulated research in Europe and, in Italy, it is estimated that sweet potato has a potential agroindustrial production yield higher than 2032 l/ha year (Montefusco *et al.*, 2014).

Sweet potatoes have two types of pigments potentially interesting as natural colouring for the food industry: carotenoids and anthocyanins (Padmaja, 2009). Carotenes in high concentration can be used for synthetic yellow or orange colorants and are suitable for colouring margarines, for example. The most practical technique for the extraction of anthocyanins involves the hydrolysis of starch with acid. Cooked, peeled roots are homogenized with an equal volume of water, then hydrolysed with sulfuric acid at 80°C for 2 h and neutralized with calcium oxide. In Japan, cv. 'Ayamurasaki' contains high amounts of anthocyanins in the storage roots and is used for making purple paste and flour. Anthocyanin composition influences not only the quality of the pigments but also the paste colour. Genotype differences in paste colour are due mainly to the anthocyanin concentration and the proportion of cyanidin and peonidin types of pigments (Yoshinaga *et al.*, 1998; Xu *et al.*, 2015).

Sports drinks are increasingly consumed and represent an interesting market for biofunctional foods, and sweet potato can be used for the development of such beverages. It has been shown that the replacement of maltodextrin by sweet potato flour is a credible alternative for these beverages (Kirchbaner Contini *et al.*, 2019).

# Section III

# Yams

Cultivated yams (*Dioscorea* spp., *Dioscoreaceae*, Monocotyledons) provide the staple food for millions of people in Africa, South America, Asia and the Pacific tropical countries. Wild yams are a reliable source of food in times of famine or scarcity and they provide pharmacologically active compounds in traditional medicine. The underground storage organs are tubers. In most species, they are renewed and produced annually, while in others they are perennial. As crops, yams are harvested every season and replanted using tuber pieces to regenerate the plant. Unlike other tropical root and tuber crop species, once harvested, yams can be stored for 4–6 months in ambient tropical conditions without significant deterioration of their nutritional properties. Tubers are also often dried and later milled into flour for reconstituting as a stiff paste (*fufu*), which is highly appreciated in West Africa. In many regions, yams play a very important part in the cultural life of the people, especially in the 'yam belt' of West Africa and in the Melanesian countries.

The English term 'yam' is most likely derived from the Portuguese word, *ynhame*, found in early documents, itself being the transcription of *niam*, the word used in the Malinké language spoken widely through the Guineas, Sierra Leone and Ivory Coast (Coursey, 1967).

# 15

# Origin and History

## DOMESTICATION

*Dioscorea* spp. are found throughout the tropics, and different species of edible yams have been domesticated independently in America, Africa, Madagascar, South and South-east Asia, Australia and Melanesia. Of the more than 640 *Dioscorea* species, 12 are staple yams, while many of the wild yams are also important plants in times of food scarcity. *D. alata*, *D. cayenensis* and *D. rotundata* are by far the major cultivated species, while the nine others are often referred to as the minor yams (Table 15.1).

It has been suggested that yams were among the first plant species to be domesticated by fishing communities that depended on the sea for their food supply. Their unbalanced diets may have obliged them to forage inland for food. Tubers may have been cooked on the fire in coastal settlements and pieces rejected from cooking might then have taken root and grown, indicating the possibility of vegetative propagation and cultivation (Coursey, 1967). This hypothesis has been challenged by recent multidisciplinary investigations that document an independent emergence of vegeculture in the highlands of Papua New Guinea (PNG), located far away from the seashore.

Humans reached Australia and New Guinea 40,000–50,000 years ago. Stone tools have been found on archaeological sites of the Ivane Valley of the New Guinea Highlands. These stone tools were used to remove trees, which indicates that the early inhabitants cleared forest patches to promote the growth of useful plants. In the Ivane Valley, abundant starch grains of *D. alata*, *D. bulbifera*, *D. esculenta*, *D. nummularia* and *D. pentaphylla* were extracted from several of the stone artefacts. It is doubtful that these vegetatively propagated species would have been introduced by humans into Sahul, the continental plate represented by Australia and the large island of New Guinea during the ice ages of the Pleistocene when these were connected by solid land. It has, therefore, been suggested that people occupied a New Guinea valley at 2000 m above sea level, soon after their arrival in Sahul and foraged for food in this high-altitude environment (Summerhayes *et al.*, 2010). These species were

**Table 15.1.** Geographic origin of the ten most important cultivated *Dioscorea* spp. Source: author's own.

| *Dioscorea* spp. | Common names | Geographical origin |
|---|---|---|
| *D. alata* | Greater, water, winged yam | South-east Asia, Melanesia |
| *D. bulbifera* | Aerial-, bulbil-bearing yam | South America, Africa, Asia, Melanesia |
| *D. cayenensis* | Yellow guinea yam | West Africa |
| *D. dumetorum* | Sweet yam | West Africa |
| *D. esculenta* | Lesser yam, Asiatic yam | South-east Asia, Melanesia |
| *D. japonica* | Glutinous yam, Japanese yam | Japan |
| *D. nummularia* | Pacific yam, spiny yam | Melanesia |
| *D. oppositifolia* | Chinese yam | China |
| *D. pentaphylla* | Five-leaved yam | South-east Asia, Melanesia |
| *D. rotundata* | White Guinea yam | West Africa |
| *D. transversa* | Pencil yam | Australia |
| *D. trifida* | Aja, aje, cush-cush, yampi | South America |

most likely well distributed in New Guinea at that time, as the major consumer, the pig (*Sus scrofa* L.), was introduced into New Guinea only 6000–12,000 years ago (O'Connor *et al.*, 2011).

A detailed analysis of prehistoric use of stone tools for processing starchy food and other plants has been conducted at Kuk Swamp in the New Guinea Highlands. The comparisons between prehistoric and botanical reference specimens indicate that morphological diagnostics for starch granules reveal the presence of yam (*Dioscorea* spp.). Residues and starch granule analyses also indicate that *Dioscorea* was processed on the wetland margin during the early and mid-Holocene. It is argued that the processing of yam commenced by at least 10,200 years ago although, on this archaeological site, the yam starch granules do not permit differentiation between wild or cultivated forms. However, from at least 7000 to 6500 years ago the processing of yam and other plants indicates that they are likely to have been domesticated and integrated into cultivation practices (Fullagar *et al.*, 2006).

*D. alata* is probably the most widely distributed cultivated yam species in the world and is also likely to be one of the oldest cultivated. It was thought, based on morphological affinities, to result from interspecific hybridization between two Asian species (*D. hamiltonii* and *D. persimilis*) (Burkill, 1960) but these two are now considered as synonyms (Wilkin *et al.*, 2007). However, amplified fragment length polymorphism (AFLP) markers indicate that *D. alata* shares a common genetic background with *D. nummularia* (Malapa *et al.*, 2005). As *D. nummularia* does not occur on the western, Asian side of the Wallace line, it is possible that *D. alata* varieties were selected after the arrival of the Australoids, 60,000 years ago on the Sahul plate, in the present-day New Guinea, or in Melanesia (Lebot, 1999). This geographic region is also the

centre of diversity of *D. alata* (Martin and Rhodes, 1977; Lebot *et al.*, 1998) and hundreds of different morphotypes exist. It is also possible that *D. alata* was already very ancient and well established in Asia and that different varieties were selected there, independently from the New Guinea domestication (Fig. 15.1).

*D. esculenta* is an ancient crop in the Pacific, as revealed by the dating of starch grains from Bourewa, south-western Viti Levu, Fiji, 3050–2500 years ago (Horrocks and Nunn, 2006). The species was most likely introduced into this archipelago by *Lapita* (Austronesian) sailors, who settled the islands of Melanesia between the Bismarck Archipelago in Eastern New Guinea and Vanuatu, from 3500 to 3000 years ago and later Fiji. *D. esculenta* was probably already being cultivated by the Australoid peoples occupying the western part of this region, and the Austronesian sailors then took it into the Pacific Islands.

In West Africa, Paleolithic man, while food gathering, most likely domesticated edible yams during his wanderings. A tuber from a wild plant can be removed without fatal damage to the vine and roots, and the plant will recover and produce another tuber in a year or so. Possibly, hunter-gatherers noticed such an interesting phenomenon and would have come back regularly to harvest edible wild forms. Selection of the most palatable genotypes would then follow naturally. It has been suggested that this process could have started c. 7000 years ago for West African yams (Dumont *et al.*, 2006), although there is no accurate dating to support this hypothesis. The domestication process has been described in great detail for West African species. Called ennoblement or

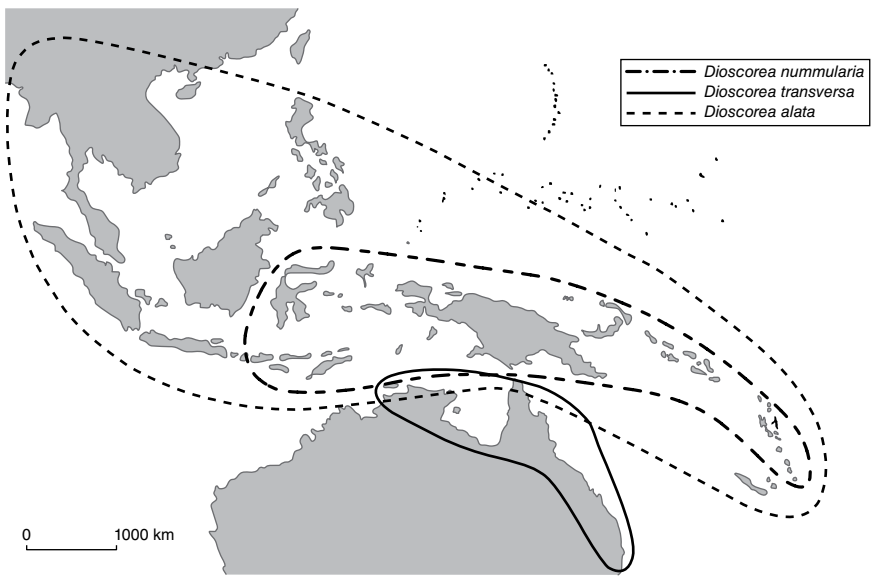


**Fig. 15.1.** Area of origin of *Dioscorea nummularia* and *D. transversa,* and area of diversity of *D. alata*.

paraculture, it is, in practice, essentially the same phenomenon. An edible wild form is vegetatively propagated and cultivated. The aerial morphological traits are not of major importance during the domestication process. When they are used, it is to identify a familiar morphotype which is known to indicate edible underground organs. The tuber's physico-chemical characteristics are the useful traits that are selected and domesticated. Cultivated and wild forms are not very different morphologically but have chemical differences. Wild species often produce some secondary metabolites which protect them from predators. *D. hispida*, for example, which occurs throughout India, South-east Asia and the Philippines, is highly toxic. It is used in times of famine because its large tubers are easily dug and it is detoxicated by prolonged soaking to remove the toxin (dioscorine, an alkaloid). In Melanesia, wild forms of *D. nummularia* oxidize readily when cut and, for this species, domestication is an ongoing process in the Solomon Islands and Vanuatu. The domestication process can be summarized as:

**1.** The domesticator recognizes a morphotype and tests its chemotype. If it seems acceptable after the flesh of the underground organ has been chewed, a propagule is collected.
**2.** Unlike the wild plant, the clone is planted into a considerably modified environment with the soil well prepared; this improved environment contributes to the ennobled development of the underground organs.
**3.** The regular vegetative propagation from a perennial wild form induces a rejuvenation process, which leads to an annual cultivar, and plants are uprooted as soon as there is a consumable yield (Lebot *et al.*, 2005).

In Benin, West Africa, the wild species most often used for domestication are *D. abyssinica*, *D. praehensilis* and *D. burkilliana*. African farmers have developed a simple test to assess the potential of the genotype they are attempting to domesticate. When they put into cultivation a propagule collected directly from the wild, an obstacle is placed in the mound under the seed-tuber. The deformed growth of the resulting tubers indicates if this particular genotype can be domesticated. Obstacles are composed of pottery pieces or flat stones and should be resistant enough to stop and modify the growth of the tubers. According to farmers from Guinea to Cameroon who use this technique, this is a fairly reliable test to decide whether or not it is worth engaging in subsequent clonal generations. The Bariba farmers of Benin argue that the purpose of the obstacle is to break the tuber's habit of deep growth. The morphological transformations induced by the domestication process may not be controlled genetically, and other biological variations such as ontogeny also play an important role (Dumont *et al.*, 2006) (Fig. 15.2).

In Benin, many cultivars are clones of edible wild forms and a few putative wild forms are probably feral plants escaped from cultivation. Some cultivars are also clones of hybrids between wild forms and feral or cultivated plants. Human selection operates on the most vigorous plants and vigour

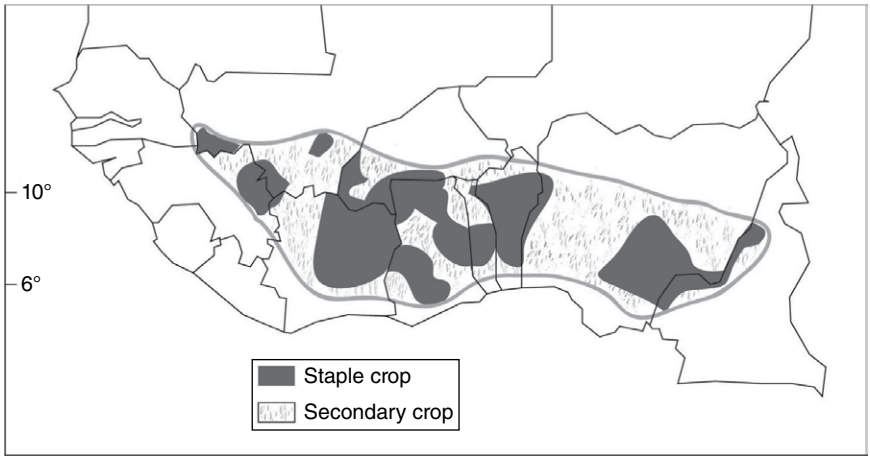


**Fig. 15.2.** Area of distribution of *Dioscorea rotundata* in West Africa (source: Dumont *et al.,* 2006).

is sometimes associated with heterozygosity or heterotic effect. However, rapid deterioration of the cultivar's attractive traits when it becomes feral may be observed. The physico-chemical characteristics of the underground organs, for example, deteriorate very rapidly if soil texture is not improved regularly. With a few minor changes, this process is common to different yam species cultivated in distant geographical regions. The domestication now observed and documented in Melanesia and Africa is most likely very similar, if not identical, to what hunter-gatherers were doing thousands of years ago.

Molecular marker studies have confirmed this process. The traditional practice of farmers involves the introduction of naturally occurring yams, supposedly wild (*D. abyssinica* and *D. praehensilis*), into varieties of *D. cayenensis* and *D. rotundata*. Through domestication, farmers influence and increase genetic diversity by using sexual reproduction of wild and possibly cultivated genotypes. Many of the spontaneous yams collected by farmers for ennoblement are wild and hybrid genotypes. This practice, used in different ecological and ethnolinguistic regions, allows farmers to create varieties with new genetic combinations via sexual reproduction of wild and cultivated yams. This system ensures cultivation of the best genotypes, while preserving the potential for future adaptation (Scarcelli *et al.*, 2005a, 2006). Whole-genome sequencing of wild and cultivated African yam provides statistically supported evidence that *D. praehensilis* is the most likely progenitor (Scarcelli *et al.*, 2019).

*D. trifida* is certainly the only American species to have been domesticated by the Amerindians. *D. bulbifera* is still under domestication in Melanesia, where wild, toxic forms occur spontaneously, but the species is pantropical and it is possible that it could have been domesticated elsewhere, as indicated by the

different gene pools revealed by intraspecific variation of chloroplast deoxyribonucleic acid (DNA) (Terauchi *et al.*, 1991).

## DISCOVERY OF THE CROP BY WESTERN EXPLORERS

Columbus referred to the cultivation of what is presumably *D. trifida*, the only cultivated yam of American origin. However, it is not known to what extent Amerindians were cultivating this yam or were merely collecting it from the wild. It is possible, however, that European and African immigrants cultivated this yam soon after their arrival in this region.

When the Austronesian peoples, originating from south-eastern Kalimantan (Borneo), colonized the great island of Madagascar approximately 2000 years ago, it was very likely that they introduced *D. alata*, along with taro (*Colocasia esculenta*) and banana (*Musa* spp.), as it was already cultivated there when French explorers first visited the island. From there, it could have spread to East Africa and later to central Africa, and thence to the yam belt of West Africa. It is not clear whether this yam was already established when Portuguese explorers visited the coast of Guinea in the 1500s. These Portuguese explorers, on the other hand, could well be responsible for the worldwide distribution of this yam species, including its early distribution along the coast of West Africa. Yams are reported by the Portuguese explorer, Pacheco Pereira, who visited the West African coast in AD 1505–1508, in a manner suggesting that they were not unfamiliar to him and his crew (Coursey, 1967). Apparently, when the Portuguese entered the Indian Ocean, they came across *D. alata* and embarked its tubers to feed their crew on their return journey to Europe.

The slave trade and the establishment of Spanish colonies in the Caribbean probably contributed to the movement of African yams (*D. cayenensis* and *D. rotundata*). Tubers were probably loaded on ships to feed the slaves during the voyage and the surplus replanted on arrival in the West Indies. At the end of the 16th century, *D. alata*, also imported from the Portuguese trading base on the island of São Tomé in the Guinea Gulf, was also cultivated in the Caribbean.

When Captain James Cook discovered the Hawaiian archipelago in AD 1778–1779, he observed that the Polynesians, who colonized these islands about 1000 years ago, had introduced *D. alata*, *D. bulbifera* and *D. pentaphylla* (Handy, 1985), probably from Tahiti or the Marquesas. The Polynesians, including the Hawaiians, descended from the *Lapita* people who spread eastwards from the Bismarck Archipelago and took yams, along with other vegetatively propagated crops, in their sailing canoes and distributed them throughout the Pacific Islands during prehistoric times. Botanists travelling with the French explorers Bougainville and La Pérouse reported that no fewer than five distinct *Dioscorea* spp. were cultivated in the Polynesian islands they visited.

The only American cultivated species, *D. trifida*, was probably taken to Ceylon by Portuguese traders during the 16th and 17th centuries. During

the 19th century it spread with missionaries throughout Asia (without much success) and all the way to the Pacific Islands, where it is still cultivated, although it is a minor yam species there. During the 19th and 20th centuries, the most important cultivated species (*D. alata*, *D. cayenensis* and *D. rotundata*) were distributed widely in all tropical countries by colonial powers and missionaries alike.

## PRESENT GEOGRAPHICAL DISTRIBUTION

Yams are now cultivated in about 50 tropical countries, but not all (e.g. China) provide their annual production statistics to the Food and Agriculture Organization (FAO). The world annual production is approximately 73 million t fresh tubers. More than 96% of this is being cultivated in Africa, where only four countries (Nigeria, Ivory Coast, Ghana and Benin) produce 90% of this output with more than 66 million t/year (FAO, 2017).

The greater yam, *D. alata*, is the most widely distributed species in the humid and semi-humid tropics and, together with *D. rotundata*, accounts for the greater part of world production. It is an important food in the Pacific Islands and the Caribbean, where it has considerable social and cultural significance, and it is also grown in parts of upland Asia. It is the preferred species in South America and in most tropical countries because of its ease of cultivation, taste and long postharvest life; but, in West Africa, it is considered inferior for the production of the national dish *fufu* (or *futu*). In Ivory Coast, however, *D. alata* is increasingly popular as a high-value crop for urban markets and accounts for 70% of overall production nationwide.

A few temperate countries also grow yam (Japan, France, China) and this is where, thanks to the long days and maximum solar radiation, the highest yields are obtained, reaching more than 20 t/ha.

Traditionally, and in most countries, yam farmers maintain a wide range of genetic diversity but, as pressures on land availability increase, so fewer varieties are grown, intensifying the effects of yam diseases. In addition, yam needs to be staked, but suitable materials are often in short supply and labour costs are high. Harvesting alone can account for 20% of total production costs.

The most important producing countries in Africa, Latin America, the Caribbean and Asia are presented in Table 15.2.

Nigeria is host country to the International Institute for Tropical Agriculture (IITA), located near the federal capital in Ibadan. IITA has been conducting long-term research programmes on yams for more than five decades. Nigerian farmers have the opportunity to be early beneficiaries of the technical packages developed by IITA scientists, and improved cultivation techniques are adopted quickly and widely. However, the increases in production in West Africa during the past two decades were due largely to increases in cultivated area rather than in yield per hectare (Table 15.2).

**Table 15.2.** Major yam producing countries in the world in 2017.

| Region | Country | Production (thousand t) | Area (thousand ha) | Average yield (t/ha) |
|---|---|---|---|---|
| Africa | Nigeria | 47,943 | 5,924 | 8.0 |
| | Ghana | 7,953 | 466 | 17.0 |
| | Ivory Coast | 7,148 | 1,239 | 5.8 |
| | Benin | 3,134 | 212 | 14.7 |
| | Ethiopia | 1,400 | 48 | 29.2 |
| | Togo | 827 | 91 | 9.2 |
| | Cameroon | 648 | 58 | 11.3 |
| | Chad | 493 | 52 | 9.6 |
| | Central Africa | 467 | 59 | 8.2 |
| | Gabon | 223 | 35 | 6.5 |
| | Sudan | 182 | 86 | 2.1 |
| | Guinea | 121 | 13 | 9.0 |
| | Congo, Dem. Rep. | 87 | 20 | 4.3 |
| America | Haiti | 439 | 55 | 7.9 |
| | Colombia | 422 | 43 | 9.8 |
| | Brazil | 250 | 26 | 9.7 |
| | Jamaica | 144 | 9 | 16.4 |
| | Cuba | 53 | 9 | 5.6 |
| | Venezuela | 48 | 5 | 9.7 |
| | Dominican Rep. | 33 | 5 | 9.7 |
| | Costa Rica | 24 | 1.6 | 15.0 |
| | Panama | 8 | 5 | 9.7 |
| | Guyana | 2.3 | 0.3 | 7.6 |
| | Saint Vincent | 2.3 | 0.2 | 12.3 |
| Asia | Papua New Guinea | 326 | 21 | 17.6 |
| | Japan | 145 | 7 | 21.7 |
| | Solomon Islands | 45 | 4.2 | 10.5 |
| | Philippines | 14 | 2.5 | 5.8 |
| | Samoa | 9 | 1.8 | 5 |

Source: adapted from FAO (2017).

Through the diversity of cultivated species, cultivars and adaptation to various ecological zones and maturity periods, yams bring great flexibility to the annual cycle of food supply. The long tuber dormancy (between 2 and 4 months at ambient temperatures) ensures sufficient storage life so that food is secured before the rainy season, when it is scarce. Traditionally, yams are planted by smallholders, but large-scale commercial plantings are also being established in response to demand by processors. Increases in area and production have also been driven by urban demand for fresh tubers as food and for use as raw material for flours. Yam cultivation is relatively intensive compared

to other root crops, and in West Africa it costs three to five times as much as an equivalent volume of cassava. However, consumers' attachment to the taste of yams is such that they are still in great demand.

Latin America and the Caribbean rank a distant second among the three producing regions. The yield levels vary substantially from close to 16 t/ha in Jamaica to as low as 4.3 t/ha in Panama. Asia and Oceania together account for less than 1% of global production, but this region enjoys higher yields than elsewhere.

Yam production faces various technical constraints in these three regions but opportunities exist for expanding its utilization. As a result of urbanization, diets are changing rapidly and the overall trend in developing countries is towards the consumption of more processed foods, such as ready-to-use yam flours.

The international trade in yam is fairly limited, probably because the product has a somewhat low value and is perishable. There are, however, some ethnic markets in Europe for West African countries (Ghana is the first exporter), in the USA for Central American countries (Costa Rica is the main exporter) and in Australia and New Zealand for the small Pacific Island countries.

# 16

# Taxonomy and Botany

## CLASSIFICATION

The genus *Dioscorea* is the type genus of the family *Dioscoreaceae* and is the largest genus within this family of about 644 species (Govaerts *et al.*, 2007). All *Dioscorea* species are dioecious twining climbers producing dry capsules, although occasionally both male and female flowers can be found on the same plant. All species of economic importance are tuberous. The genus *Dioscorea* is divided into sections which have a taxonomic status. There are 12 main food yam species and they belong to five different sections: Enantiophyllum (*D. alata*, *D. cayenensis*, *D. japonica*, *D. nummularia*, *D. oppositifolia*, *D. rotundata* and *D. transversa*), Combilium (*D. esculenta*), Opsophyton (*D. bulbifera*), Macrogynodium (*D. trifida*) and Lasiophyton (*D. dumetorum* and *D. pentaphylla*).

*Dioscorea* spp. produce a tuber as an annual underground storage organ, which shrivels away when regrowth commences, and a new tuber can be formed simultaneously. The yam tuber, unlike the Irish potato (*Solanum tuberosum*), lacks the anatomical characteristics of a modified stem structure: it has no buds or eyes, no scale leaves and no terminal bud at the distal end of the tuber. Some species form perennial tubers, which become larger and more lignified as the plant ages. There is tremendous variation in size, form and number of tubers per plant within and between species. The Enantiophyllum species usually produce one to three large tubers, while *D. esculenta* (Combilium) and *D. trifida* (Macrogynodium) produce a greater number of smaller tubers. The shape of the tuber in species producing small tubers is generally regular and their skin usually thinner than in species producing large tubers.

The roots and the stems are renewed annually. Both type of species, annual- or perennial-producing tubers, spend the dry part of the year in dormancy, which can vary from 1 to 6 months. The root system is very superficial. Several thick and long roots develop rapidly after sprouting and reach considerable distances, 3–4 m in radius around the plant, ensuring that the developing vine is anchored firmly. When plants are cultivated in mounds, this

 

development is somewhat constrained. Some species, including the cultivated *D. esculenta*, produce roots near the surface that are armed with spines.

The stems are unable to support the weight of the leaves and have to climb by twining, but there are no specialized organs such as tendrils. The direction of twining, anticlockwise or clockwise, is a characteristic of each taxonomic section. Species of the Enantiophyllum section twine to the right (clockwise) and those of the Combilium, Opsophyton, Macrogynodium and Lasiophyton sections twine to the left. The stems may be winged, spiny or spineless; hairy or glabrous; and circular, rectangular or polygonal in section (Coursey, 1967). After sprouting, the stem can remain erect to a height of almost 1 m before it reaches a support. Some species (*D. cayenensis*, *D. esculenta* and *D. nummularia*) have spiny stems, especially at their base, to protect the plant and to assist in supporting the young stem. The length of the stem varies greatly between species, from a few metres for *D. esculenta* to more than 15 m for *D. nummularia*.

Some species (*D. alata*, *D. bulbifera* and *D. pentaphylla*) produce bulbils in the axils of the leaves. These bulbils are formed when the growth of the stems and leaves is complete and just before the aerial organs start to senesce. They contribute to the vegetative propagation of the plant in natural conditions and, being less dense (lower content of dry matter, DM) than the underground organs, they can float on water, allowing dispersion of the species. From a morphological point of view, they correspond to a condensed stem. Depending on genotypes, some are toxic, while others are produced in great number and are appreciated for their fine texture and taste (*D. bulbifera*).

The leaves are always carried on long, not sheathing, petioles and are usually simple and cordate, but can also be lobed, consisting of three leaflets (*D. trifida*). Each leaf or leaflet has three primary veins joining at the tip of the lamina. The leaves vary in size between species, between cultivars within species and between different parts of a single plant. Their average area is in the range 50–200 $cm^2$. Many species, including cultivated ones, have glands on the leaves producing extrafloral nectaries attractive to ants. The arrangement of leaves on the stems (phyllotaxy) is spiral, although it appears either opposite or alternate, depending on species, and quite often it can be alternate on the lower part of the stem and opposite on the upper part.

The flowers are usually unisexual. Many cultivars flower only rarely and, even more rarely, set fertile seeds. Within all species, there are more male than female plants and male flowers are usually more numerous than female ones. The individual flowers are small (2–4 mm in diameter). The male and female flowers are borne in axilliary spikes. The male flower is composed of a calyx of three sepals and a corolla of three petals. There are usually two whorls of three stamens each. The stamens are usually erect and inserted towards the centre of the receptacle. The female flower has a trilocular ovary located below the corolla and there are three stigmas. The flowers are supposedly entomophilous (Coursey, 1967) and, being insignificant in colour but sweetly scented, are thought to be pollinated by night-flying insects

which do not require visual attraction. Each loculus of the ovary contains two ovules (Govaerts *et al*., 2007).

The fruits are dry dehiscent trilocular capsules (1–3 cm long) and, theoretically, each fruit can produce six seeds. They are not more than three times as long as they are wide, with two ovules in each of the three locules. The seeds are usually lenticular, not ridged, with wings all round the margins or restricted to their base or apex. They are flat and light and their wings are an efficient aid to their wind dispersion. When seed germinates, the plantlet establishes itself with the emergence of a radicle outside the thin seedcoat, which is followed immediately by the emergence of the first chlorophyllous leaf. The hypocotyledon zone develops and the leaf spreads out as the petiole extends. The first radicle then produces two or three roots and, during the following weeks, a complete root system develops rapidly.

## MORPHOLOGICAL DESCRIPTION OF MAJOR CULTIVATED *DIOSCOREA* SPP.

### *D. alata* L. (Enantiophyllum) (Fig. 16.1a, b, Fig. 16.2a, b)

The stem cross section is square, with the corners being in the form of wings. Tremendous intraspecific variation exists and several hundred different morphotypes are cultivated. The tubers can be very large (up to 40 kg in weight and 2 m long), with an average of 3–5 kg/plant in 6–9 months, and present

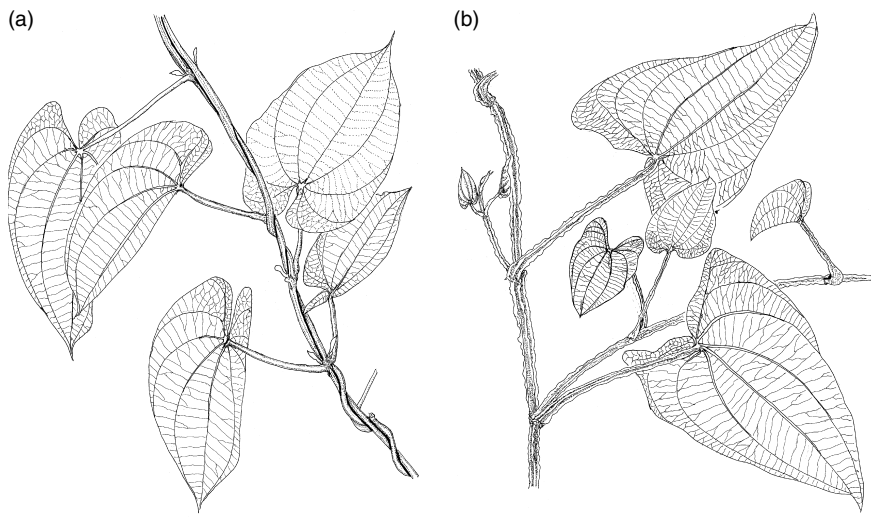


**Fig. 16.1a, b.** *Dioscorea alata* (Enantiophyllum), stem and leaves of two different genotypes.

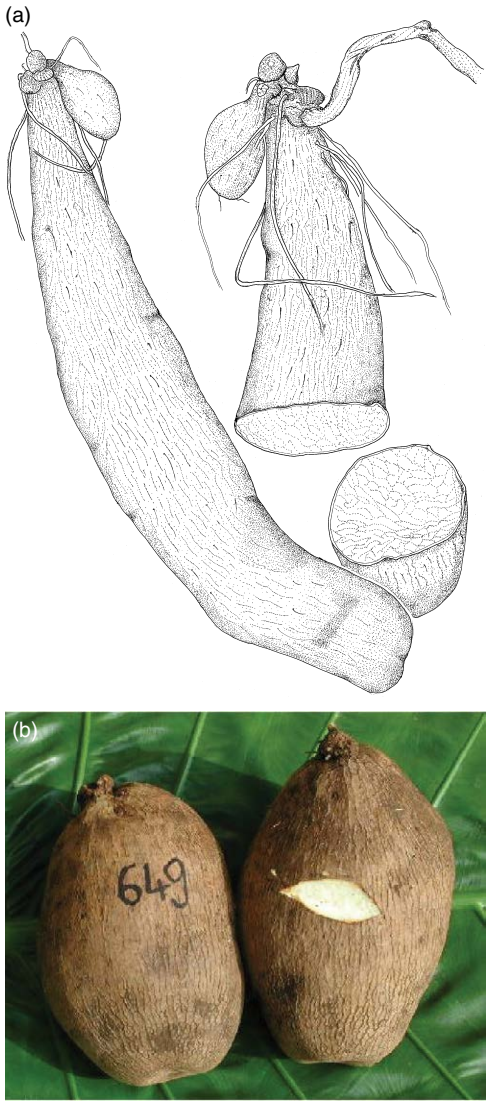


**Fig. 16.2a.** *Dioscorea alata* tubers and cross section; **b** variety with compact tuber shape (photo: V. Lebot).

all sorts of shapes and a vast continuum of variation. The flesh colour can vary from homogeneous white to a deep purple. The shape of the leaves is very variable in size and form, with some rounded, elongated, uplifted or sharply pointed with a deep sinus. The phyllotaxy is opposite. The female flowers are carried in spikes which are up to 30 cm long and the male flowers are borne in shorter panicles. Most of the cultivars are sterile, but those that flower are mostly males. There is, therefore, an unbalanced sex ratio within diploids where male plants are dominant (3:1) (Abraham and Nair, 1990).

Although often described as a cultigen, *D. alata* has all the attributes of a normal species. When flowering male and female plants of equivalent ploidy levels are planted together, the female cultivars produce several hundred fertile seeds every year. The seeds have no dormancy, germinate readily at a high rate and it is not uncommon to find $F_1$ plants which can flower as early as their seminal generation, before being cloned and propagated.

A comprehensive comparison of morphological variation in a germplasm collection of 235 accessions from different geographical origins, including the Caribbean, West Africa, India, South-east Asia and Melanesia, led Martin and Rhodes (1977), to identify Papua New Guinea (PNG) as the centre of greatest variation. It is cultivated by the Aborigines of northern Australia and its presence on that continent is likely an ancient introduction (Yen, 1995), probably by Australoids directly from the north of the Sahul plate (PNG) before the last rise in sea levels, more than 10,000 years ago. In Melanesia, the gene pool includes a particularly confusing array of local cultivars with primitive forms and more than 1000 cultivars maintained in traditional gardens and in the feral state through reproduction from aerial bulbils. Various attempts to determine the intraspecific classification of *D. alata* using a morphological description of aerial and underground organs have failed to produce a clear structure. Martin and Rhodes (1977) suggested three groups:

- *Primitive*: very vigorous foliage; coarse, often feral plants; tuber flesh with anthocyanins, bulbils and becoming gluey when cooked.
- *Feo* (from the vernacular name of one cultivar): stem containing anthocyanins; unobtrusive wings; thorns; short leaves; dark green, triangular or digitate tubers with white flesh producing irritating exudates.
- *Selected*: pleasant aroma when cooked; few anthocyanins and phenols; no oxidation of the white tuber flesh.

The use of morphological traits for classifying cultivars seems to be rather unreliable within *D. alata* because it is extremely widespread and variable. In practice, it is more appropriate to classify the numerous cultivars in different ploidy levels and to identify the male and female plants within each group, as this system is meaningful for breeding purposes (Malapa *et al.*, 2005). The same classification system should be used for other major cultivated yam species.

### *D. bulbifera* L. (Opsophyton) (Fig. 16.3a, b, Fig. 16.4a, b, c)

The stems twine anticlockwise, are cylindrical and spineless and may climb up to 8 m. The leaves are large and simple, either opposite or alternate. The flowers are larger than other *Dioscorea* spp. and have spreading perianths. The female flowers are usually paired. Fertile seeds are produced easily and, in some cases (in Melanesia for example), *D. bulbifera* can be very invasive and behave as a weed that farmers have to remove. This species is characterized

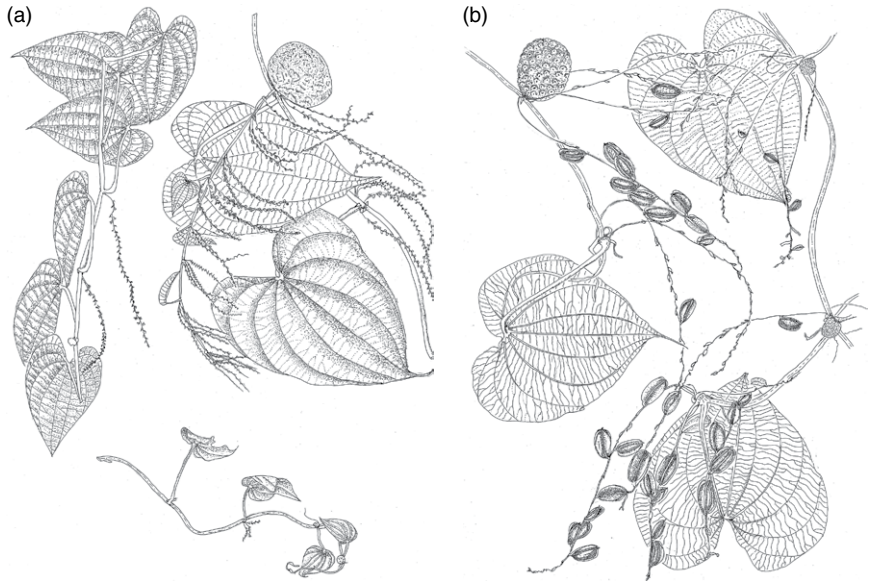


**Fig. 16.3a.** *Dioscorea bulbifera* (Opsophyton), stem, leaves and flowers; **b** capsules.

by the profuse production of large bulbils located at the base of the petioles. The largest bulbils can reach a diameter of 15 cm and a weight of 2 kg, but 300–500 g is the average size. Wild forms require detoxification by soaking sliced bulbils or tubers in water before boiling. Bulbils vary in shape, colour of skin, texture of skin and flesh colour and taste. The tuber has a reduced size: the largest ones reach 5 kg, but they can be very small. It is usually bitter but some cultivars produce palatable tubers that are sold in markets. The species is found in the wild state in Africa, Asia and Oceania and is now cultivated throughout the tropics. Chloroplast deoxyribonucleic acid (DNA) studies have shown that the African and Asian genomes diverged from each other in very ancient times, indicating independent domestication. A genome occurring in South-east Asia appears to be the most ancient Asian genome from which others found in insular regions (Melanesia and Polynesia) have been derived (Terauchi *et al.*, 1991).

### *D. cayenensis* Lam. (Enantiophyllum) (Fig. 16.5, Fig. 16.6)

The stems are slender, cylindrical and mostly glabrous, but covered with spines on the first 1 m above ground. Some cultivars carry very few spines, while others are armed with numerous and remarkable spines. The stems are covered with opposite petiolated leaves with a hastate heart shape and

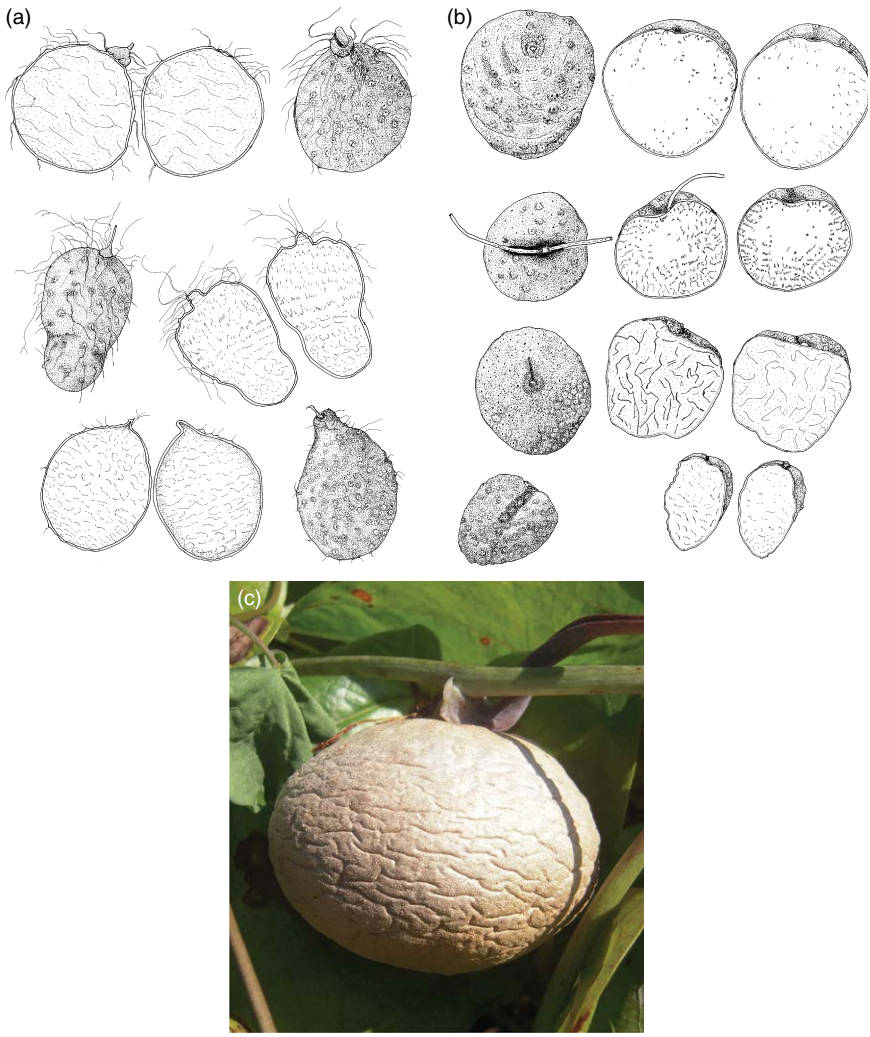


**Fig. 16.4a, b.** *Dioscorea bulbifera*, cross sections of bulbils from different genotypes; **c** full aerial bulbil (photo: V. Lebot).

are truncated at their base with two short auricles. The new shoots are thick, sometimes with a purplish green appearance. The leaves are glabrous and have five or seven clearly apparent veins which start from the base but of which only three join at the tip of the lamina. The leaves are usually flat, broad and acuminate. Inflorescences are produced towards the distal parts of the branches. Male spikes can be single or up to four at the axil of each leaf. They can reach up to 6–8 cm in length and bear more than 40 sessile male flowers with white sepals and brownish petals. The plant matures in 8–12 months. In its natural

**Fig. 16.5.** *Dioscorea cayenensis* (Enantiophyllum), stem, leaves and male flowers.

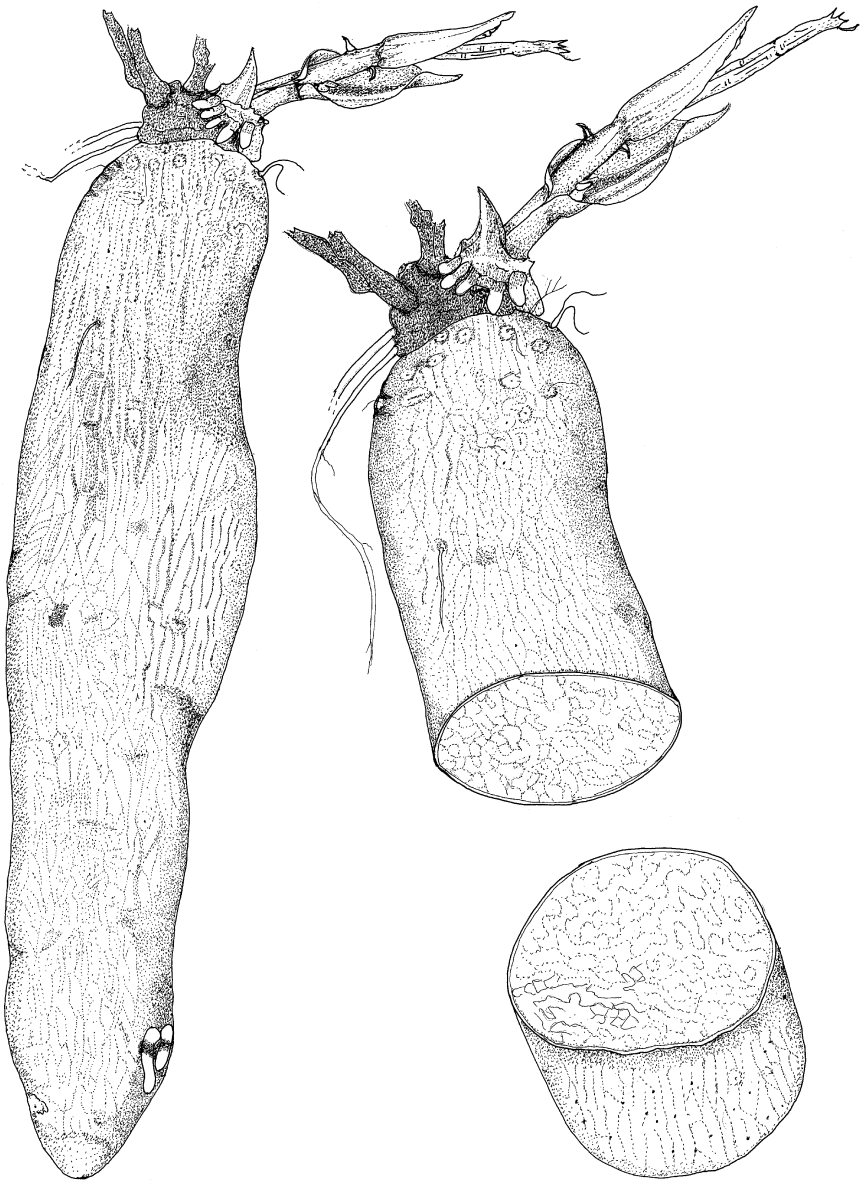

**Fig. 16.6.** *Dioscorea cayenensis*, tubers. Previous primary nodal complex (PNC) and new PNC.

habitat, the West African forest zone, its growth is almost continuous and a new stem arises as soon as the old one has senesced. Tubers have a short dormancy period and do not store well. This is not a highly regarded species but it is robust, hardy, anthracnose resistant and high yielding. Its great advantage is that it can be harvested at almost any time of the year by 'milking' the plant: that is by cutting one tuber from the living plant, which will form a new tuber.

Hundreds of cultivars of *D. cayenensis* exist and are highly variable in their aerial and underground traits. In most cases, the tuber flesh is yellow, or with some traces corresponding to carotenoid compounds, and the species is, for that reason, known under the name of yellow Guinea yam. It has been shown, however, that the contents are not higher than in the white Guinea yam (Price *et al.*, 2018). Numerous studies using morphological, isozyme and DNA markers and various numerical taxonomy techniques have attempted to classify them, with somewhat disappointing results. The species is native to West Africa, where farmers have put into cultivation genotypes collected in the wild and resulting from spontaneous sexual recombinations. *D. cayenensis* bears the same chloroplast DNA as *D. rotundata* (Terauchi *et al.*, 1993; Ramser *et al.*, 1996; Chaïr *et al.*, 2005) but other studies clearly separate cultivars belonging to the two taxa (Asiedu and Sartie, 2010).The species status of *D. cayenensis* is debatable and corresponds most likely to a group of cultivars rather than to a true species (Dumont *et al.*, 2006).

### *D. rotundata* Poir. (Enantiophyllum)

The stems are glabrous, fistulose and streaked. When a new stem develops, it is thick with abundant prickles and pairs of cataphylls (large, broadly ovate bracts). Stout branches develop at right angles from the axils of these cataphylls. The bracts will then give place to paired leaves. These leaves are opposite, with a long petiole, and are oval or almost round in shape. The petioles are almost as long as the leaves, which are almost as long as they are wide, glabrous and poorly indented at their base. The laminas have seven veins and their lower surface is much paler than the upper surface. The male flowers are white, borne on axillary spikes always shorter than the length of the lamina, filiform and glabrous. The flowers are sessile, scattered and solitary. The male inflorescences are approximately 5–8 cm long and can carry 20–30 flowers with three yellow sepals and petals. The female flowers are borne on spikes measuring up to 15–20 cm long and resulting in capsules with a cordate apex.

The growth cycle is of approximately 6–8 months and varies, depending on the numerous cultivars. The tubers may be produced in pairs or in small groups of four or five and have a long dormancy period of up to 5 months. Tuber shapes are varied but the flesh of the white Guinea yam does not vary much in colour. The tuber skin is dark and smooth and nearly free of rootlets.

Cultivars are grouped into the double-harvest or early-maturing yams and the single-harvest or late-maturing yams. Some morphotypes are bitter, and bitterness is attributed to physiological immaturity and unfavourable environmental conditions, although this phenomenon is still poorly documented. Differences between *D. cayenensis* and *D. rotundata* are presented in Table 16.1, but there is often more variation within than between the two groups (Dumont *et al.*, 2006).

### *D. dumetorum* (Kunth) Pax (Enantiophyllum)

This species is widely cultivated in Eastern Nigeria and in Benin. It is very high yielding and the tubers may be single or form a cluster. Bulbils are rarely found. The vines twine clockwise and all the leaves are trifoliate, which differentiates this species from the other edible and cultivated African yams. There are some toxic wild forms unsuitable for consumption. The leaves are affected by anthracnose. The tubers can be boiled without being peeled. There is remarkable varietal diversity in Benin (Laly *et al.*, 2019).

### *D. esculenta* (Lour.) Burkill (Combilium) (Fig. 16.7a, b, c)

This species is distributed widely throughout the tropics but is less cultivated than *D. alata*, *D. cayenensis* and *D. rotundata* because, although it is hardy and high yielding, its tubers have somewhat limiting physico-chemical characteristics. The stems of the vine are cylindrical and very spiny, although the size and density of spines vary between genotypes. They twine in an anticlockwise direction. The emerging leaves are covered with small hairs and show a light brown pigmentation. The leaves are cordate, simple, alternate and have a smooth, leathery and shiny texture and a light to dark green colour, depending

**Table 16.1.** Differences between *Dioscorea cayenensis* and *D. rotundata*.

| Characteristics | *D. cayenensis* | *D. rotundata* |
|---|---|---|
| Climatic adaptation | Long rainy season | Short rainy season |
| Earliness of production | Late | Early |
| Dormancy | Short | Long |
| Number of harvests | One | Two |
| Colour of tuber | Yellow | White |
| Shape of leaves | Orbicular | Ovate |
| Starch granule | Small, triangular | Large, ovoid |
| Smell when cooked | Strong | Delicate |
| Number of stems | Approx. 8 | 4–12 |

Source: adapted from Martin and Rhodes (1978).

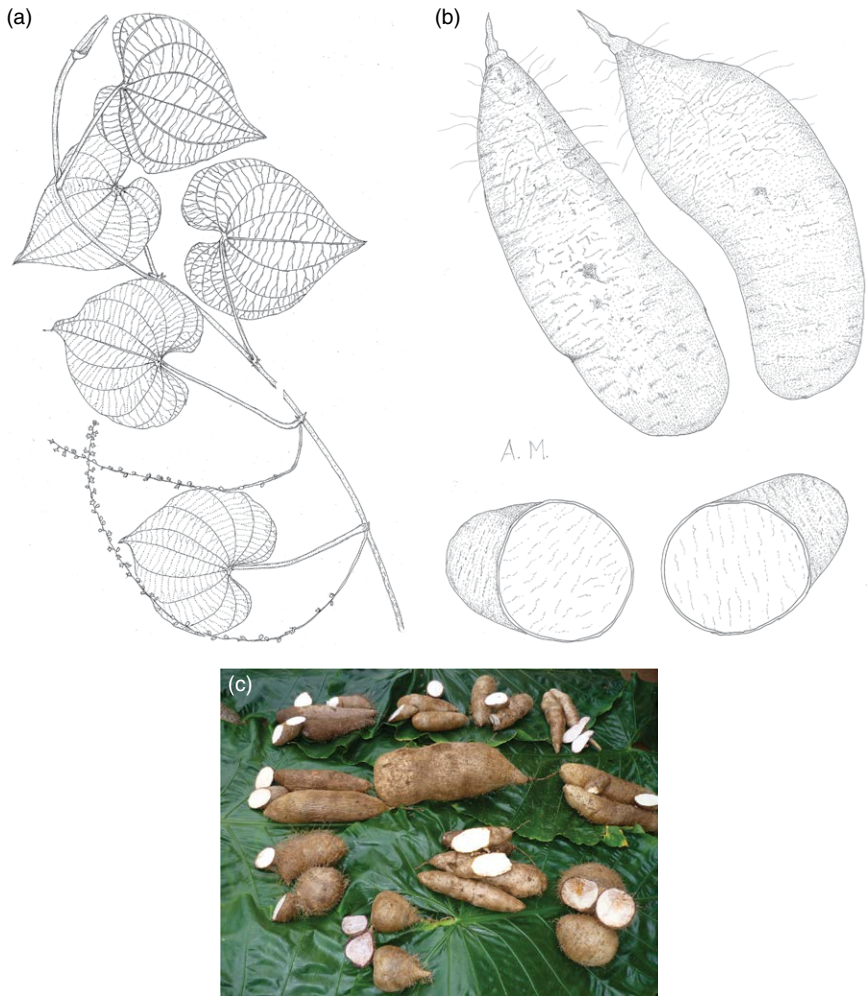


**Fig. 16.7a.** *Dioscorea esculenta* (Combilium), male inflorescences; **b** tubers; **c** different varieties (photo: V. Lebot).

on genotypes. The male flowers are borne on spikes 10–15 cm long and female flowers are, so far, unknown. Numerous cultivars exist from India, through South-east Asia, Melanesia and the Pacific Islands, where it is a very ancient crop (Horrocks and Nunn, 2006). However, compared to other major cultivated species, morphological variation is limited.

The individual tubers are quite small compared to other species but are produced in a considerable number per plant, from 5–20 annually. The tuber flesh colour varies from pure white to a deep purple. The total yield per plant is very high and the yield per ha can reach more than 128 t in 10 months. The

tubers are of good palatability and they are often the yams preferred by westerners as they have a soft flesh texture similar to the Irish potato (*S. tuberosum*) and are free from toxicity and bitterness. However, they tend to become very fibrous if left in the ground for too long. The species is hardy, is resistant to most yam diseases and has the advantage of being well adapted to mechanized cultivation. In Hawaii, the tubers are harvested with an ordinary potato uplifter or ginger harvester. In PNG, the species is becoming so popular that it is replacing *D. alata* in traditional agroforestry systems, thus contributing directly to its genetic erosion. In West Africa, however, this species is not appreciated because its chemotype has a low DM content, which makes it unsuitable for producing good *fufu*. The dormancy period is rather short and, in storage, tubers start to sprout after only 1–2 months, depending on the temperature.

### *D. japonica* Thunb. (Enantiophyllum)

This species is mostly cultivated in Japan (where it is called 'Yamaimo'), in Korea, Taiwan, the Ryukyu and Bonin Islands. It is morphologically very similar to *D. oppositifolia* and some authors consider the two species as being conspecific. The fact that hybrids between species can be produced may confirm this (Araki *et al.*, 1983). However, they are considered as clearly different species in the most recent taxonomical review of *Dioscoreacea*e (Govaerts *et al.*, 2007). This species is also important as a medicinal plant and is rich in antioxidants. There are four botanical varieties: var. *japonica*, var. *nagarum*, var. *oldhamii* and var. *pilifera*. The plant produces bulbils and the long smooth tubers can be eaten raw.

### *D. oppositifolia* L. (Enantiophyllum)

This species, often called *D. opposita*, is the major yam of economic importance grown in temperate regions. The stems are round and the vines can climb up to 3–4 m, but not as high as other species. The leaves are acuminate and opposite. Aerial bulbils are produced at the axils of the leaves and are often used for propagation, although they result in a much lower tuber yield. The tubers are spindle shaped and can reach 1 m long but are relatively thin, with an average diameter of 8–10 cm. They descend vertically into the ground and their cultivation requires intensive land preparation to ease harvest, which often involves considerable labour. There are numerous cultivars and the trend is to select those with a more compact tuber shape. The tuber surface, especially towards the head, is quite hairy because of numerous small roots.

This species is also known as *D. batatas* and is cultivated throughout China. It tolerates much colder temperatures than other *Dioscorea* spp. It has been introduced into France, where it is cultivated in the light, sandy soil of

the Loire-et-Cher around Saint Claude-Montlivault and is exported annually to urban supermarkets in the French West Indies (Guadeloupe and Martinique).

### *D. nummularia* Lam. (Enantiophyllum) (Fig. 16.8a, b, Fig. 16.9, Fig. 16.10)

It is likely that different species are, in fact, misidentified under this binomial. The stems are round in cross section with dense and usually numerous pronounced spines at their base. The upper portion of the vines is glabrous but some cultivars (e.g. 'Lapenai' in Vanuatu) have no spines at their base. The leaves are large, cordate and elliptic, with those located on the lower portion of the stem being opposite, while the upper ones are alternate. The tubers have a dark, rough and thick skin and are very large and almost independent. They vary in number and shape, some being round in cross section, others flat or oval, generally shallowly placed for cultivars and deeply placed for wild forms. True wild forms tend to produce deformed tubers of 2 m long and only 2–3 cm thick. The tuber flesh varies in the numerous cultivars, being white to purple in colour, and some cultivars oxidize faster than others. Male inflorescences are single or up to four and measure up to 5 cm long. The female inflorescences can measure up to 15–20 cm long and are always single or in pairs. Numerous fertile seeds are produced every year.

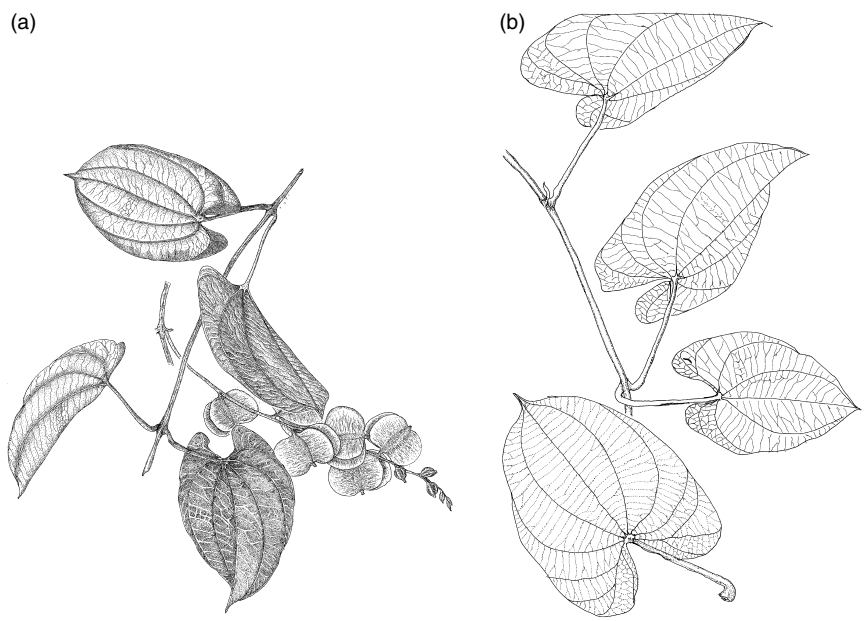


**Fig. 16.8a.** *Dioscorea nummularia* (Enantiophyllum), capsules (cv. 'Lapenai'); **b** leaves.

**Fig. 16.9.** Pluriannual cultivar of *D. nummularia* (photo: V. Lebot).

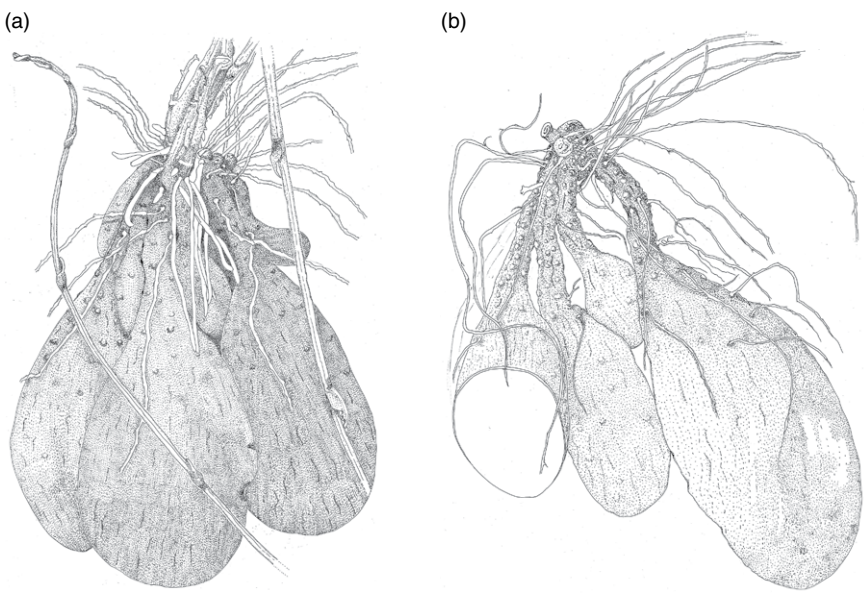


**Fig. 16.10a.** Interspecific hybrid (Enantiophyllum), cultivar 'Marou' tubers; **b** cross section.

*D. nummularia* is a very polymorphic species in the Pacific and has also been reported from Indonesia. It is the most important yam species in some parts of PNG, the Solomon Islands and some islands of Polynesia (e.g. Samoa) (Cable and Wilson, 1984). In Vanuatu, it is highly valued for the quality of its tubers and is used in wedding ceremonies in gift exchanges for the bride (Malapa *et al.*, 2005). It is very hardy, resistant to diseases and high yielding.

Annual and perennial cultivars are known and can produce between 15 and 50 kg tubers/plant (Lebot *et al.* 2017).

There are natural interspecific hybrids between *D. nummularia* and *D. alata* (Chaïr *et al.* 2016a). These cultivars are late maturing (9–12 months) compared to *D. alata* and are greatly valued for their high DM content and good organoleptic quality, which are similar to those of *D. nummularia*. Tuber shape varies according to the cultivar, the most common ones having a long neck. There are also attractive cultivars with neckless and compact tubers, with smooth epidermis. There are few cultivars and all have white tuber flesh. These cultivars are cultivated in Australia and Melanesia. The cultivar 'Marou' ('Wael') has been introduced into the French West Indies without evident success, but is hardy, drought tolerant, high yielding and resistant to anthracnose. Confusion over the morphology of *D. alata*, *D. nummularia* and *D. transversa* has been reported in the Philippines (Cruz and Ramirez, 1999), in Indonesia (Sastrapradja, 1982), in New Caledonia (Bourret, 1973) and in Vanuatu (Malapa *et al.*, 2005).

### *D. pentaphylla* L. (Lasiophyton) (Fig. 16.11a, b)

The stems are very spiny, especially on the part close to the ground. The leaf is peculiar for a *Dioscorea* species and, as the name suggests, is composed of five leaflets arranged in palmate form, although some occasionally may

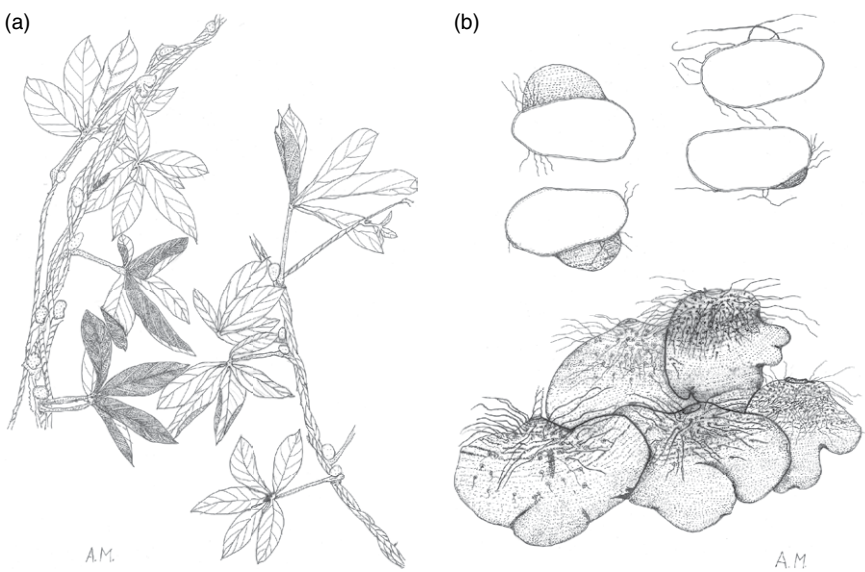


**Fig. 16.11a, b.** *Dioscorea pentaphylla* (Lasiophyton).

produce only three. Numerous small bulbils are produced on the vines, too small to be eaten, and contribute to its natural vegetative propagation. It is a highly polymorphic species with numerous cultivars and no fewer than five botanical varieties have been proposed by taxonomists (*javanica*, *malaica*, *palmata*, *papuana* and *sacerdotalis*), but their value is debatable as a vast continuum of variation exists. It is cultivated in Indonesia but it is in Melanesia that it is widespread and important. It is an important food in times of scarcity and, unlike the other Lasiophyton species, the tubers are not toxic. A plant can produce, after a growth cycle of 10 months, an average yield of 5–10 kg of only one or two tubers per plant.

### *D. transversa* R. Br. (Enantiophyllum)

The pencil yam produces long and slender edible tubers. The tubers were a staple of the Aborigines but are now rarely consumed in Australia. They are known for their very tasty flesh after boiling or baked in a ground oven without any particular preparation. Leaves are alternate basally on stems and opposite distally on stems. They are similar in shape to those of *D. alata* (elongate to cordate) but with thick and shiny, leathery laminas. Spines are few at stem base and present on both sides of the junction between stem and petiole, as in *D. nummularia*. The aerial parts contain anthocyanins and the young leaves and stems are bronze or poppy-brown. The stems twine towards the right, with alternate, cordiform, shiny leaves with purple lamina. *D. transversa* is immune to anthracnose. This is probably the least cultivated of all species but its potential remains to be investigated thoroughly.

### *D. trifida* L. (Macrogynodium) (Fig. 16.12)

The stem has a square section and is spineless. Its angles are frequently extended into wings broader than those of *D. alata*. The leaves may be opposite or alternate and are divided into three to five lobes, but not into separate leaflets (as in *D. pentaphylla*). Many individual, small but uniform tubers are produced, each measuring between 20–40 cm long. Numerous cultivars exist with tuber flesh varying from white, yellow and pink to purple and all have a pleasant aroma and highly appreciated taste. This species, which originates from northern South America (probably the Guyanas), is very popular in the West Indies (it is called *cousse couche* in Guadeloupe). It has been introduced into Melanesia, where it is also appreciated for its taste but cannot become a leading crop because of its comparatively low yield and DM content. This species is highly susceptible to viruses, especially to yam mosaic virus (YMV), which are responsible for the decline of its cultivation in the West Indies.

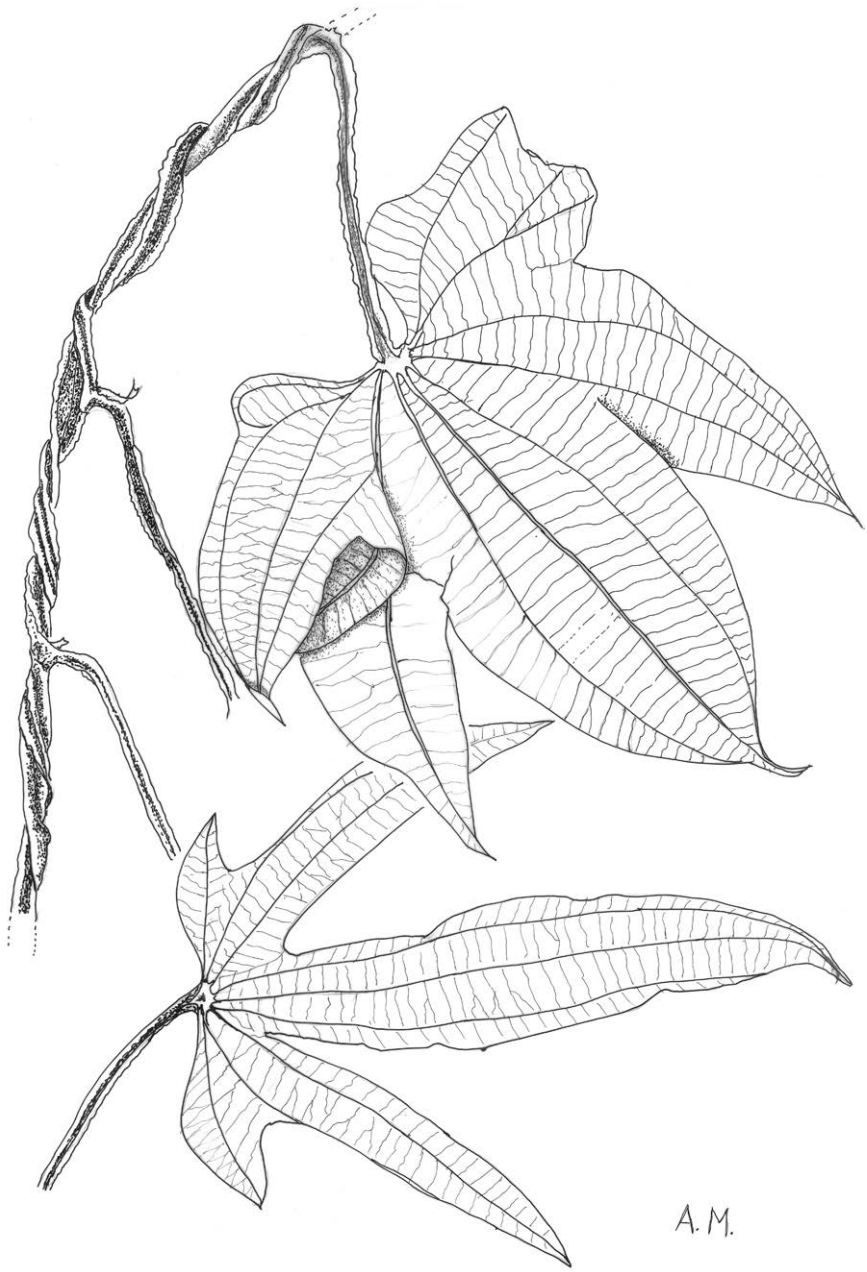


**Fig. 16.12.** *Dioscorea trifida* (Macrogynodium).

## RELATED SPECIES

*Dioscorea* spp. are difficult to describe and, within each section, the taxonomy is fairly complex. In PNG, for example, several species related to *D. alata* and *D. nummularia* are not yet identified. Confusion also exists among the wild African yams. Molecular markers provide an alternative classification of the genotypes but it is often observed that the two systems, molecular and morphological, do not necessarily produce matching groups. Gene flows occur between wild and cultivated genotypes of the same species (Scarcelli *et al.*, 2006) and it is possible that they also occur between distinct species within the same section if these are sympatric.

An impressive amount of research has attempted to clarify the taxonomic positions of the two Guinea yams (*D. cayenensis* and *D. rotundata*). A controversial debate is still ongoing and emphasizes the complexity of *Dioscorea* taxonomy and the endless discussion between 'splitters' and 'lumpers'. According to Miège (1982), *D. cayenensis* was described by Lamarck in 1792 and *D. rotundata* was described by Poiret in 1813 but their descriptions were not sufficient to define the two species correctly and strictly because some characters, such as phyllotaxy, were not stable (e.g. leaves may be alternate or opposite on the same plant).

If the morphological descriptions are not conclusive, the molecular markers hardly clarify the debate. Hamon and Touré (1990) consider that the two species belong to the complex *D. cayenensis–rotundata* rather than to two well-differentiated species. In Benin, however, isozymes (leaf proteins) differentiate *D. rotundata* from *D. cayenensis* accessions, supporting the idea that the two forms of Guinea yam represent distinct genetic entities (Dansi *et al.*, 2000). DNA marker (random amplified polymorphic DNA, RAPD) analyses used to investigate genetic relationships of the two Guinea yams concluded that accessions could be clearly separated into two major groups corresponding to *D. rotundata* and *D. cayenensis*. Cultivars of *D. rotundata*, however, showed a high degree of DNA polymorphism and were separated into two major groups that appeared most closely related to *D. praehensilis* and *D. liebrechtsiana* rather than to *D. cayenensis*. It was, therefore, proposed that cultivars classified into *D. cayenensis* should be considered as a taxon separate from *D. rotundata* (Mignouna *et al.*, 2007).

On the other hand, studies conducted using chloroplast DNA simple sequence repeats (cpSSR) show that *D. cayenensis* and *D. rotundata* share the same haplotype. The morphotype *D. abyssinica* appears to be subdivided into two haplotypes. One of these haplotypes shares the same haplotype with *D. cayenensis* and *D. rotundata* and with morphotypes of *D. praehensilis*, suggesting that the three may belong to the same species. A similar case involves the three wild species, *D. minutiflora*, *D. smilacifolia* and *D. burkilliana*, which may be considered as one single genetic group, and are thought to belong to the same species (Chaïr *et al.*, 2005).

For taxonomists, *D. alata* is unknown in the wild state and it has been considered as a cultigen (Coursey, 1967). It has been postulated that *D. alata* originated in cultivation in Assam or Burma, where the related species *D. hamiltonii* and *D. persimilis* are found growing wild. Taxonomists now consider these two species to be synonyms (Wilkin *et al.*, 2007). New molecular tools have been used to clarify *Dioscorea* spp. phylogeny and relationships between wild and cultivated species. For Asian species, 72 accessions representing 48 species from seven different sections (*Botryosicyos*, *Combilium*, *Enantiophyllum*, *Lasiophyton*, *Opsophyton*, *Shannicorea* and *Stenophora*) were analysed with chloroplast markers. The results of the DNA phylogeny confirm the taxonomic, infrageneric, classification of *Dioscorea* into the seven sections analysed. Among the Enantiophyllum section, the species were found to be closely related, with *D. japonica* clustering with *D. batatas* (syn. *D. oppositifolia-opposita*), *D. formosana* and *D. cirrhosa*. *D. alata* was found to be closer to *D. hamiltonii* (syn. *persimilis*) than to *D. nummularia* although the distances between the three species were small (Hsu *et al.*, 2013).

Four plastid DNA markers and SSRs were used to understand the historical evolution of *Dioscoreaceae* in a family-wide analysis. These markers were selected to provide phylogenetic resolution at different levels, from basal family level to shallow, species-level relationships. The Enantiophyllum section was clearly differentiated from the other sections, but *D. alata* was found to be closer to *D. calcicola*, *D. fordii* and *D. glabra*. *D. hamiltonii* and *D. nummularia* were found to be quite distant from this group, with *D. nummularia* being closer to *D. hastifolia*, an endemic species of Western Australia (Viruel *et al.*, 2016), which is morphologically very different.

Phylogenetic diversity estimated for African species based on chloroplast DNA markers for eight *Dioscorea* spp. of Cameroon supported the monophyly of three out of four sections (Enantiophyllum, Combilium, Osophyton), but section Lasiophyton was found to be paraphyletic owing to the grouping of some *D. dumetorum* individuals with the Combilium section (Ngo Ngwe *et al.*, 2015).

It is, however, difficult to compare the results of these phylogeny studies because they are conducted with different markers and different species samples. Their aim is often to attempt to pinpoint the geographical origin of the major species, *D. alata* for example, but this appears as a rather complex task. The overall picture is that most yam species were probably naturally widespread over wide geographical areas well before the two major consumers (man and pig) started to exploit this natural resource. The shallow tubers of the major yam species do not present toxic secondary metabolites and can be easily cooked by roasting them directly on the fire (a preparation still practised). It is, therefore, possible that these species were exploited by hunter-gatherers well before the invention of pottery. For some medicinal *Dioscorea* species, over-exploitation of the natural resource is still ongoing, and valuable species such as *D. villosa* and *D. zingiberensis* are in danger of extinction in America and Asia, respectively.

## CYTOLOGY

Various protocols have been developed to count chromosomes in root tips at meiosis. Tuber pieces are germinated in a light substrate and root tips of approximately 1.5 cm long are treated in a suspension of α-monobromo- or chloro-naphthalene. The tips are then fixed in alcohol:acetic acid (3:1) and preserved at 5°C. The samples are hydrolysed for 6 min in HCl (hydrochloric acid) at 60°C and stained with Feulgen (Essad, 1984). An alternative, simplified protocol involves the fixation of root tips in alcohol:acetic acid (3:1) without any pretreatment, their storage at room temperature for 48 h and squashing in 2% acetocarmine (Abraham and Nair, 1991).

Two base numbers ($x = 9$ and $x = 10$) have been determined and the two are present in America, Europe and Africa, while only $x = 10$ is present in Asia and Oceania (Essad, 1984). However, there has since been a debate regarding the base number of major cultivated species, which is now considered as being $x = 20$. The situation has been clarified for *D. alata*. Abraham and Nair (1991), while studying meiosis in 61 accessions, reported that all showed 20 bivalents at diakenesis or metaphase and concluded that the $2n = 40$ males may be considered as diploidized tetraploids. When studying the genetic relationships among 269 cultivars of *D. alata* from the South Pacific, Asia, Africa and the Caribbean, Lebot *et al.* (1998) observed that the MDH (malate dehydrogenase) enzyme system patterns exhibited a typical diploid segregation with the homozygous and heterozygous states of each locus. They also noted that the existing variation was due to numerous ancient sexual recombinations, and that therefore *D. alata* was probably a true species and not a putative cultigen, as previously reported. Abraham (1998) observed that the $2n = 40$ chromosome types of *D. alata* produced bivalent formation and high fertility.

He further observes that the $2n = 60$ chromosomes are trivalent forming. The diploid nature of $2n = 40$ chromosome types of *D. alata* is also evidenced from the microsatellite marker inheritance; and *D. alata* is, in fact, a polyploid species with di- (40), tri- (60) and tetraploid (80) cultivars with a chromosome number of $x = 20$ (Arnau *et al.*, 2009). It is assumed that the *D. alata* polyploids would have appeared through the formation of unreduced gametes. Triploids would have been produced and diversified through the formation of $2n$ gametes in diploid females caused by the non-viability of seeds resulting from the formation of $2n$ sperm and of the non-viability of intercytotype crosses. The tetraploids would have appeared through sexual polyploidization caused by unreduced gametes and the sterility of triploids (Nemorin *et al.*, 2013).

It is observed that higher ploidy levels tend to produce larger tubers. This is quite clear for *D. alata* tetraploids (with 80 chromosomes) which produce long and large tubers, penetrating deep into the soil, often used as gifts and for ceremonial purposes. If tetraploids with compact tuber shape could be developed, they would present a definite advantage in cultivation. The fact that fertile tetraploid males with 80 chromosomes are absent from India (Abraham

and Nair, 1991), but present in Melanesia (Abraham *et al.*, 2013), may be an indication of an independent and early domestication process in the northern part of the Sahul plate (now New Guinea and Melanesia).

The most cultivated yam in West Africa, *D. rotundata*, has 40 chromosomes. Diploid segregation of isozymes (Zoundjihékpon *et al.*, 1994) and amplified fragment length polymorphism (AFLP) (Mignouna *et al.*, 2002a) have been observed, and Daïnou *et al.* (2002) suggest that this species is diploid ($2n = 2x = 40$). The segregation studies of two isozyme loci and six microsatellite markers, both co-dominant, in the progeny of a self-fertilized, monoecious plant has confirmed these previous observations. For the eight markers, segregation patterns could be explained by only two genetic models: diploidy or tetraploidy with two null alleles. However, given the nature of studied markers, the simplest hypothesis was that the parental plant was diploid. These results, combined with data from a diversity survey and results of other authors, led to the conclusion that *D. rotundata* is a diploid species with $2n = 2x = 40$ chromosomes (Scarcelli *et al.*, 2005b).

Microsatellite marker segregations have been used and suggest that the American species *D. trifida* also has a base chromosome number of 20 (Boussalem *et al.*, 2006).

While the situation is relatively conclusive for *D. alata*, *D. rotundata* and *D. trifida*, it is not yet confirmed for other species, but it is reasonable to assume that other Enantiophyllum species may also have a base number of $x = 20$ rather than $x = 10$. Numerous chromosome counts have been produced and it is therefore possible to hypothesize that most cultivars could be di-, tri- or tetraploid rather than tetra-, hexa- or octoploid, as reported in the literature. Whatever the exact chromosome number in *Dioscorea* spp. is, this information is of academic rather than practical interest and will not change the way breeders recombine and improve yam genotypes.

It appears that polyploidy operates actively and that accessions with 40 chromosomes are the most numerous, followed by accessions with 20, 60 and 80 chromosomes. Accessions with 100 chromosomes (*D. bulbifera* and *D. esculenta*), 120 (*D. hastata*, *D. minutifolia* and *D. smilacifolia*) and 140 chromosomes (*D. opposita*, *D. pentaphylla* and *D. cayenensis*) have also been encountered. It is suggested that the variation in ploidy levels observed within some species, and the obvious lack of correlations between polyploidy and food value, indicate that polyploidy variation has not been involved in the process of speciation (Table 16.2). It may, however, have played a major role in the domestication and cultivar selection process.

Flow cytometry is a rapid and reliable technique that allows the quantification of DNA content in a large number of nuclei. This technique has been applied successfully to yams. Three different ploidy levels were detected using flow cytometry in Guadeloupe for *D. alata* (Gamiette *et al.*, 1999) and in Cameroon in *D. cayenensis* and *D. rotundata* (Dansi *et al.*, 2001). It was concluded that the use of an appropriate flow cytometry technique gave results which were

**Table 16.2.** Reported chromosome numbers and ploidy levels in cultivated yams.

| *Dioscorea* spp. | 2*n* chromosome numbers | Reported ploidy levels |
|---|---|---|
| *Dioscorea alata* | 40, 60, 80 | 2x, 3x, 4x |
| *D. bulbifera* | 40, 60, 70, 80, 100 | 4x, 6x, 7x, 8x, 10x |
| *D. cayenensis* | 18, 36, 54, 60, 80, 140 | 2x, 3x, 6x, 8x, 14x |
| *D. dumetorum* | 40 | 4x |
| *D. esculenta* | 40, 60, 90, 100 | 4x, 6x, 9x, 10x |
| *D. japonica* | 80 | 8x |
| *D. oppositifolia* | 40, 140 | 4x, 14x |
| *D. nummularia* | 60, 80, 100, 120 | 6x, 8x, 10x, 12x |
| *D. pentaphylla* | 40, 70, 80, 140 | 4x, 7x, 8x, 14x |
| *D. rotundata* | 40, | 2x, 4x |
| *D. transversa* | 80 | 8x |
| *D. trifida* | 54, 72 | 6x, 8x |

Source: adapted from Araki *et al*. (1983); Essad (1984); Zoundjihékpon *et al*. (1994); Daïnou *et al*. (2002); Mignouna *et al*. (2002a, b); Scarcelli *et al*. (2005b); Boussalem *et al*. (2006).

in agreement with chromosome counts and offered a reliable tool for routine ploidy determination in *Dioscorea* spp. It can, therefore, provide the necessary data for breeding programmes where the screening of large collections is a prerequisite before sexual recombination.

# 17

# Breeding and Genetics

Several research institutes have contributed to yam breeding, working with the most economically important species (*Dioscorea alata*, *D. cayenensis* and *D. rotundata*) in various environments (Nigeria, India, Guadeloupe and Vanuatu), and numerous hybrids are now being evaluated. The other cultivated species (*D. bulbifera*, *D. dumetorum*, *D. esculenta*, *D. japonica*, *D. nummularia*, *D. oppositifolia*, *D. pentaphylla*, *D. transversa* and *D. trifida*), however, have been neglected and their germplasm is poorly documented.

## OBJECTIVES AND SELECTION CRITERIA

The productivity of yam cultivation is under increasing pressure owing to the shortening of fallows and because of reduced soil fertility, and pest and disease build-up. Labour inputs can be reduced when selecting genotypes that do not need expensive staking and produce shallow-growing tubers that are easy to harvest. There are, however, numerous pests and diseases that are increasing in importance. Nematodes (*Scutellonema bradys* and *Meloidogyne* spp.) often interact with fungi (*Botryodiplodia*, *Fusarium*) and bacteria (*Erwinia* spp.) to damage *D. cayenensis* and *D. rotundata* tubers in the field and in storage. Anthracnose (*Colletotrichum gloeosporioides*) and viruses infect *D. alata* foliage, and insect pests (*Adoretus versutus*) also damage it.

An international *D. alata* germplasm collection was maintained and evaluated by the US Department of Agriculture in Mayaguez, Puerto Rico, in the 1970s. Each of more than 300 varieties collected throughout the tropics have been evaluated for 100 traits in the field, at harvest, and in the laboratory and kitchen. This work resulted in the selection of five elite varieties: 'Florido', 'Forastero', 'Veeven', 'Gemelos' and 'Leone Globe'. They have since been distributed in many countries (Martin *et al.*, 1975). Because of its compact size and tuber shape, the 'Florido' variety was introduced into Ivory Coast from Puerto Rico in the early 1970s for a yam production mechanization project to be developed in the northern part of the country. For various reasons,

the mechanization of the harvest was never implemented, but 'Florido' was adopted widely by farmers. It has since spread throughout the country and is spreading to other countries in West Africa. The reasons for its popularity include its flexibility of planting time, good storability and postharvest life, and its tolerance to the internal brown spot disease (IBS), which usually affects other *D. alata* varieties in Ivory Coast. A good yam variety with superior attributes is adopted readily by farmers and spreads rapidly, even though the multiplication rate is low (Doumbia *et al.*, 2004).

It is, therefore, important to create and distribute new, improved yam varieties and, in doing so, breeders have to take into consideration both the agronomic constraints and the tastes of consumers, who may be hard to please. New modern uses by urban dwellers also necessitate improvements in the physico-chemical characteristics of the tubers to extend their storage life.

A significant contribution to *D. trifida* breeding was made in Guadeloupe by INRA (Institut National de la Recherche Agronomique) in the 1960s. Various selections were obtained in 1971 with yields of approximately 30 t/ha unstaked; but since then no progress has been made in solving the major problem of the great sensitivity of *D. trifida* to viruses (Degras, 1993).

The breeding and selection of yams has been carried out by the International Institute for Tropical Agriculture (IITA) since the early 1970s, with the objective of improving yam-based systems and with the primary focus on *D. rotundata*, the most important species throughout the yam belt (Mignouna *et al.*, 2007). The principal objectives include:

- High and stable yield of marketable tubers.
- Suitability for prevalent cropping systems (plant architecture).
- Good quality (dry matter (DM) content, texture, taste, rate of oxidation).
- Resistance to biotic stresses in the field.
- Good postharvest storage.

Harvesting being the most expensive operation (in man days) throughout the crop cycle, the long-term objectives are to release genotypes adapted to non-staked conditions and to partial or complete mechanical harvesting. Tubers that have shallow setting, and which are oval or round and tough-skinned are preferred, and plants with several smaller tubers per plant rather than one large one are preferable.

The objectives of INRA, IITA, the Centre de Coopération Internationale en Recherche Agronomique pour le Développement (CIRAD) and the Central Tuber Crops Research Institute (CTCRI) for the genetic improvement of *D. alata* are almost identical, except for an emphasis on the major disease of this species, the anthracnose caused by *C. gloeosporioides* (Arnau *et al.*, 2010). The physico-chemical characteristics of *D. alata* are a major challenge for West African breeders. This species has very desirable agronomic attributes but its suitability to traditional processing is far from good. In Nigeria, improving the food quality of *D. alata* is a priority, as this species is gaining in popularity among

farmers because of its ease of cultivation, a situation observed throughout the yam belt from Cameroon to Guinea. Local Nigerian accessions are being evaluated for the suitability of their tubers to preparation of boiled and pounded yam, the national dish. Mealiness, colour and taste are important in the general preference for boiled yam but the consistency, colour and stickiness determine the general preference of the pounded yam. Although *D. alata* is an introduced species in Nigeria with a genetic base assumed to be narrow, two-thirds of the accessions have been identified as being suitable for the preparation of boiled tubers, while only half were assessed to be good for the popular pounded yam. The challenge now is to breed varieties good for pounded yam that are also resistant to anthracnose (Egesi *et al.*, 2003).

There have been few attempts to improve the other minor, neglected *Dioscorea* species, either through evaluation and selection or breeding. These collections are important and need to be evaluated as there is anecdotal evidence that genetic resources of the minor *Dioscorea* species are being lost, and this will affect any future improvement programmes where broad genetic diversity will be needed. The importance of *D. nummularia* in the Pacific has been greatly underestimated (Lebot *et al.*, 2017). It is a highly polymorphic species with high yield potential. Genetic resources are now being collected and thoroughly evaluated in Vanuatu for their agronomic and breeding characteristics. In Africa, *D. dumetorum* has a recognized potential for wider utilization (Laly *et al.*, 2019) and *D. esculenta* could be used for processing into flour and for bread making (Ukpabi, 2010).

## SEXUAL REPRODUCTION AND STERILITY

There are large germplasm collections and thousands of accessions have been screened to identify, over the years, parental genotypes with breeding potential. Advances have been made in understanding the reproductive biology of yams, especially of *D. alata*, *D. cayenensis* and *D. rotundata*.

In India, clones of *D. alata* flower from mid-September to the end of November. In Vanuatu, in the southern hemisphere, they flower from mid-April to the end of June. Flowering is synchronized between clones of the same genotypes and, in large collections, this trait is an easy way to trace duplicates. After the initiation of the floral primordia, the maturation period for male flowers is about 4 weeks (Fig. 17.1) and for female flowers about 3 weeks.

Anthesis of the male flowers occurs around noon and the pollen remains viable for about 4 h. Both male and female flowers produce a strong pleasant scent upon anthesis. The male flowers remain open for only 4 h, while the blooming duration of the female flowers can last 10 days (Abraham and Nair, 1990). After pollination there is usually a high percentage of fruit set, unless different ploidy levels are involved (Fig. 17.2). High relative humidity usually favours high fruit set in polycross plots.

**Fig. 17.1.** *Dioscorea alata* spikes of male flowers (photo: V. Lebot).

A few techniques have been developed to extend the pollination period and improve synchronization between male and female plants of *D. rotundata*. It appears that hermetic cold storage of the pollen, without pre-drying and in viable condition, at −20°C or −80°C for periods as long as 2 years or more is an efficient means of conservation. Hand pollination with *D. rotundata* frozen pollen kept at −80°C for 1 year gave more than 69% fruit set; and after 2 years of preservation it gave about 50% of fruit set. This simple technique allows the pollination of non-overlapping male and female plants (Daniel *et al.*, 2002).

Unfortunately, quite often the varieties with the most desirable characteristics, either agronomic (e.g. compact tubers) or palatability (e.g. appropriate chemotype) are those that do not flower. Different flower induction techniques have been attempted, with disappointing results. In experiments in 2001–2003, 50-day-old plants of four varieties of *D. rotundata* were exposed to 10 h (short) day length for 15 days, 14 h for 30 days or for constant 24 h, with natural day length as the control. Under natural day length, the male varieties flowered earlier than the female. A short day length delays and reduces

**Fig. 17.2.** *Dioscorea alata* female flowers developing into capsules after pollination (photo: V. Lebot).

the intensity of development of inflorescences, but response to 14 h and 24 h treatments differs between varieties, some being more sensitive than others (Shiwachi *et al.*, 2005a). To promote flowering, planting large tubers and trellising the vines on long stakes and wires (along with gibberellic acid spraying) have been tried, but with disappointing results.

## CROSSING TECHNIQUES AND TRUE SEED PRODUCTION

An efficient and reliable controlled pollination technique is necessary to produce full sibs and progenies aimed at Mendelian segregation studies. Abraham and Nair (1990) compared two methods of pollination for *D. alata*: the so-called 'pencil method' and the 'brush method'. For the first, the tiny male flower is held between the fingernails of thumb and index fingers on the left hand while the anthers are scooped out of the flower using a sharpened lead pencil held in the right hand. The female flower is then held upright with the left hand and the excised anther is applied to the stigma by inserting the pencil tip between the perianths of the female flower. It is easier if two people are involved as one person can perform the pollination while the other person lifts out the anther with the pencil tip to pass it over for transfer on the stigma. The second method uses a camel-hair brush with only a few bristles whose length is reduced to 3 mm. The pollen from dehisced anthers is taken out and deposited on the stigma with the brush. There are significant differences in fruit set rates between the two methods (Table 17.1). The pencil method proves to be more efficient but, for the two methods, productivity is improved if two persons are involved.

In Nigeria, and for *D. rotundata* (which has male flowers of a comparable size), the brush method has been found superior to two other methods producing only 27.8% of fruit set (Akoroda *et al.*, 1981).

**Table 17.1.** Comparison of the two hand-pollination methods for *Dioscorea alata*.

| Pollination method | Flowers pollinated by hour | | Fruit set %* |
|---|---|---|---|
| | 1 person | 2 persons | |
| Pencil | 98 | 240 | 74.2* |
| Brush | 86 | 208 | 51.4* |

Note:*Averages of columns 2 and 3, significant at 5% level. Source: adapted from Abraham and Nair (1990).

In India, the absence of efficient pollinators contributes to low seed set and, although it is time consuming and expensive in terms of labour, artificial pollination without bagging the female flowers is the only efficient way of producing hybrids. The rather long period of stigma receptivity of *D. alata* (Abraham and Nair, 1990) and *D. rotundata* (Akoroda, 1983a) is an advantage for breeders.

In Ivory Coast, it has been shown that for *D. cayenensis* and *D. rotundata*, polycross nurseries composed of parents selected carefully for their ploidy level and sex, and established in plots isolated from pollen pollution, can set fruits and produce considerable quantities of viable botanical seeds in normal conditions. This field design offers the possibility of producing substantial populations of half sibs (only the mothers being known) and initiating a cycle of recurrent selection (Zoundjihékpon, 1993).

In Vanuatu and New Caledonia, open and natural pollinations are very successful in *D. alata*, and numerous seeds are produced in polycross nurseries in years where anthracnose damage is low. Profuse fruit set occurs naturally, but plants bearing capsules tend to be burnt by the anthracnose epidemy when the weather is wet, and weekly fungicide sprays are necessary to keep plants alive until the seeds are fully mature. Flowering ability is improved in the hybrids, and flowers can be observed as early as the first clonal generation, and occasionally as early as the $F_1$, in the seminal generation.

The rate of flowering increases with the number of crossing cycles with a sex ratio tending to balance and to be less favourable to the males. In most breeding programmes, the number of seed-setting cultivars is limited but, in the breeding process, it soon becomes possible to choose from clones resulting from crossing. Tremendous variation is, in fact, found in the progenies because of the highly heterozygous genetic make-up of yams.

However, one should take care that dehiscing capsules do not open in the field, releasing their seeds, which will be lost. Capsules are harvested when fully mature, which is approximately 12 weeks after pollination, and can be kept in well-aerated bags. Yam seeds are fairly easy to germinate (Fig. 17.3).

*D. alata* seeds do not show any form of dormancy and can be sown directly after harvest on any commercial seed-raising substrate, similar to those used for vegetable species. Seeds germinate between 2 and 3 weeks after sowing and their germination can continue for several weeks (Fig. 17.4).

**Fig. 17.3.** *Dioscorea alata* seeds are surrounded by a circular membrane to allow wind dispersion. They have no dormancy and will germinate as soon as the conditions are favourable (photo: V. Lebot).

**Fig. 17.4.** Yam seeds are germinated in trays before being transplanted to small pots in a nursery prior to being planted in a field (photo: V. Lebot).

When the seedlings have reached the 2- to 3-leaf stage, they are transplanted into small pots for 4–6 weeks before being transplanted to the field (1 × 0.50 m). In IITA, when large populations of 10,000 or more seedlings are managed, a procedure involving high-density nursery beds is giving interesting results. Seedbeds are covered with palm leaves. When seedlings reach the 2- to 3-leaf stage, they are thinned out to leave 15 cm between each plant and the extra plants are transplanted in other nursery beds. The vines are trained on strings 1.5 m high and the palm leaves are removed when the seedlings are well established. Tubers produced in this way are smaller because of the close spacing.

In Vanuatu, young seedlings raised in Jiffy® pots are transplanted directly into the field at wide spacings (1 × 1 m) and produce large tubers (from 200 g to 3 kg) after 8 months of growth when staked.

## SELECTION METHODS AND PROGRAMMES

A critical step involves the identification of flowering genotypes with good tuber quality and equivalent ploidy levels. Parents showing traits relevant to the objectives of the breeding programme are then selected for hybridization.

The breeding process of *Dioscorea* spp. is very long, between 8 and 10 years, because of the very low multiplication rate of propagules and the existence of a juvenile phase during the seminal generation. Plants resulting from true botanical seeds cannot be evaluated properly during their first generation ($F_1$) and have to be propagated clonally before a reasonable assessment of their characteristics can be done during the first clonal generation ($C_1$). As with other root crop species, there are no means for evaluating accurately the important physico-chemical characteristics of the tubers in early screening of the progenies. Present techniques are based on the sensory evaluation of food products and cannot be applied to large numbers at the early stages of the selection process when the tubers per clone are still few and small.

In Nigeria, selection trials start with an unreplicated evaluation of the numerous hybrids with usually only one plant per genotype. The first clonal evaluation is followed by preliminary (PYT), advanced (AYT) and uniform yield trials (UYT) conducted with randomized complete block design composed of three to six replications. After 5 years of field evaluation, the selected genotypes can pass through a series of cooking and processing tests aimed at evaluating their properties. In the meantime, field evaluation proceeds with scoring of pest and disease tolerance. Because the multiplication rate is very slow, it is necessary to go through intensive propagation over 6 years to obtain sufficient material for the establishment of multi-locational trials. A collaborative evaluation of IITA breeding lines conducted with the National Root Crop Research Institute of Nigeria (NRCRI) permitted the release of new varieties (Mignouna *et al.*, 2007; Lopez-Montes *et al.*, 2012) and new ones are being evaluated every year.

In India, CTCRI in Trivandrum (Kerala) has developed *D. alata* hybrids and several improved varieties have been officially released to growers. Remarkable differences are observed in the performance of sexually propagated seedlings of *D. alata* and their subsequent clonal derivatives. Seedlings are generally poor in field vigour, flowering and tuber yield, whereas their clonal descendants are vigorous and characterized by greater flowering and yield. In the second clonal generation ($C_2$), the majority of genotypes flower, facilitating hybridization, and tuber yield increases significantly, aiding selection of high yielders. Sexually propagated seedlings of *D. alata* have genetic potential that requires at least two generations of clonal propagation to be expressed fully (Abraham, 2002).

The evolution of important morphological characteristics has also been studied with *D. alata* progenies. Among the sexual progenies, oval and irregular-shaped tubers often undergo changes of shape through seedling to clonal generations, whereas the cylindrical tuber shape seems to be fairly stable across generations. In two families, approximately 56% and 67% of the seedlings, respectively, had cylindrical tubers which remained stable. Among the remaining seedlings having oval and irregular tubers, approximately 75% of the oval tubers and 47% of the irregular tubers changed their shape between

the first and second clonal generations. However, after the second and subsequent clonal generations, the tuber shapes remained stable as a clonal character. Thus, in the third clonal generation, there were only 24% and 30% of the original population having oval and/or irregular tuber shapes, respectively. Since compact tuber shape is one of the most desirable attributes of a good cultivar, direct selection can be practised, starting from the second clonal harvest or later, along with other desirable attributes (Abraham *et al.*, 2006).

In Guadeloupe, *D. trifida* is highly valued for its organoleptic qualities but is too sensitive to viruses, especially to YMV (yam mosaic virus), to be cultivated widely. INRA has attempted to ascertain from 222 hybrids of seed origin whether any had a level of resistance to viruses or merely a more tardy appearance of symptoms. The field study showed that no hybrids were truly resistant but some had tolerance and could therefore be useful for future research (Arnolin and Lombion, 2005). From 1966 until 1980, INRA introduced cultivars of *D. alata* resistant to anthracnose. In 1989, new strains of the disease became virulent on the resistant cultivar 'Plimbite'. After 4 years of trials, only three cultivars were still resistant to the disease: 'Belep' (from New Caledonia), 'Oriental' and 'Kinabayo' (from the Philippines). In 1993, INRA initiated a breeding programme to create resistant cultivars. Despite the small number of resistant females that could be used as parents, numerous resistant cultivars were obtained. Two of these new hybrids: 'Boutou' and 'INRA 15' are, at present, cultivated but their comparative advantages over others are not clear-cut.

In Guadeloupe, CIRAD has developed a breeding programme aiming at producing varieties of *D. alata* resistant to anthracnose and with high-quality tubers (Arnau *et al.*, 2009, 2010, 2017). Improved hybrids are now being evaluated in farmers' fields.

At present, farmers' varieties (landraces) are the dominant varieties in Western Africa and this is thought to be due to the limited dissemination rate of improved varieties. One major constraint is the breeding period needed to develop improved varieties with consumer-preferred traits. It is anticipated that developing a participatory value chain strategy could set priorities. It is recognized that different varieties are needed for food security, processing (flour, pasta, noodles, pancakes) and pharmacology (drugs, cosmetics). Rapid seed yam propagation systems could then support variety development and dissemination efforts. In IITA, it is expected that the implementation of a new scheme could reduce the time to develop and recommend new varieties from 9 to 3.5 years (Lopez-Montes *et al.*, 2012). However, the greater yam, *D. alata*, was introduced clonally in Africa and its genetic base is narrow (Otoo, 2017). There are many *D. alata* landraces around the world, especially in Melanesia: this is an area of diversity, with attractive traits which could be introduced to Africa and distributed directly to farmers, and this could complement the current breeding efforts. A first experiment conducted in Benin with varieties introduced from Vanuatu has shown that the local genetic base was broadened successfully (Adoukonou-Saogbadja *et al.*, 2014).

## HERITABILITY OF MAJOR TRAITS

Yam breeding is constrained by the lack of knowledge on the heritabilities of major traits, and this is due to the practical difficulties in generating full-sib progenies through controlled pollination between selected parents. *Dioscorea* spp. being dioecious, it is often difficult to identify diploid parents with synchronous flowering to produce enough seedlings to establish conventional heritability trials. Most germplasm collections are poorly characterized and, when the information is available, the number of female parents with known ploidy information is often very limited. This represents the first constraint for breeders and there is a need to exchange female plants to broaden the genetic bases of breeding programmes. In many countries, the female plants used for crosses are selected because of their sex and flowering ability but not necessarily because of their agronomic value.

In *D. rotundata*, heritability has been found to be high for eight agromorphological traits (Table 17.2). However, although heritability was high for leaf size, plant leafiness and tuber yield, only the latter had a corresponding high genetic advance. For this species, rapid genetic advance can be achieved for yield under uniform environment by single plant selections followed by clonal propagation (Akoroda, 1983b).

For *D. cayenensis*, various phenotypic variances, coefficients of variation, expected genetic advances and correlation coefficients have been estimated for seven agronomic traits. Plant leafiness, virus infection, number of tubers per plant and tuber yield show high expected genetic advances, while highly significant positive correlations are observed between tuber yield, plant leafiness and vine dry weight. It is also suggested that resistance to leaf virus infection, as expressed by foliage vigour, is the most important trait for selecting high-yielding genotypes (Akoroda, 1984).

**Table 17.2.** Mean, phenotypic and genotypic coefficients of variation, heritability and expected genetic advance of eight characters in *Dioscorea rotundata*.

| Character | Mean | Phenotypic (CV%) | Genotypic (CV%) | Heritability (%) | Expected genetic advance (% of mean) |
|---|---|---|---|---|---|
| Time to vine emergence | 6.94 | 22.3 | 17.4 | 38.0 | 22.0 |
| Leaf size | 2.30 | 12.4 | 18.0 | 67.8 | 30.5 |
| Leaf virus infection | 1.66 | 32.2 | 28.2 | 43.4 | 38.2 |
| Plant leafiness | 2.86 | 20.6 | 15.5 | 66.8 | 26.0 |
| Shoot height | 2.59 | 17.3 | 15.7 | 45.1 | 21.7 |
| Vine dry weight | 74.65 | 41.3 | 39.2 | 47.4 | 55.5 |
| No. of tubers/plant | 1.24 | 39.8 | 10.6 | 6.6 | 5.6 |
| Tuber yield/plant | 2.13 | 40.1 | 47.3 | 58.1 | 74.3 |

Source: adapted from Akoroda (1983b).

In Nigeria, a study aimed at understanding the *D. rotundata* genetic control of YMV resistance has shown that it can be expressed by the action of a single dominant gene in simplex condition or a major recessive gene in duplex condition (Mignouna *et al.*, 2001a). In some genotypes, the recessive state of YMV resistance means that this type of resistance is difficult to trace in field screenings and necessitates molecular tools for accurate identification. Resistance of *D. alata* to a moderately virulent strain of *C. gloeosporioides* was found to be strain specific and appeared to be controlled by a single major dominant locus (Mignouna *et al.*, 2001b). Breeding for anthracnose resistance will have to develop varieties carrying many different genes for resistance in order to provide a fairly sustainable advantage against a fungus with many different strains (Mignouna *et al.*, 2007).

For *D. alata*, successful crosses between diploids × tetraploids and tetraploids × tetraploids have been conducted in addition to diploid × diploid crosses to develop hybrids resistant to anthracnose. Parents from India (IN) and Vanuatu (VU) have been used. Parents from India are resistant to anthracnose, while those from the Pacific are susceptible but present high-quality tuber flesh (no oxidation, high DM content and high starch). A total of 10,410 controlled hand pollinations were carried out and resulted in very low numbers of individual hybrids selected because of the severity of the anthracnose impact in $F_1$s. A higher seedling survival percentage in the IN × IN group (67.3 vs 47.8%) was owing to the higher anthracnose resistance of the seedlings in the nursery stage. The Vanuatu female plants were susceptible to anthracnose and the maturing fruits with developing seeds were destroyed by the disease. All VU × VU crosses failed to produce seeds. Overall, the mean seedling survival varied from 28% to 70% (Table 17.3). However, remarkable variation was observed between different parental combinations even when the same pollen parent was used. Anthracnose-resistant *D. alata* hybrids have been produced,

**Table 17.3.** Number of *D. alata* flowers pollinated, fruit set (% capsules), seed set (% seeds) and seedling survival (% seedlings) for the different ploidy groups.

| | Parental combinations | | | Flowers | Capsules | | Seeds | | Seedlings | |
|---|---|---|---|---|---|---|---|---|---|---|
| Ploidy groups | *n* | Female | Male | *n* | no. | % | no. | % | no. | % |
| IN2x × IN2x | 20 | 11 | 6 | 3184 | 1826 | 57.4 | 3172 | 28.9 | 2137 | 67.3 |
| IN2x × VU2x | 12 | 8 | 5 | 1393 | 760 | 54.6 | 1050 | 23.0 | 502 | 47.8 |
| VU2x × VU4x* | 3 | 3 | 1 | 1189 | 770 | 64.8 | – | – | – | – |
| VU4x × VU4x* | 2 | 1 | 2 | 234 | 123 | 52.6 | – | – | – | – |
| IN2x × VU4x | 12 | 7 | 3 | 3596 | 1689 | 47.0 | 3329 | 32.8 | 2386 | 71.7 |
| Hybrids** × 2x | 4 | 4 | 3 | 292 | 91 | 31.2 | 143 | 26.2 | 80 | 56.0 |
| IN2x × numm. | 4 | 4 | 1 | 522 | 231 | 44.2 | 330 | 23.8 | 144 | 43.6 |

*Mother plants perished owing to anthracnose before seed maturation; **$F_1$ hybrids crossed again; numm = *D. nummularia* (source: adapted from Lebot *et al.*, 2019a)

utilizing the tetraploid fertility in the species. The desired trait of oval, compact tuber shape for ease of harvest was found to occur in less than 10% of the evaluated hybrids. Flowering ability is transferred to the hybrids and flowers are produced profusely in their first clonal generation (Lebot *et al.*, 2019a).

## GENOTYPE × ENVIRONMENT (G × E) INTERACTIONS

G × E interactions are a major challenge to breeders and farmers alike because they cause serious difficulties in selecting cultivars for diverse environments. Resistance or tolerance to anthracnose is a typical example and, for a given variety, the incidence of the disease on the foliage of a clone varies greatly, depending on the environment. Sources of virus inoculum also differ from one place to another, and so does the susceptibility of a given genotype. It is, therefore, necessary to assess – early in the selection process – adaptation and yield stability across different environments of promising genotypes evaluated on research stations. There are numerous reports of varieties performing well on a station and being disappointing when distributed and, vice versa, some varieties perform surprisingly well in farmers' fields.

Significant G × E interaction for a quantitative trait reduces the usefulness of the genotype over all locations. It reduces the correlation between agronomic and genotypic values and confuses yield evaluation. As most yam cultivars are present in the field for 8–10 months, they are exposed to numerous stresses. In Nigeria, *D. alata* yield stability has been studied using six different genotypes, across five major yam-growing areas and two cropping seasons. It appears that G × E interaction affects fresh tuber yields significantly. Genotype performance stability is affected by biotic and abiotic stresses (Egesi *et al.*, 2005).

In Ghana, some work has been done to assess G × E interaction on the tuber yield of 18 *D. cayenensis* varieties. Different experiments were conducted in 12 different environments and the analysis identified three *D. cayenensis* mega-environments. Two-thirds of the tested genotypes were identified as redundant (Otoo *et al.*, 2006a). Multi-locational evaluation has also involved six *D. rotundata* hybrids and one cultivar, which were evaluated across 13 environments. Highly significant G × E effects were observed on the yield of the tested genotypes. However, a high and stable yielding hybrid (89/02665) was identified and released formally in 2005 (Otoo *et al.*, 2006b; Otoo, 2017).

These conclusions have obvious bearings on breeding programmes and tend to emphasize the importance of decentralizing agronomic evaluation as soon as possible in the slow improvement process. The variability required to suit different agroecological conditions and climatic changes can be obtained only by segregating populations of parents of diverse geographical origins. If crosses focus on a few traits known to be important, then progress might be rapid for these traits. Broadening the genetic base of the breeding programmes, however, needs to take account of the possible introduction of viruses or virus

strains. Although guidelines exist for the safe movement of yams (Brunt *et al.*, 1989), there has been little official sharing of germplasm between countries.

In the 'yam belt' of West Africa, bioclimatic variables, soil properties, and remote sensing vegetation layers combined with topographic variables are used to identify the different yam mega-environments suitable for testing hybrids produced by breeding programmes. Most often trial sites are chosen for their ease of access, but cluster maps provide valuable indicators for site selection for varietal testing to represent the optimum target set of yam production environments. This environment mapping approach is used to optimize varietal testing programmes (Alabi *et al.*, 2019).

## USE OF RELATED SPECIES

Farmers' use of genotypes resulting from gene flows between cultivated and wild yams has been described profusely in the case of West Africa (Dumont *et al.*, 2006). Wild related species are not used yet in breeding programmes, although it is quite clear that they exhibit useful traits. For example, for the African Enantiophyllum (*D. cayenensis* and *D. rotundata*), the wild reservoir composed of *D. abyssinica* and *D. praehensilis* offers opportunities for capturing resistance to some virus strains. There are, however, some limits to doing so, such as the possible introduction of deleterious physico-chemical characteristics of tubers. It has been shown, using microsatellite markers, that many of the spontaneous yams collected for domestication by farmers in Benin are wild or hybrid genotypes. Through this capture process, farmers can create new varieties and this practice permits the cultivation of the best genotypes (Scarcelli *et al.*, 2006).

For *D. alata*, the situation is somewhat similar and interspecific hybridization with the related Enantiophyllum species, *D. nummularia*, may well produce anthracnose resistance. As many genotypes present 40 chromosomes ($2n = 2x = 40$), the two major Enantiophyllum gene pools, the African one (*D. cayenensis* and *D. rotundata*) and the Asian one (*D. alata* and *D. nummularia*) can be combined. There are intermediate morphotypes between *D. alata* and *D. nummularia*, which have been shown by deoxyribonucleic acid (DNA) studies to be natural interspecific hybrids (Chaïr *et al.*, 2016a), and it is possible to create more through controlled pollination. Attempts to hybridize fertile *D. alata* females with pollen from *D. nummularia* were found to be successful in producing interspecific hybrids (Table 17.3). A total of 522 interspecific pollinations was done by controlled hand pollination with substantial fruit set (44.2%) but reduced seed set (23.8%). The hybrids exhibited spiny basal stems and very vigorous vegetative growth, but deformed hairy tubers with high browning and oxidation of tuber flesh, and presented very poor tuber shapes and oxidizing tuber flesh (Lebot *et al.*, 2019a).

In Japan, crosses conducted between *D. japonica* and *D. oppositifolia* (syn. *D. opposita*) have produced interesting hybrids (Araki *et al.*, 1983). The *in vitro*

ovule culture technique was used to obtain interspecific hybrids between *D. rotundata* and *D. bulbifera*. Ten days after pollination, ovules were excised and cultured onto Murashige and Skoog (MS) medium, and 40 days after pollination, germination was observed from cultured ovules. The hybridity of the regenerated plant was checked by flow cytometry. The obtained ovule culture-derived *in vitro* plantlets were successfully hardened, acclimatized and transferred to the field, where they survived and grew normally (Saini *et al.*, 2016). Species barriers are probably less solid than initially thought. Enantiophyllum male and female plants of the same ploidy levels could probably be crossed and, if diverse attempts conducted in IITA and CTCRI have failed so far, success is not excluded if breeders are able to access appropriate germplasm. Wide crosses with a great number of related species will give breeders access to a wide range of useful genes. It may be necessary, however, to develop some embryo rescue techniques first. Breeding programmes also depend on the efficiency of the rapid propagation technique, either to propagate recently introduced genotypes which will be used as parents in the selection cycles, or to propagate a recently improved hybrid for advanced clonal evaluation or distribution.

## POLYPLOIDY BREEDING

Almost two decades of data recording on the harvest of the Vanuatu germplasm collection composed of more than 300 accessions of *D. alata* has shown that, on average, plants with 40 chromosomes (diploids) yield 2 kg fresh tubers/plant, while plants with 60 chromosomes (triploids) yield 2.5 kg/plant and plants with 80 chromosomes (tetraploids) can yield more than 3 kg/plant. These are low yields obtained with low inputs, and the yield potential of these varieties is higher, but the influence of the ploidy level on the yield seems to be confirmed. Breeders are attempting to produce round and compact cultivars with 80 chromosomes, as it is most likely that this type of genotype will be useful. The occurrence of fertile male and female plants having 80 chromosomes offers great perspectives for the improvement of the crop. These plants usually produce an exuberant foliage with large leaves. This is the case, for example, for two recommended varieties in New Caledonia, 'Nouméa blanc' and 'Nouméa rouge', which both have 80 chromosomes and are very high yielding. In yams, as in other plant species (e.g. bananas and the Irish potato), an elevation of the ploidy level and chromosome number is associated with yield increase. This is also quite obvious when comparing different *Dioscorea* species with low (*D. tokoro*) and high (*D. nummularia*) chromosome numbers.

In *D. alata*, the observation of quadrivalents in the tetraploids provides cytological evidence for autotetraploidy. The autotetraploid males and females are highly fertile and produce viable seeds on controlled hand pollination. Pollination between diploids and tetraploids are also successful via embryo rescue, producing triploid progenies. The discovery of sexually fertile natural

autotetraploids of *D. alata* is of great interest because polyploidy breeding by conventional hybridization may produce tetraploids and triploids which are more vigorous and higher yielding than diploids (Abraham *et al.*, 2013).

## USE OF MOLECULAR MARKERS

Isozymes have been used successfully to characterize the genetic diversity of African yams and to clarify their traditional classification system (Hamon and Touré, 1990). The most widespread *D. alata* cultivars seem to present a narrow genetic base, but the existing variation is obviously due also to ancient sexual recombinations, as demonstrated by the isozyme patterns (Lebot *et al.*, 1998).

DNA markers (restriction fragment length polymorphisms, RFLPs; amplified fragment length polymorphisms, AFLPs; random amplified polymorphic DNA, RAPD; and simple sequence repeats, SSRs) are useful for demonstrating the relationships between cultivated yams (*D. cayenensis* and *D. rotundata*) and wild relatives in West Africa (Mignouna *et al.*, 2007), between yams of Jamaica (Asemota *et al.*, 1996) and varieties of *D. bulbifera* (Ramser *et al.*, 1996) and *D. alata* (Malapa *et al.*, 2005). Comparison of pairwise distance averages between *D. alata* and the other species showed the decreasing genetic similarities of 54%, 26%, 15%, 9%, 8%, 6% and 5% with the *D. nummularia* interspecific hybrids: *D. persimilis*, *D. cayenensis* and *D. rotundata*, *D. pentaphylla*, *D. bulbifera*, *D. esculenta* and *D. trifida*, respectively. AFLPs confirm the close relationship between *D. alata* and *D. persimilis* (syn. *D. hamiltonii*).

These results are consistent with the biosystematics of the genus *Dioscorea* in respect of the botanical sections and the geographic origins of these species. Comparison of AFLP genetic similarity between *D. alata* and *D. persimilis* did not support previous hypotheses involving *D. persimilis* in the origin of *D. alata* (Coursey, 1967; Mignouna *et al.*, 2001b). It appears that *D. persimilis* is closely related but the two taxa are clearly different species. AFLP markers employed to assess intraspecific variability among 83 accessions of *D. alata* could not differentiate Asian, African and Melanesian cultivars, confirming that clones have been distributed widely but that the diversification process is still ongoing, involving fixed somatic mutations, polyploidization and sexual recombination (VandenBroucke *et al.*, 2015). Hence, the tremendous variation observed in *D. alata* at the morphological level may also reflect a genomic plasticity magnified by the outcrossing mating system (Malapa *et al.*, 2005).

Another AFLP study involving 53 accessions of diverse geographic origins in West and Central Africa, and in Puerto Rico, revealed similar results. The accessions could be clustered into groups that were a mixture of accessions of different geographical origins, indicating that geography has not played a major role in the differentiation of the species. A few accessions clustered very tightly, suggesting that there may be duplicate accessions in the collection. Although *D. alata* was an introduced species in Africa, the genetic variation observed at

the AFLP level was found to constitute a good basis for genetic improvement (Egesi *et al.*, 2006).

AFLP markers have been used also to investigate the genetic diversity in 48 yam accessions from Ethiopia, and to assess their relatedness to commonly cultivated species in West Africa, and reveal that Ethiopian accessions are significantly distinct. The groups detected by AFLP markers are, however, highly consistent with the local yam classification system and also reflect the main structure of morphological diversity (Tamiru *et al.*, 2007). Finally, AFLP and chloroplast DNA (cpDNA) were used to study the genetic diversity of *D. dumetorum* from six countries in West and Central Africa. Three major genetic groups were identified. The highest genetic diversity in accessions from Nigeria and Togo suggests that these countries are the centre of origin and diversity of *D. dumetorum* (Sonibare *et al.*, 2010).

Microsatellite markers have been developed for yams for phylogenetic studies. Microsatellite markers with a higher resolution than other co-dominant markers, such as isozymes, have also been developed for *D. japonica* (Mizuki *et al.*, 2005) and for the Guinea yams and *D. alata*. The structure of the genetic diversity revealed with these markers in Benin appears to be the result of farmers' crop management practices, and cultivar diversity has a geographical component (Tostain *et al.*, 2006, 2007). In Benin, several *D. alata* accessions from the Pacific have been introduced *in vitro*, field evaluated for their major morpho-agronomic traits, fingerprinted with ten SSRs to assess their genetic diversity and compared with local clones. It appears that the introduced accessions are morphologically and genetically well diversified and contribute significantly to germplasm base broadening (Adoukonou-Sagbadja *et al.*, 2014).

In China, ISSR (inter-simple sequence repeats) and SPRAP (sequence related amplified polymorphism) markers have shown that *D. alata* and *D. persimilis* are well differentiated with low genetic diversity within each species (Wu *et al.*, 2014). An SSR study of 384 *D. alata* cultivars from Asia, Africa, the Caribbean and the Pacific revealed wide genetic diversity and structuring associated with geographic origin and ploidy levels (2x, 3x, 4x). No centre of origin was identified, but two genepools (Vanuatu and India) were differentiated (Arnau *et al.*, 2017). In Vanuatu, SSR (simple sequence repeat) and DArT (diversity arrays technology) markers were used to fingerprint 80 *D. alata* cultivars and the local diversification seems to be dominated by the contribution of somaclonal variation, while the selection of seedlings played a minor role. However, when male and female plants of equivalent ploidy flower, natural fruit set occurs and several hundred fertile seeds are produced per plant (VandenBroucke *et al.*, 2015). The same phenomenon probably occurred elsewhere and volunteer seedlings were clonally propagated, evaluated and selected.

In Taiwan, the genetic diversity and phylogenetic relationships of *D. japonica* were evaluated by ISSR markers. Accessions belonging to var.

*oldhamii* and var. *pseudojaponica* were clearly separated into different groups, and var. *japonica* was identified as a possible intermediate variety between var. *oldhamii* and var. *pseudojaponica*. The results revealed that genetic variation was high within counties and subpopulations and low among counties and regions. The northern region of Taiwan is proposed as the genetic diversity centre of the species owing to the greatest number of varieties and high genetic diversity (Kung *et al.*, 2016).

Next-generation sequencing (or genotyping by sequencing, GBS) has been used to attempt to clarify the patterns of genetic diversity within and between the two guinea yams (*D. rotundata* and *D. cayenensis*). Interestingly, a single ploidy level was detected in *D. cayenensis*, whereas both diploid and triploid accessions were present in *D. rotundata*. It appears that the wild species *D. togoensis* and *D. burkilliana* were most distant from the two cultivated yam species; whereas *D. abyssinica*, *D. mangenotiana* and *D. praehensilis* were closest to cultivated yams (*D. rotundata* and *D. cayenensis*). While *D. cayenensis* formed a single genetic group, it seems that *D. rotundata* is composed of diploids genetically similar to *D. praehensilis*, diploids genetically similar to *D. cayenensis* and triploids. When used in combination with morphological data, GBS seems to be a powerful tool for studying the evolution and domestication of guinea yams (Girma *et al.*, 2014). Whole-genome sequencing provides statistically supported evidence that the forest species *D. praehensilis* is the most likely progenitor of *D. rotundata* (Scarcelli *et al.*, 2019).

The genome sequence of *D. rotundata* has been produced and markers suitable for sex determination have been identified (Tamiru *et al.*, 2017). For *D. alata*, a high-density single nucleotide polymorphism (SNP) genetic map has been developed covering 94% of the genome, and a locus determining sex was identified (Cormier *et al.*, 2019). Quantitative trait loci (QTL) related to the resistance of yam to anthracnose (*Colletotrichum gloeosporioides*) and to YMV have been identified (Pétro *et al.*, 2011; Saski *et al.*, 2015; Bhattacharjee *et al.*, 2017) using AFLPs (amplified fragment length polymorphism) and EST sequences (expressed sequence tags).

In practice, however, and despite the significant investments made by various institutions, molecular marker-assisted selection (MAS) is not used for yam breeding. There is no released variety whose development utilized these markers, and conventional breeding is still the most efficient approach to produce improved varieties.

## TRANSGENIC TECHNOLOGIES

Yam genome mapping has been initiated (Mignouna *et al.*, 2002a, b) but needs to be continued. Candidate gene identification has yet to be done to locate the genes involved in important agronomic traits. Reliable systems of regeneration and the use of efficient *in vitro* techniques will have to be developed if

we are to realize genetic transformation. It is first necessary to improve meristem culture techniques, and there are some technical problems in culturing protoplasts of *Dioscorea* spp., because of persistent contamination with bacteria. A significant amount of research was invested in the 1990s, but with limited results (Mantell and Boccon-Gibod, 1998). Cultured cells of *D. alata* have been bombarded, using a particle gun, with microprojectiles coated with DNA; and histochemical assays have been carried out to show GUS ($\beta$-glucuronidase) expression in the bombarded cells (Tör *et al.*, 1993, 1998). No genetically modified yam has been produced so far, but this approach could be useful for transferring virus and anthracnose resistance to commercial varieties more efficiently.

## GERMPLASM CONSERVATION

IITA holds in its genebank the world's largest collection, which includes eight species in more than 4000 accessions. CTCRI in Trivandrum (India), VASI (Vietnam Agricultural Sciences Institute) in Hanoi (Vietnam), PhilRootCrops in Baybay (the Philippines), VARTC (Vanuatu Agricultural Research and Technical Center) in (Santo) Vanuatu, INRA and CIRAD in Guadeloupe (West Indies) also maintain several hundred *Dioscorea* spp. accessions each in *ex situ* collections. Small collections of *D. oppositifolia* and *D. japonica* are maintained in China, Taiwan and Japan.

Once established, *ex situ* collections are described morphologically using internationally standardized morphological descriptors (IPGRI/IITA, 1997). Important databases are then submitted to various multivariate analyses but, in many cases, this has failed to produce a useful image of the variation (Martin and Rhodes, 1977; Malapa *et al.*, 2005). Comparisons between national collections using morphological descriptors are, however, unreliable.

In West Africa, several national collections of *D. cayenensis*, *D. rotundata* and related species have been assembled and characterized in Ivory Coast (Hamon and Touré, 1990), Benin (Dansi *et al.*, 1999) and other countries, but their maintenance has been difficult and numerous accessions have been lost. The core collection concept has been applied to the IITA collection in order to identify a set of genotypes representative of the global diversity maintained in the whole collection. An attempt was made to compose a core collection using 56 morphological traits, information on new germplasm and the presence of duplicates. About 70% of the entire collection is represented by *D. rotundata* (3113 accessions with only 343 females and 1121 males). The core collection is composed of 843 accessions representing about 20% of the entire collection (4,156 accessions). Among the 620 *D. rotundata* accessions of the core collection, 88.6% are diploid ($2n = 40$) and 11.4% were triploid ($2n = 60$). Among these, 300 accessions are flowering (230 male, 64 female) (Girma *et al.*, 2018).

*D. alata* collections were made in Fiji, New Caledonia, PNG, the Solomon Islands and Vanuatu as part of the regional root crop programmes of the 1980s (Jackson, 1994). Most have been documented using international descriptors. In some cases, evaluations have been made for yield and disease resistance, and data from Vanuatu include information on ease of harvest. This region is fortunate in that considerable variation in the germplasm is present and more than 1000 cultivars are grown in the Pacific Islands. In the early 2000s, the South Pacific Yam Network (SPYN) coordinated characterization and clonal selection efforts and a core sample was assembled. These selected genotypes are maintained *in vitro* in the regional germplasm centre managed by the Secretariat of the Pacific Community in Suva, Fiji (Kenyon *et al.*, 2008) and are available for international distribution. Some of these selected genotypes have been introduced in Guadeloupe and are used by the CIRAD breeding programme (Arnau *et al.*, 2017).

When combined with virus eradication and indexing, molecular technologies have the potential to rationalize collections and facilitate exchange between countries. International guidelines exist for the safe movement of yam (Brunt *et al.*, 1989) but, in reality, exchanges are very limited. Virus indexing is not only essential for plants moved internationally, but also for those conserved in active and base genebanks. Conservation *in vitro* can be done at ambient temperatures (Malaurie *et al.*, 1993), on slow-growth medium (Nair and Chandrababu, 1994) or at lower than ambient temperatures, but losses may occur and subculturing is required at 6–12-month intervals. *In vitro* conservation can be done on slow-growth medium at lower than ambient temperatures, but subculturing is required at 6–12-month intervals (Malaurie *et al.*, 1993). By contrast, cryopreservation offers a more cost-effective alternative for cultivars that are not in constant use. To date, methods of encapsulation in alginate beads (Malaurie *et al.*, 1993) or vitrification have shown a 50% success rate; but this work has been carried out with only the most economically important species, *D. alata*, *D. cayenensis* and *D. rotundata*. Therapies for infected plants of the minor *Dioscorea* species have not been tested to determine if meristem culture techniques or antiviral compounds are needed to raise healthier planting materials.

Conservation of germplasm of the minor species (*D. bulbifera*, *D. esculenta*, *D. nummularia*, *D. trifida* and *D. transversa*) is fraught with difficulty: *ex situ* collections are expensive to maintain and methods of on-farm conservation have not been studied.

# 18

# Developmental Physiology

## GROWTH CYCLE

After a growth cycle of approximately 6–8 months, *Dioscorea alata* seedlings can produce tubers ranging in weight from 300 g to 2 kg, but the thinness of their stems and the limited leaf area characterize this seminal phase where plants are far less vigorous than those obtained from tubers.

The growth cycle of any of the 12 cultivated food yam species follows a cycle repeating a rhythm of growth and dormancy every year. Annual cultivars are characterized by the dormancy phase of their tubers, starting at harvest. The perennial cultivated forms of *D. nummularia* go through a dormancy phase of their tubers, remaining in the ground, before they produce new stems. The growth cycle can be described, therefore, as the transfer of nutrients from tuber to stems and leaves at the beginning of the plant's development and in the reverse direction at the end of the cycle.

During the growth cycle, there are five distinct phases, which can vary according to growing conditions, species and genotype.

### Phase one: tuber germination

This may occur from a bud or from differentiated cell masses within the cambium. A bud can develop within a few days, then another bud will appear in the vicinity of the first one, and so on. This group of buds constitutes the primary nodal complex (PNC) from where the primordia of the roots will emerge (Degras, 1993). It consists of an apical bud with one or more axillary buds located on tissues with scattered vascular bundles in parenchymatous cells. This meristematic region has the capacity to produce roots, shoots, tubers and bulbils during seedling germination, and the tuber and stem cutting will also sprout during tuber and bulbil development (Wilson *et al.*, 1998). This PNC is, in fact, a corm-like structure with a very corky bark and a periderm about

1 mm thick. The size of this corm varies greatly according to species and cultivars. It is very large in wild species but relatively small in *D. alata*.

The initial stem emerging from the PNC does not produce true leaves at its nodes but one or two cataphylls. Very soon after that, the stems sprout and the root systems develop rapidly with vigorous growth and ramification, sometimes before field emergence. During this phase, the stem is still devoid of expanded leaves, reducing the transpiring surface as much as possible to optimize the reserves for root development. Such stems without leaves can reach impressive heights of up to 4 m for perennial forms of *D. nummularia*. As leaf growth is negligible, there is almost no photosynthesis and plant development depends almost exclusively on tuber reserves for nutrients and moisture. This phase can last about 6 weeks. Growth often starts during storage, in the absence of light, soil or water.

### Phase two: foliage development

This second phase of growth is characterized by a very rapid and massive increase in leaf area and ends the dependence of the yam plant on the tuber sett. The plant reaches self-sufficiency (autotrophy). Approximately 6 weeks after emergence, leaf development starts and continues up until the 14th week (for *D. alata*) or 18th week (*D. nummularia*), when there is not much more growth in leaf area. Foliage development is accompanied by elongation of stems; increase in stem number and their branching; increase in leaf initiation; and, for some genotypes, the production of bulbils. The growth of the stem is very rapid and can reach 15 cm/day. It starts to grow orthotropically and, as soon as the apex touches a support, it twines around it. During this phase, root development continues but, after 12–14 weeks, it reduces. Towards the end of this phase, the plant tends to accumulate carbohydrates in excess and this triggers tuber initiation, which occurs between 10 and 12 weeks. It is also approximately at this time, or a little later, that plants initiate their flowers.

### Phase three: tuber bulking

During this phase, nutrients are translocated from the canopy to the tuber and the larger the leaf area, the more rapid is tuber development, and the greater its final size. Early canopy development is therefore important. The increase in tuber size is due to the proliferation of new cells and their subsequent enlargement. Tuber growth is slow during the period that follows tuber initiation, is very rapid for several weeks following full development of the canopy and then slows down towards the end of the phase.

### Phase four: foliage senescence

Senescence of foliage starts as early as 5–6 months after planting for early-maturing genotypes. Desiccation starts with the fall of the older, basal leaves and drying of the apices. Usually, foliage senescence is synchronized with suberization of the tuber's surface. This senescence is probably initiated by photoperiod, but there is a genetic component as well. It is, of course, accelerated by foliar diseases. In most cases, however, foliar senescence starts 7 months after planting and finishes during the 10th month. At that time, the stems of the leaves are completely dry. The maturation of the tuber corresponds to the end of the photosynthate translocation, which also corresponds with foliage senescence.

### Phase five: dormancy

The tuber is mature when the distal meristematic area at its tip changes in colour from light to dark, and produces a cork layer and a suberized bark. Mature, freshly harvested tubers cannot sprout and they enter a dormancy phase which can last for less than 1 month to up to 5 months. The dormancy period varies according to temperature.

Sprouting occurs between 25°C and 30°C and is delayed below 15°C and above 35°C. Moisture needed for the sprouting process is supplied endogenously by the tuber itself. The appearance of small protuberances under the skin layer is an indication of the end of dormancy.

Three phases of tuber dormancy have been identified for *D. rotundata*. A first phase from tuber initiation to the appearance of the tuber germinating meristem, a second phase from the tuber germinating meristem to initiation of foliar primordium and a third phase from foliar primordium to appearance of the shoot bud on the surface of the tuber. The first phase can last 220 days and is thought to be an endo-dormant phase. The second and third phases last less than 70 days each, are influenced by plant growth regulators and environmental conditions, and are therefore endo-/eco-dormant phases. It is suggested that the duration of the first phase would need to be shortened to manipulate dormancy, and allow off-season planting, to enable more than one generation of *D. rotundata* per year to be grown (Ile *et al.*, 2006).

Seedlings and plants derived from tubers of *D. rotundata* have two distinct root systems. The first is the temporary root system which is small and short lived, and the second is the definitive root system with a larger and longer lifespan than the temporary root system. The temporary and definitive root systems possess the same structural and functional properties and become established following an identical developmental sequence. The tuber development is coupled with the root system development (Charles-Dominique *et al.*, 2009).

Field experiments have been conducted with *D. esculenta* in Vanuatu to quantify dry matter (DM) production relative to time and plant part (Fig. 18.1). *D. esculenta* develops more than ten primary roots 11 weeks after planting (WAP); the average number of roots per plant increases until 24 WAP and then remains stable. The roots occupy the top 7–10 cm of the soil 11 WAP and do not send secondary roots deeper into the soil. They do not explore the planting mound extensively, but radiate horizontally from the tuber seed sett. They reach an average length of 120 cm, which increases until 21 WAP, but not significantly thereafter. After reaching a maximum distance, the roots go deeper into the soil and, at 24 WAP, the root tips penetrate to a depth of approximately 30 cm. Roots reach a maximum length at 20 WAP (5 months, with the longest measured at 436 cm in a field experiment). The first tubers appear 21 WAP. The number of tubers increases significantly over the following months and can reach a maximum of 27 tubers per plant between 37 and 41 WAP. Yellowing of leaves becomes evident between 33 and 41 WAP. By 45 WAP, many leaves are shed and vine dry weight is less than half its maximum. Vines are completely dead by 50 weeks. Dry weight production is rather slow in the first 4 weeks

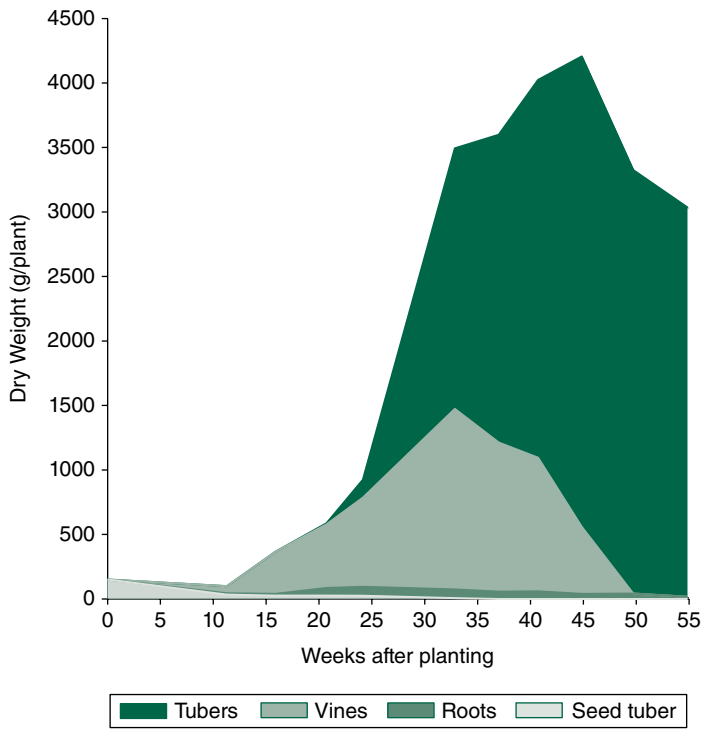


**Fig. 18.1.** Cumulative dry matter production of *Dioscorea esculenta,* relative to time and plant part development (Source: Melteras *et al.*, 2008).

and then increases rapidly from 24 to 33 WAP, when vine growth has ceased. Before the senescence of the vines, 60% of the final dry weight has been stored but, during the senescence of the vines, 40% of the final dry weight is stored. After 45 WAP, DM content declines, probably owing to tuber respiration during dormancy. Crop growth rate (CGR) reflects photosynthetic capacity. It follows a similar pattern to vine dry weight and declines rapidly during the vine senescence period. Relative growth rate is steady during the initial vegetative stage, but declines during tuber bulking. The tuber bulking rate, however, remains high after vine growth has ceased but declines rapidly only in the last stages of vine senescence (Fig. 18.2) (Melteras *et al.*, 2008).

## PHOTOPERIODISM

Most cultivated *Dioscorea* spp. seem to have a $C_3$ photosynthetic type (Cornet *et al.*, 2007). Photoperiod plays an essential role in yam tuber formation and growth. Numerous studies have attempted to understand how yam production could be de-seasonalized by planting every month or so, with the ultimate aim of producing the whole year around. All have failed. Long days promote vegetative development of the aerial parts, foliage and stems, while short days trigger senescence of the foliage and tuber bulking. Of course, different yam species differ in their reaction to photoperiod. The phenology of the temperate species *D. opposita*, its flower induction and tuber bulking, have been found to be highly influenced by photoperiodism (Yoshida *et al.*, 1999, 2000, 2001); but these results can hardly be transposed to the tropical species, which are probably influenced less, though still significantly. In the case of *D. opposita*, it is also observed that more aerial bulbils are produced in plants grown in short days (10–11 h) than those in days of more than 12 h. For the pantropical *D. bulbifera*, it is likewise observed that the production of bulbils occurs in the season when days are shortening.

In the West Indies, there is a significant effect of the planting date on the final yield (Degras, 1993). *D. alata* plantlets produced *in vitro* and subsequently established in the field in successive plantings do not initially differ in morphology. However, after a few months, the architecture and the maximum size of both the aerial and underground parts are quite different. The duration of the vegetative growth phase and of tuber dormancy also varies between planting dates, but tuber sprouting always occurs in April, as in normal cultivation. It is concluded that the problems encountered when attempting to cultivate this species out of season are related mostly to its sensitivity to photoperiodism (Lacointe and Zinsou, 1987).

The effects of photoperiod on the development of *in vitro* grown plantlets of *D. alata* has been studied and reveal that the formation and development of underground tubers is only induced under 12 h photoperiod. The tuber initiation is not related to the initial vegetative stage of plants, and the tubers are

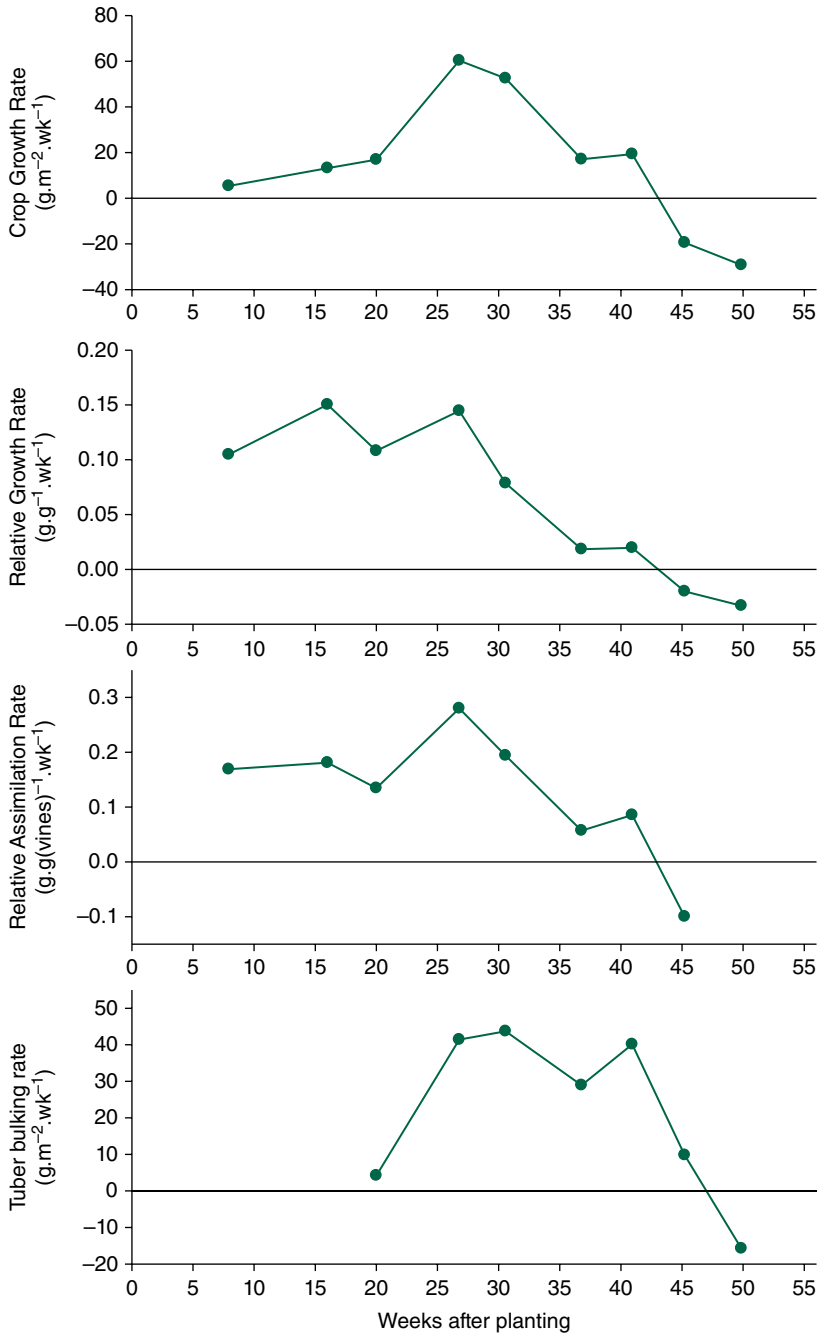


**Fig. 18.2.** Growth analysis parameters for *Dioscorea esculenta* (data are averages across two sampling intervals (Source: Melteras *et al.*, 2008).

visible at about 20 days. However, when the photoperiod reaches 16 h, tuber formation is inhibited and the vine leaf and growth is stimulated. The total DM production and the number of leaves per plant are 50% and 30% lower, respectively, after 44 days under 12 h photoperiod compared to 16 h. It is assumed that the effect of 12 h photoperiod on DM is due to the early initiation of tuberization. When plants grown under 12 h photoperiod are transferred to 16 h photoperiod, they stop their tuber growth and starch accumulation, but shoot and root growth is stimulated (Vaillant *et al.*, 2005).

The effect of light on the development of plants produced by stem-cutting propagation has also been investigated. During long days, there is a connection between root growth and raising the level of the cutting, while during short days the stems emerge more quickly. During short days, the tuber grows to over four times the volume of tubers developed during long days. This illustrates the superiority of tuberization during short days compared to long days (Degras, 1993) (Table 18.1).

Yam is not a shade-tolerant plant. Experiments conducted in greenhouses have shown that the plants can produce normal foliage development but very poor yield in shaded conditions. Yams growing unstaked, with a reduced leaf area, produce lower yields than staked plants; this is thought to be due also to mutual leaf shading and, consequently, reduced light interception in unstaked plants. In Papua New Guinea (PNG), field experiments were carried out to determine the effects of shading on the stomatal density, leaf size, leaf DM and leaf lamina thickness of *D. esculenta*. Shading was found to decrease the stomatal density in the lower epidermis (the upper epidermis of yam being devoid of stomata). Shading generally resulted in the production of larger (in terms of surface area) but thinner leaves, with a decreased DM content. Since shading often occurs under normal growing conditions in various traditional cropping systems (for example, intercropping and alley cropping), *D. esculenta* yield is affected directly (Onwueme and Johnston, 2000).

Field experiments conducted in Guadeloupe have shown that the light interception coefficient across the yam leaf canopy is quite high ($k = 0.64$). Radiation use efficiency (RUE) is, on the other hand, quite low, although highly variable from one genotype to another. Leaf area index (LAI) is estimated using the relation between the lamina area and two measurements: the length and

**Table 18.1.** Dry matter weight (in g) of *Dioscorea alata* plantlets subjected to different photoperiodisms.

| Day length | Stem | Tuber | Root | Total |
|---|---|---|---|---|
| 11.5 h | 17.0 | 34.9 | 4.3 | 56.2 |
| 12 h | 28.2 | 50.6 | 7.4 | 86.2 |
| 12.5 h | 48.7 | 9.1 | 24.9 | 82.7 |

Source: adapted from Degras (1993).

the width of the lamina. This simple technique appears to be reliable in three different *Dioscorea* spp. However, for *D. alata* and *D. rotundata*, a power regression was found appropriate to predict leaf area (LA) from leaf measurements, while linear relationships were sufficient to predict the relationship between crop LA and leaf and stem mass. Species-specific models for the estimation of leaf and stem mass were found to be more accurate. These models provide a nondestructive and reliable alternative to estimate LA and leaf and stem biomass for different cultivars and sites (Cornet *et al.*, 2015).

Change in the RUE as a function of the planting date and its effect on *D. alata* growth and yields has been studied in Guadeloupe. The RUE was relatively stable in the vegetative phase, but increased after tuber initiation to reach a maximum value during the tuber growth phase and then decreased towards the end of growth. Maximum RUE was negatively correlated with photoperiod. It is hypothesized that RUE values were induced by a source–sink interaction which was controlled by crop development and photoperiod. Yields varied little between early and intermediate planting dates and this is thought to be due to an offset between the length of the vegetative phase which determined LA, and the level of RUE after tuber initiation, which determined the capacity of the plant to fill tubers. However, growth and yield decreased for the late planting dates because photoperiod induced fast tuber initiation which ultimately affected the LA (Marcos *et al.*, 2011).

The photosynthetic capacity of *D. alata* leaves has been estimated through the specific leaf N, leaf stomatal conductance and leaf C content under field conditions. It is observed that the LA and chlorophyll meter readings increase with plant age, while leaf N content decreases. Also, leaves at different positions on the vine differ in their photosynthetic capacity. The yam leaves reach their maximum photosynthetic capacity between the 4th and 7th position and these are, therefore, the optimal position for the prediction of plant N response using a chlorophyll meter. The photosynthetic performance of mature leaves is related to the plant growth stage and its nutritional status, being higher under fertilization and at tuber bulking phase. It is thought that the tuber bulking phase is a critical period in which changes in photosynthetic capacity of leaves due to N deficiency may compromise the tuber yield (Hgaza *et al.*, 2009).

## TEMPERATURE

Temperature has a major effect on the dormancy phase. Dormancy is prolonged between 15°C and 17°C. No cultivated species, apart from *D. oppositifolia* and *D. japonica*, can tolerate frost conditions. Vegetative growth is affected severely by mean temperatures of less than 20°C and most species generally require temperatures of 25–30°C for normal development. For a given species, there is a decline in vigour, foliage and tuber yield when the plants are grown in regions with lower temperatures. This is often manifested in a reduction

in the individual LA and in the total number of leaves, and in thinner stems growing to a lower height. Although warm temperatures promote vegetative growth, plants need a marked reduction in mean temperature to promote tuber bulking, which usually occurs during the cool season.

## NUTRITION

*Dioscorea* spp. are demanding on soil fertility and, in traditional cropping systems, they are always placed first in the cropping cycle, just after the fallow. When human pressure increases and fallow periods reduce, yields tend to decline. Symptoms of deficiencies are not obvious but the most significant have been recorded in the field for *D. rotundata* (Table 18.2).

Some experiments have been conducted to study the nutritional disorders of *D. alata*. A range of nutrient deficiencies were generated in small plants grown in solutions in a greenhouse and the associated changes in leaf-nutrient concentrations in leaves of different ages were quantified. For practical purposes, it is recommended that a sample from the sixth node be used as an index leaf. This may provide a good compromise (O'Sullivan and Jenner, 2006). Table 18.3 summarizes the DM yield from each treatment at harvest.

These experiments have induced severe chlorotic symptoms, particularly for Mn and Cu. Most deficiencies increase the chlorosis of young leaves. Deficiencies of N, S and Ca produce symptoms on the shoots, as well as on the

**Table 18.2.** Symptoms seen in the field on leaves of *Dioscorea rotundata*.

| Deficiency in | Symptoms on leaves |
|---|---|
| Nitrogen | Very small leaves, light green or yellowish at first and then drying out from the tip to the edges before falling off. The new leaves are translucent, contain anthocyanins and do not fall |
| Phosphorus | Purple or violet leaves when young; dark, shiny, green leaves when mature. Senescence is marked by scattered yellow to light brown and dark brown leaf areas, then the area becomes yellow, the leaves fall, starting from the bottom to the top |
| Calcium | The leaf is small and leathery, the older ones are mottled and yellow. They become necrotic at their end, along the main vein, on the underside of the leaf |
| Potassium | Small, round, brownish spots appear, then the leaves roll up and turn necrotic with a yellow background |
| Sulfur | Generalized yellowing, including the veins, with leaves narrower than normal |
| Manganese | Internerval chlorosis of the young leaves. Adult leaves are light to yellow |

Source: adapted from Degras (1993).

young leaves, which are pale green to light cream in colour. Generous N nutrition tends to promote aerial growth while causing yield decline, and Ca deficiency restricts shoot production while increasing the size of underground organs. Plants deficient in Ca produce smaller leaves with necrotic lesions and very thin vines. P-deficient plants have necrotic young leaves of a reduced size, while older leaves are stiff and thickened. K deficiency results in overall growth reduction. Colour plates have been produced and may help further deficiency identification in the field. It appears that, in well-nourished plants, mobile macronutrients follow a decline in concentration from the youngest to the oldest leaves.

In deficient plants, concentrations are similar in the youngest and the oldest leaves. This would indicate that, in *D. alata*, the remobilization of nutrients is inefficient (O'Sullivan and Jenner, 2006).

## WATER DEFICIT AND STRESS

*Dioscorea* spp. are tolerant of dry conditions and, in most countries, planting occurs during the dry season. The moisture content of the tubers is sufficient to initiate root growth and it is observed that larger tuber setts have to be planted when drier conditions are expected. The young plant is relatively tolerant to drought because it can tap some of the moisture present in the seed tuber to satisfy its requirements. As the first phase of growth focuses on the development of a root system, with vigorous ramification, the young plant is able to exploit the moisture present. Drought tolerance of the young plant is also improved by the fact that the young stem is devoid of leaves and the transpiring area is consequently limited. When plants are under severe water stress, the lowest, oldest leaves turn yellow and fall off. The abscission of these leaves is a practical indicator of field water deficit. If moisture stress occurs during the first two phases of the growth cycle, tuber initiation will be delayed and final yield reduced. Yams can grow in areas with as little as 500–700 mm of rainfall (e.g. in southern Madagascar), but yields are low. Well-distributed rainfall, or the irrigation amount equivalent of 1500 mm during the total growth cycle, is needed for high yields and commercial production.

A study was conducted in Osun State, southwestern Nigeria, to assess the feasibility of producing different *D. alata* varieties in both wet and dry seasons (planting seedlings already sprouted). As expected, varieties performed better during the wet season than in the dry season in terms of yield of ware tubers, yield of seed tubers, total fresh tuber yield and moisture content. It was, however, observed that these varieties presented an increased percentage DM yield during the dry season. It is hypothesized that the ability to produce higher DM yield in the dry season may be owing to longer hours of sunshine and that the rate of photosynthesis may be higher during the dry season. As higher DM yield is a desirable characteristic, especially for *fufu*, the ability of some *D. alata*

**Table 18.3.** Dry matter yield of *Dioscorea alata* plants grown in full nutrient solution or in solutions omitting one nutrient.

| | Dry weight in g | | | | |
|---|---|---|---|---|---|
| Treatments | Total | Vines | Tubers | Roots | Harvest index* |
| All | 26.3 a | 17.6 a | 5.9 ab | 2.8 a | 0.22 b |
| Minus N | 16.7 bc | 6.1 cd | 8.6 a | 2.0 abc | 0.52 a |
| Minus P | 14.5 bc | 8.9 cd | 3.4 bc | 2.2 abc | 0.22 b |
| Minus K | 11.9 c | 7.3 cd | 3.5 bc | 1.2 cd | 0.30 b |
| Minus Ca | 10.4 c | 3.5 d | 5.8 abc | 1.2 cd | 0.56 a |
| Minus Mg | 17.7 abc | 10.3 bc | 5.3 abc | 2.07 abc | 0.32 b |
| Minus S | 15.9 bc | 8.7 bcd | 4.6 abc | 2.6 ab | 0.30 b |
| Minus Fe | 25.1 ab | 15.2 ab | 7.7 ab | 2.2 abc | 0.32 b |
| Minus B | 15.6 bc | 8.7 cd | 5.3 abc | 1.7 bcd | 0.29 b |
| Minus Mn | 8.9 d | 6.4 cd | 1.6 c | 0.9 d | 0.18 b |
| Minus Zn | 14.9 bc | 1.7 bcd | 3.5 bc | 1.9 bcd | 0.27 b |
| Minus Cu | 14.4 bc | 9.9 bc | 2.9 bc | 1.6 bcd | 0.18 b |
| Minus Mo | 19.9 abc | 12.4 abc | 5.7 abc | 1.84 abcd | 0.26 b |

*Harvest index is the weight of the tubers divided by the total plant weight (numbers followed by the same letter are not significantly different at $P < 0.05$). Source: adapted from O'Sullivan and Jenner (2006).

varieties to consistently produce tubers with higher DM yield indicates their potential value for commercial production (Adeniyan, 2017).

## CLIMATE CHANGE ADAPTATION

It is expected that global warming will be associated with an increase in $CO_2$ and rising air temperatures, which are predicted to be about 0.3–1.7°C by 2100 and 2.6–4.8°C under high $CO_2$ emission scenarios. Changes in both $CO_2$ and temperature are expected to affect yam production. The final yield of yam is influenced by a range of physiological and environmental factors whose interactions are not well documented; their relative contribution is, therefore, difficult to understand. These interactions, however, will play a major role in yam adaptation to climatic change.

Despite a long growing season, the size of the initial tuber sett has a great influence on the final yield: the heavier it is, the higher the yield. The way nutrients are captured and assimilated remains poorly documented and it is quite surprising that the influence of sett size on early root growth appears to have a larger and more reproducible impact on final yield than do fertilizer applications (Onwueme and Haverkort, 1991). Well-organized seed systems will, therefore, play a major role in strengthening growers' capacity to adapt to climatic change. The quality of the planting material will be one of

the major determinants. There is a limit to the average density per unit of area and it depends on species and varieties. In addition, there is tremendous variability among plants of the same clone, resulting from significant differences in sprouting time and vigour, which are influenced directly by the sett's dormancy status and which part of the tuber is used (whole or top, middle or tail) and its nutrient content. To make matters worse, virus and nematode loads undoubtedly add to variability; and staking, mounding and mulching practices are known to influence yield. However, yields of more than 50 t/ha fresh tubers can be obtained for *D. rotundata*, 80 t/ha for *D. alata* and up to 120 t/ha for *D. esculenta* when soil and climate conditions are optimum.

A number of studies attempting to characterize the agronomic determinants of yield have shown that an early development of the root system occurs during the period of dependence on the planted tuber sett, followed by a period of rapid vine growth and LA acquisition and, finally, tuber development. For *D. alata*, there is a correlation between LA duration and tuber yield. For *D. esculenta*, there is a strong relationship between the final number of tubers and the LA at the time of tuber initiation. There is also a high correlation between final tuber yield and LA duration over the period from tuber initiation to harvest. The LAI is an important component of the ideotype and the yield potential is closely related to its value. Table 18.4 presents a few LAI measurements, although very little is documented on this index, which is particularly difficult to measure in yam owing to the complexity of its canopy. The LAI is highly variable and differs according to genotypes within species. It is, therefore, possible that there is sufficient variation in the germplasm to improve earliness of canopy expansion and its total area.

In Bayelsa State, Nigeria, climatic and yam crop production data over the last three decades were analysed using trend analysis and growth models for the prediction of change in climatic factors and yield. The results revealed that the projected future values witnessed an increasing trend in temperature and rainfall, while statistical yield data recorded a decreasing trend in yam yield (Ike, 2012). Another study conducted in the Federal Capital Territory of Nigeria aimed at establishing the relationship that exists between rainfall, temperature and yam yield. Two sets of data on climatic records (rainfall and temperature) and yam yield were collected over 10 years and it was concluded

**Table 18.4.** Leaf area index (LAI) of *Dioscorea* spp.

| Species | LAI | Month |
|---|---|---|
| *D. alata* | 8 | 5th |
| *D. esculenta* | 0.75 | 5th |
| *D. rotundata* | 6 | 6th |

Source: adapted from Suja *et al.* (2000).

that changes in rainfall and temperature have a significant influence on yam production (Zakari *et al.*, 2014).

In Benin, a study attempted to elucidate the effects of the projected climate variables and $CO_2$ on *D. alata* yield in relation to three major soils. The scenario with highest increase in temperature and extreme decline in rainfall exhibited a decrease of 33% in yield until 2050 under ambient $CO_2$ concentrations, while under a moderate increase scenario a decline of 27% was registered. Analysis of the growth constraints suggested that, besides water stress, the indirect effect of reduced rainfall on the release of N from soil organic matter and N deficiency were the major constraints for the ferruginous soils impoverished without concretions type (Srivastava *et al.*, 2012a).

In Japan, the results of similar studies gave different results. The effect of elevated $CO_2$ on *D. oppositifolia* was studied under high- (24–29°C) and low-temperature (20–25°C) regimes, in summer and autumn, and rice was also grown for comparison under the same conditions. In summer, yam vine length, LA, leaf dry weight and total dry weight were higher under elevated $CO_2$ than under ambient $CO_2$ in both temperature regimes. In autumn, tuber dry weight was higher under elevated $CO_2$ than under ambient $CO_2$ in the high-temperature regime. Hence, these interesting results indicate that yam shows a positive response to elevated $CO_2$. Elevated-to-ambient $CO_2$ ratios of all growth parameters in the summer experiment were found to be higher in yam than in rice. Yam net photosynthetic rate was also higher under elevated $CO_2$ than under ambient $CO_2$ in both temperature regimes in summer. It is suggested that these results can be explained by the fact that yam tubers have a large sink capacity, whereas the sink capacity of rice is relatively small during the vegetative phase (Thinh *et al.*, 2017).

# 19

# Agronomy

High yam yields depend on good planting material and husbandry and, in particular, timely weed control to permit establishment of a sufficient leaf area (LA). They also depend on adequate and near optimum temperatures (25–30°C) during the period of maximum growth potential between 14 and 20 weeks after planting (WAP). The most important constraints to production are the high labour requirements, the quality of the planting material and difficulties in mechanization.

## SEED SYSTEMS AND PROPAGULE SELECTION

Multiplication of yam by *in vitro* growth of nodal segments is a practical way for rapid clonal multiplication but, in tropical countries, only a few agricultural research stations can afford to do it. *In vitro* techniques are used for the rapid propagation of virus-free clonal material (Kenyon *et al.*, 2008). Antisera have been produced for several of the viruses infecting cultivated yams, and diagnostic protocols have been developed. However, for all species, meristem culture techniques or antiviral compounds are needed to raise healthier planting materials, faster and in greater numbers (Fig. 19.1a,b).

For rapid propagation, plants are grown in quarantine glasshouses from small tuber pieces. Nodes taken from these plants are surface sterilized and transferred to a range of tissue culture media of different compositions and incubated under controlled light and temperature (14 h light at 29°C and 10 h darkness at 25°C). Despite taking great care over the surface sterilization of nodes, several accessions can fail to be established in tissue culture. Many nodes simply fail to grow and are subsequently overgrown with what is believed to be endophytic fungi, bacteria or yeasts.

The medium that gives the most consistent regeneration rates for meristem tips is composed as follows: Murashige and Skoog- (MS-) based medium, 30 g/l sucrose, 20 mg/l cysteine, 100 mg/l inositol, 80 mg/l adenine, 0.2 mg/l naphthaleneacetic acid (NAA), 0.15 mg/l 6-benzyl-aminopurine and 0.08 mg/l


**Fig. 19.1.** (a) *In vitro* culture of yam meristems and (b) *in vitro* plantlets for germplasm conservation (photo: D. Filloux).

gibberellic acid ($GA_3$). Dissected meristem tips are placed either on filter paper bridges in liquid medium or on the surface of medium of the same composition but solidified with 2 g/l phytogel. For nodal vine segments of *Dioscorea alata* used as explants and nodal segments grown on MS medium, the best shoot proliferation occurs with MS medium containing 1.5 mg/l kinetin + 2 mg/l indole acetic acid. The best rooting is also observed in medium supplemented with 2.5 mg/l indole acetic acid. The plantlets are easily regenerated when transplanted in hardening medium containing brick bats + charcoal + dried moss + leaf mould + soil in 1:1:1:1:1 proportions. After 1 month of transfer in this medium a survival rate of about 85%–87% is observed for transplanted *in vitro* plantlets (Das *et al.*, 2013).

*In vitro* microtuber production has been studied as an alternative for safely propagating and distributing germplasm, as microtubers have been reported as being less vulnerable to transport conditions and easier to establish in the soil (John *et al.*, 1993). In Ghana, various attempts have been made to improve the efficiency of the technique. The effect of sequential treatment (6, 8 or 10 weeks) with tuberization medium (T-medium) followed by MS medium on the sizes and weights of microtubers in shoot cultures of *D. rotundata* has been evaluated on three local cultivars. Culturing the plants on T-medium for 8 and 10 weeks, followed by MS medium, gave the highest induction of microtubers, the best frequency and yield, and highest individual microtuber weights (Klu *et al.*, 2005).

Morphogenesis, growth and *in vitro* microtuber formation have been found to be controlled by external factors. The number of shoots and nodes is increased by the addition of jasmonic acid, which also induces an increase in microtuber numbers (Ovono *et al.*, 2007). However, this technique is not being used routinely, and *in vitro* plantlets are still the most practical way of distributing germplasm internationally.

The culture system type in liquid media influences the growth of the yam plant. Two systems have been tested: the temporary immersion system

(TIS) and the constant immersion system (CIS). Higher results were obtained with TIS compared with plants obtained in culture systems with passive renewal of internal atmosphere in culture flasks or static liquid system (SLS). In TIS, the best results were obtained after 6 weeks of culture. With TIS, the depletion of reducing sugars and the lower mineral nutrients of contents in the culture medium were thought to be related to fast plant growth (Cabrera *et al.*, 2011).

The use of rooted stem cuttings for the production of planting setts is a technique first developed at the International Institute for Tropical Agriculture (IITA) (Akoroda and Okonmah, 1982; Wilson, 1982). It not only accelerates propagation of selected clones but, if carried out with sterilized substrate, produces minitubers free of nematodes. The best results are obtained when the cuttings are taken from plants in full vegetative phase, before tuber initiation. Sections of young vine bearing four to five nodes are cut with a clean, sharp knife and the leaves from the bottom three nodes are removed. The laminas of the upper ones are reduced by half. The prepared cuttings are then planted in a slanting position in trays filled with steam-sterilized shredded coir (coco peat) or carbonized rice husk and maintained in a healthy condition by spraying fungicides at regular intervals. These vine cuttings can be used to produce minitubers within 100–120 days, which can be replanted to produce tubers large enough for planting. It is, however, observed that some genotypes perform much better than others (Acha *et al.*, 2004; Shiwachi *et al.*, 2005b).

IITA has recently transferred to yam a technique originally developed for potato and tested successfully on cassava. Semi-autotrophic hydroponics (SAH) is a novel, low-cost, licensed technology for rapid micro-propagation of clonally propagated crops. SAH is among the various high-ratio propagation technologies showing great potential for addressing tuber seed production for yam seed systems in Nigeria (Olugboyega *et al.*, 2019). It needs a good laboratory infrastructure and skilled human resources, however, and it is too soon to say if it can be readily adopted by the private sector in West Africa.

In traditional cropping systems, farmers usually save and separate from their harvest the planting material they plan to use for the following crop. Considering an average density of 10,000 plants/ha, the seed weight is considerable. For an average individual seed sett weighing between 100 and 500 g, between 1 and 5 t of planting material is required, which means that, depending on crop yield, the farmer has to put aside approximately 10%–30% of the harvest. When farmers lose their planting material for one reason or another, they then have to purchase it and the costs can be very high compared to other inputs, especially if this occurs late in the season. In practice, small tubers are kept as planting material while larger ones are sold at markets. Unfortunately, this approach – if repeated year after year – tends to favour the selection of small leftover tubers that have deteriorated and accumulated viruses and nematodes. Table 19.1 presents the effect of sett weight and plant density on yield.

**Table 19.1.** Effect of sett weight and plant density on the yield of *Dioscorea alata* and *D. rotundata*.

| | 1 × 1 m (10,000 plants/ha) | | 1 × 1.2 m (8,000 plants/ha) | |
|---|---|---|---|---|
| Sett weight (kg) | t/ha | kg/plant | t/ha | kg/plant |
| *D. alata* | | | | |
| 0.2 | 18.1 | 1.8 | 18.9 | 2.4 |
| 0.5 | 29.3 | 2.9 | 20.3 | 2.5 |
| 0.9 | 37.1 | 3.7 | 34.1 | 4.3 |
| 1.8 | 35.6 | 3.6 | 33.0 | 4.2 |
| 4.0 | 42.1 | 4.2 | 34.5 | 4.3 |
| *D. rotundata* | | | | |
| 0.2 | 6.7 | 0.7 | 3.2 | 0.4 |
| 0.5 | 14.1 | 1.4 | 10.1 | 1.3 |
| 0.9 | 20.6 | 2.1 | 13.5 | 1.7 |
| 1.5 | 25.3 | 2.5 | 26.5 | 3.4 |
| 3.4 | 31.9 | 3.2 | 32.9 | 4.1 |

Source: adapted from Akoroda (1995).

In many cases, and especially for the major species *D. alata* and *D. cayenensis-rotundata*, the tuber is fragmented and the propagule is a 200–300 g fraction of a larger tuber: the head (proximal part), the tail (distal part) or the centre. It is observed, for all species, that heads sprout faster and more homogeneously than central parts and tails. The cut sections are often healed with fire ashes and can be sold as planting material in baskets, at markets. They tend to lose water rapidly when cut, and are therefore prepared just before planting, when the small protuberances appearing under the tuber skin indicate that germination will start soon.

In Nigeria, IITA and the National Root Crop Research Institute (NRCRI) have jointly developed the mini-sett technique, which is an efficient seed-tuber production system. Selected mother tubers are cut into 20–40 small pieces called mini-setts. With appropriate treatment, each develops into a full plant producing a seed tuber in a few months. The tubers are selected when dormancy stops, approximately 2–3 months after harvesting, depending on species and countries. The mother tuber is cut into several cylindrical pieces, each about 5 cm long. Each of these is cut again longitudinally into two, three or four pieces, each with a portion of skin, or periderm. These freshly cut mini-setts are soaked in any wide-spectrum fungicide and allowed to dry in light shade for 1–2 h. In some cases, healing is improved by applying wood ash to the fresh cuts. The mini-setts are then spread in nursery beds on 2–3 cm of moist sawdust for sprouting. They can also be sprouted in baskets or boxes, or even in polyethylene bags. When they just start to sprout, the mini-setts are transplanted

into the field, under natural or plastic mulch (at a density of 80,000 plants/ha, 1.00 × 0.25 m). Five months after planting, it is possible to harvest seed tubers weighing up to 1 kg from mini-setts as small as 20–30 g. In most breeding programmes, the multiplication in the field to obtain planting material is carried out routinely using mini-setts (Otoo *et al.*, 1987) (Table 19.2).

The mini-sett technique is now used increasingly by commercial growers in West Africa, and the mechanization of their planting and weeding, and the harvest of seed tubers resulting from them, can reduce production costs. One of the major constraints of this technique, however, is to make sure, before multiplication, that virus-free plants, resulting from tissue culture and virus indexing, are used.

Nursery techniques are also very important for the mini-sett technique, and the use of an infected sprouting medium can have disastrous consequences. Significantly higher percentage of rot is recorded when mini-setts are planted in unsterilized sprouting media. Different methods of sterilizing sprouting media for the control of rot have been studied for *D. rotundata*. The incidence of rot is higher in unsterilized topsoil than in unsterilized sawdust. Roasting is the most effective way of sterilizing the sprouting media, followed by fumigation, while solarization is of low efficiency. There are, however, significant differences between genotypes (Asare *et al.*, 2007). So, first of all, farmers have to experiment to discover which varieties within their portfolio are the most adapted to this type of manipulation.

In Nigeria, seed-tuber production of *D. rotundata* and *D. alata*, using the mini-sett technique, has been tested on-farm and on-station in different agroecological zones. A lower mini-sett sprouting rate is observed in the southern Guinea savannah than in the tropical forest zone. When using the direct mini-sett field planting technique, sprouting and tuber yield are influenced strongly by the cultivar of *D. rotundata*, but *D. alata* is less affected by sett size. An increase in mini-sett size in some cultivars of *D. rotundata* can enhance their sprouting potential; but agroecological conditions, temperature and relative humidity also play a determining role (Ayankanmi *et al.*, 2005).

The quality of the planting material depends on the way this material has been handled during its dormancy period. When temperatures increase, farmers can remove the sprouts by hand to prolong dormancy and delay planting out.

**Table 19.2.** Comparison of multiplication rate per hectare between the traditional seed yam method and the mini-sett technique over 3 years.

| Year | Traditional (A) | Mini-sett (B) |
|---|---|---|
| 1 | 10,000 | 60,000 |
| 2 | 50,000 | 1,800,000 |
| 3 | 250,000 | 54,000,000 |

Source: adapted from Otoo *et al.* (1987).

**Fig. 19.2.** *Dioscorea esculenta* small tubers are calibrated and cleaned to be used as seed setts for field planting (photo: V. Lebot).

An Ivory Coast study has examined the effect on the quality of *D. cayenensis* and *D. rotundata* setts of postharvest gibberellic acid ($GA_3$) treatment just after harvest, and manual desprouting of seed tubers. Although postharvest losses were reduced slightly after 4 months of storage by both treatments, this had no effect on subsequent tuber yield. Field emergence and yield are, however, influenced significantly by sprouting state at planting and the origin of the sett with respect to its position on the mother tuber (proximal, central, distal). Also in Ivory Coast, it is recommended that farmers use apical setts and sprouted setts, which have the highest yield potential (Tschannen *et al.*, 2005).

For *D. alata* varieties producing bulbils, and for *D. bulbifera*, bulbils represent an interesting planting material and give even emergence in the field. For *D. alata*, however, their weight is often quite low (30–100 g) and so is the final yield, but they are a good source of seed setts and some varieties are favoured by farmers because of this attribute (Girma *et al.*, 2015). Species such as *D. trifida* and *D. esculenta* produce a large number of individual tubers, which are ideal propagules for the next crop and as easy to handle, store and replant as full tubers (Fig. 19.2).

## SOIL PREPARATION

Yams, being light-loving and shade-sensitive plants, require sites that are well exposed to solar radiation. If planted in traditional agroforestry systems, they

need to be established in the middle of the plot and to be staked in order to benefit from maximum sunlight. Unlike cassava and sweet potato roots, which initially penetrate the soil and then expand, the yam tuber penetrates the soil while expanding. It is, therefore, important that the soil is light, well drained and friable. Land preparation is the most important input and necessitates almost half of the total 1800 man-hours/ha in West Africa (Orkwor and Adeniji, 1998). In Jamaica, West Indies, inputs are more important but land preparation (clearing + breaking up the soil + ridging) also represents more than half of the time spent on the crop (Table 19.3).

Because yams are placed first in the cropping cycle, land preparation usually involves traditional slash-and-burn techniques. In most countries, land preparation occurs during the dry period, which often corresponds to the cool season of the year during which tubers are dormant. Farmers often have some sort of plant indicator (e.g. the blooming of *Erythrina* spp. trees) that guides them on the most appropriate time to prepare the plot. Bushy fallow and any small trees that are present are cleared with machetes, and the stumps or small trunks are left on the spot until they are burnt. The surface of the soil is then cleared of debris and the soil can be worked very superficially if the plot is intended to satisfy domestic consumption. For higher yields and commercial production, however, the same plot will require further soil preparation.

The construction of mounds (also called hills) is preceded by hand digging a small pit which varies in depth according to the species involved, *D. esculenta* requiring less depth than some elongated varieties of *D. alata* and *D. rotundata*. In most cases, the pits are 0.30 m deep and the mounds are 0.5–1.2 m high, sometimes higher. Mounds are made by drawing the organics-rich topsoil together with the hoe. In general, large hills give the highest yields but this also depends on the characteristics of the soil (Table 19.4; Fig. 19.3). In West Africa, thousands of these impressive mounds can be hand prepared by a single commercial farmer with a simple hoe.

**Table 19.3.** Time spent on *Dioscorea cayenensis* production in Jamaica.

| Operations | H/ha |
|---|---|
| Clearing | 198 |
| Breaking up the soil | 791 |
| Ridging | 791 |
| Preparing planting setts | 119 |
| Weeding | 791 |
| Staking | 237 |
| Tying lianas | 158 |
| Harvesting | 296 |
| Total | 3381 |

Source: adapted from Degras (2003).

**Fig. 19.3.** When hills are planted with calibrated seed setts of a single clone (here cv. 'Wailu' of *D. rotundata*) the intraclonal variation is significant: two tubers *vs* one (left) and forked tuber *vs* cylindrical (right) (photo. V. Lebot).

**Table 19.4.** Effect of mound size on tuber yield.

| Mound size | Density plants/ha (spacing m) | *D. rotundata* | | | *D. alata* | | |
|---|---|---|---|---|---|---|---|
| | | t/ha | kg/mound | kg/tuber | t/ha | kg/mound | kg/tuber |
| Small | 2,500 (2 × 2) | 11.8 | 2.4 | 1.3 | 18.5 | 3.1 | 2.4 |
| Medium | 5,000 (1.4 × 1.4) | 15.8 | 3.1 | 1.5 | 25.2 | 5.0 | 3.5 |
| Large | 10,000 (1 × 1) | 24.3 | 4.7 | 1.9 | 30.9 | 7.5 | 5.0 |

Source: adapted from Akoroda (1995).

Ridges are also used, although not as frequently as mounds, and can be between 1 m and 1.5 m wide and 0.5 m high. In very humid areas (2–3 m rainfall per year), they are established in the direction of the slope to improve drainage. In areas where yams are an expensive product, for example in the West Indies or New Caledonia, land preparation can be mechanized and this necessitates an average area of 25–30 h/ha. A first ploughing is usually followed by a rotavator to turn the soil into a loose and fine texture. Long ridges, spaced approximately 1.2–1.5 m apart, are then produced mechanically by pulling a special tool (a ridger) behind a tractor. For this type of soil preparation, ploughing is often more important than ridging, which is never very high and tends to erode rapidly with the first rains.

## PLANT DENSITIES AND CROP ESTABLISHMENT

In most countries, yams are planted individually by hand, with one plant per mound, or spread out at regular spacings on ridges. Mechanical planting is very rare but has been developed in France for *D. opposita* and in Guadeloupe for *D. alata*, *D. cayenensis* and *D. rotundata* (Joachim *et al.*, 2003). Average density is 10,000 plants/ha when yams are planted on mounds, but it can reach 20,000 plants/ha when ridges are used. The placement depth of the sett depends on its size and

weight, but farmers always make sure that the sprout is covered gently with 5–10 cm loose soil. It is safer to plant too deep than too shallow, to avoid drying out of the shoots. In Melanesia, for example, farmers plant the head end towards the bottom of the hole for the same reasons, but also because it is claimed that the elevation of temperature on the part near the surface accelerates sprouting.

The time of planting depends on the cultivar, species, length of the dormancy period, tolerance of the removal of sprouting in storage, agroecological conditions and, of course, market demands. Farmers can also speed up the sprouting process with traditional techniques aimed at raising the temperature. The main advantage of pre-sprouting the setts before planting is that variability in emergence can be reduced. If the freshly cut setts are planted directly in the field, there is no way for unsproutable setts to be detected and discarded (Onwueme and Charles, 1994). For those that do sprout, time to sprouting may vary by several weeks.

The Tongans in Polynesia have developed a traditional method to break dormancy, known as *tanu*. Although this is not traditional in many countries, farmers may wish to consider adopting it. It involves burying the tubers for several days in a pit covered with banana leaves and soil. The heat of their respiration breaks dormancy and heals cut surfaces. A shallow pit of approximately 4 $m^3$ is dug in the soil and its bottom covered with banana leaves, on which the seed tubers are placed. Location is an important factor and the pit has to be placed somewhere dry under a tree, or where rain will not make it damp. Three to four layers of tubers are placed, along with a few hands of maturing bananas, before they are all covered with more banana leaves and a thick (15–20 cm) layer of topsoil. In some cases, a vent to allow the escape of excess hot air is added to the system in the form of a hollowed-out papaya tree trunk. After 7–15 days, the pit is opened and the tubers are found either ready to sprout or sprouting. This gives an even emergence in the field and is used traditionally in the Pacific for *D. alata* and *D. esculenta*.

Planting dates are controlled largely by photoperiod, but other factors can influence the farmer. Anthracnose and virus diseases can have devastating impacts on yam production in many regions. The complexity of the epidemiology necessitates the use of integrated approaches to counteract their impact, and the date of planting has a significant effect on incidence. In countries where the wet climate favours the development of anthracnose, in Melanesia or in the West Indies, it is generally more appropriate to plant as soon as possible during the dry season, so that the plant has a well-developed canopy before the disease strikes during the wet season.

This recommendation does not, however, appear to be suitable for growers in Nigeria (northern hemisphere). A comparison of the performance of six cultivars of *D. alata*, planted on six different dates (from March to August) reveals a different trend. It confirms that the date of planting has a profound influence on anthracnose severity and, as expected, the genotype effect is more determining with respect to virus severity. Planting late, in August, seems to

produce the least anthracnose development; early plantings in April and May result in the least severity of virus diseases. If the selection of planting time can be used to manage anthracnose, its application is influenced significantly by the prevailing weather conditions at a particular location (Egesi *et al.*, 2007). Table 19.5 summarizes the months of planting and harvesting in the northern and southern hemispheres.

In West Africa, farmers mulch their mounds just after planting their setts. They place a layer of dried grass or leaves at the summit of the mound and cover it with mud, soil or stones to make sure that it will not be blown away by the wind. This mulch reduces the soil temperature in the mound. In these areas, mulching is so critical that drastic yield reduction occurs if it is not done. Mulching is of limited advantage in the wet climates of the West Indies or in the Pacific Islands, except in comparatively dry New Caledonia, where it has been shown to be very advantageous. Mulching is, however, an expensive operation as it has to be carried out carefully by hand.

Staking is done after field emergence and represents 5% of the total manhours. When the species providing the stakes is not cultivated, as in some countries, the use of stakes poses environmental hazards because of the effect on deforestation. Staking is a cumbersome practice, labour intensive and costly. Various attempts to identify genotypes that are tolerant to non-staked cultivation have been made, but the results show that, for most cultivars, there is a significant yield difference between staked and unstaked plants. In Nigeria, a few recently released hybrids seem promising, however, and trials are going ahead. In the savannah, most production is now unstaked, or staked on cereals such as maize or sorghum, because of the scarcity of wooden stakes (Agbaje and Adegbite, 2006). As cereals grow faster than yams, they are sown when the setts are planted and harvested before the yam canopies fully develop. The dried stalks then collapse and the vines grow on each other. This is a popular and efficient cropping system.

Within forest areas, the plots prepared for yams are often cleared incompletely, so that a few trees and bushes can be used to support the vines. Any convenient timber, bamboo or wild cane can be used as stake material as long as they are robust enough to support a large and heavy canopy. Three or four stakes, each supporting a different plant, can be bound together near the top to form a pyramid-like structure, which is fairly resistant to high winds. Various elaborate staking and trellising techniques involving wires and poles have been experimented with by researchers and transferred to growers, with mixed results as they always tend to increase labour inputs and costs.

## INTERCROPPING

*Dioscorea* spp. are rarely intercropped, except in traditional agroforestry systems. Farmers have developed their own associations and continue to experiment with all sorts of crop combinations. Table 19.6 presents the effects of such intercrops.

**Table 19.5.** Planting and harvesting months in northern and southern hemispheres. Source: author's own

| Species | J | F | M | A | M | J | J | A | S | O | N | D | J | F | M | A | M | J | J | A | S | O | N | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Northern hemisphere | | | | | | | | | | | | | | | | | | | | | | | | |
| *D. rotundata* | P | | | | | | H | H | H | H | | | P | | | | | | H | H | H | H | | |
| *D. alata* | H | H | H | H | P | P | P | | | | H | H | H | H | | | P | P | P | | | | H | H |
| *D. trifida* | H | H | H | P | P | P | | | | | | | H | H | H | P | P | P | | | | | | |
| *D. esculenta* | | H | H | P | P | | | | | | | | | H | H | P | P | | | | | | | |
| Southern hemisphere | | | | | | | | | | | | | | | | | | | | | | | | |
| *D. alata* | | H | H | H | H | P | P | P | P | | | | | | H | H | H | H | P | P | P | P | | |
| *D. cayenensis, D. rotundata* | | | H | H | P | P | | | | | | | | | | H | H | P | P | | | | | |
| *D. esculenta* | | | | | H | H | H | P | P | P | | | | | | | | H | H | H | P | P | P | |
| *D. trifida* | | | | | | | | H | H | P | P | | | | | | | | | | H | H | P | |
| *D. transversa* | | | | | | | | | H | P | | | | | | | | | | | | H | P | |
| *D. nummularia* | | | | | | | | | | H | P | | | | | | | | | | | | H | |

When new hybrids of *D. rotundata* are evaluated for tuber yield, response to mosaic diseases and soilborne pests under three different cropping systems (yam alone; yam and maize; yam, maize and melon), the results show that tuber yields decrease under intercropping. There is a reduction of up to 22% in yam and maize and 33% in yam, maize and melon, when compared with yam alone (Agbaje *et al.*, 2002).

In Nigeria, an experiment conducted to evaluate the influence of intercropping on tuber yield and yield components of *D. rotundata* revealed higher values of tuber yield and yield components when yam was interplanted with cowpea compared to monocropping. Cowpea was not detrimental to yam and it was suggested that it could improve soil N status through biological N fixation. The complete ground coverage of cowpea may minimize leaching and excessive water evaporation from the soil, as well as increasing soil organic matter content. The higher tuber yield of sole-cropped yam compared to yam/maize, yam/cassava and yam/maize/cassava associations was thought to be due to competition among yam, maize and cassava (Osundare, 2014).

In Benin, the impact of yam-based systems with herbaceous legumes on DM (dry matter) production of tubers and leaves was studied to assess the levels of nutrients removed and recycled, and the soil fertility changes. The comparison focused on smallholders' traditional systems (1-year fallow of *Andropogon gayanus*–yam rotation, maize–yam rotation) with yam-based systems integrating legumes (*Aeschynomene histrix*–maize and *Mucuna pruriens*–maize). It was observed that DM was removed and recycled; total N, P and K were recycled or removed; and soil chemical properties were significantly improved on yam-based systems with legumes (Maliki *et al.*, 2016). Although there is sufficient research data to demonstrate the positive impact of legume cover crops in fallows and rotations, these techniques are not readily adopted. More research is needed to convince smallholders to adopt new associations and rotations.

**Table 19.6.** Sole and intercrop yield of *Dioscorea rotundata* and intercrops.

| Cropping system | Yam tuber yield (t/ha) | Sweet potato yield (t/ha) | Maize cob yield (t/ha) | Cassava (t/ha) |
|---|---|---|---|---|
| Yam alone | 15.8 | – | – | – |
| Yam + cassava | 7.5 | – | – | 10.8 |
| Yam + maize | 5.5 | – | 7.8 | – |
| Yam + sweet potato | 5.8 | 14.55 | – | – |
| Sweet potato + maize | – | 56.06 | 4.4 | – |

Source: adapted from Akoroda (1995).

## WEEDING

Weeding by hand using a hoe is carried out at least two or three times during the growth cycle, depending on the weeds present in the field. Unstaked plants established at high density are less demanding, as the vines cover the soil and each other fairly rapidly. Staked plants established on ridges require maintenance of the inter-rows, as well as the ridges. The growth habit of *Dioscorea* spp. and their inability to shade the ground completely when staked makes them susceptible to weed competition. Fields that are not weeded properly during the first 3–4 months after planting produce lower yields than weed-free plots. Intercropped yam fields have fewer weeds, and intercropping with maize during the first 3 months minimizes yield reduction, because weed competition is at the early development stage (Table 19.7).

In the West Indies, various rates of active ingredient are used to control weeds (especially grasses) in yam fields, and the products mentioned in Table 19.8 are recommended.

In Nigeria, fluometuron mixed with metolachlor at a dose of 2 + 2 kg a.i./ha, respectively, and Primextra™ (atrazine + metolachlor) give good results at a rate of 3.0 kg a.i./ha (Table 19.9).

Some pre-emergence herbicides (ametryne, atrazine and diuron) can keep weeds under control during the first 3 months of growth if close spacing and

**Table 19.7.** Effect of weed control method and cropping system on *Dioscorea rotundata* yield (t/ha).

| Treatment | Yam alone | Yam and maize | Yam, maize, cassava | Mean |
|---|---|---|---|---|
| Weeding at 3 and 5 WAP | 21.0 | 16.3 | 17.0 | 18.1 |
| – at 3 and 8 WAP | 20.3 | 15.0 | 17.4 | 17.5 |
| – at 3 and 12 WAP | 26.0 | 17.8 | 18.7 | 20.8 |
| – at 5 and 12 WAP | 21.7 | 17.9 | 18.1 | 19.2 |
| – at 3, 5 and 12 WAP | 26.3 | 18.0 | 17.1 | 20.5 |
| Melon and weeding at 3 WAP | 18.9 | 18.4 | 13.7 | 17.0 |
| Melon, sweet potato with yam | 23.4 | 16.7 | 17.4 | 19.2 |
| Melon, herbicide, sweet potato and weeding at 3 WAP | 22.2 | 18.8 | 17.9 | 19.7 |
| Sweet potato and weeding at 3 WAP | 18.9 | 13.8 | 16.5 | 16.4 |
| Herbicide | 24.4 | 17.4 | 15.7 | 19.2 |
| Weed-free control | 28.6 | 17.7 | 20.9 | 22.4 |
| Weedy control | 22.5 | 17.0 | 17.3 | |
| Mean | 22.5 | 17.0 | 17.3 | |

Source: adapted from Akoroda (1995). WAP, weeks after planting.

**Table 19.8.** Active ingredients used in yam fields.

| Active ingredient | Type | Efficiency | Impact | Doses of a.i./ha |
|---|---|---|---|---|
| Glyphosate | Systemic, total | All species | Last 60 days | 1.1–4.2 kg/ha |
| Paraquat™ | Contact, total | All species | Last 30 days | 0.6–0.8 kg/ha |
| Diquat-Paraquat™ | Contact, total | All species | Last 30 days | 0.4 + 0.2 kg/ha |

Source: Joachim *et al.* (2003). a.i., active ingredient.

vigorous growth succeed in covering the ground rapidly. However, if applied too soon, they may not have much impact since yams take quite a long time to emerge (sometimes more than 1 month between planting and field emergence). A practical solution may be to apply a contact herbicide (e.g. Paraquat™) combined with a pre-emergence herbicide just before anticipated emergence. The very heterogeneous emergence rate between heads, central parts and tails of tubers, however, is another factor causing difficulties. The early sprouting setts run the risk of being killed by the contact herbicide and the late sprouting ones run the risk of being invaded by weeds. It is, therefore, important to calibrate planting materials and – as much as possible – to plant full tubers or heads only so that emergence is quick and even.

In Nigeria, it has been found that there is no economic benefit in keeping yams weed-free during the whole cropping period. The investment is high and the return is unsatisfactory. After the critical period (4–16 WAP for commercial tubers and 6–16 WAP for seed tubers), the reduction in tuber yield due to uncontrolled weeds is not significant (Orkwor and Adeniji, 1998).

## FERTILIZATION AND NUTRIENT DISORDERS

Degradation of soil fertility is the major constraint identified by growers in yam production in West Africa (Table 19.10). Although farmers perceive the decline in soil fertility as their most important difficulty in improving yield and profit, they often lack suitable and practical solutions to correct the situation.

Responses to fertilizers are erratic and usually much less significant than the effects of sett size or staking (Oyolu, 1982).

No responses to N fertilization or even depressive effects have been reported. Kang and Wilson (1981) reported no significant effect of NPK fertilizer on tuber yield at all three locations where their experiments were conducted and noticed some depression in the yield of plants grown on flats. In Puerto Rico, Lugo *et al.* (1993) showed that the response to fertilizer application on *D. alata* was significant at only one location, where low natural fertility was confirmed by a soil test conducted at the beginning of their study. *D. alata* yields increase with P fertilization, whereas those of *D. esculenta* and *D. rotundata* do not. To complicate the situation, yams appear to depend on an effective mycorrhizal association to meet their P requirements. Apparently, yams respond well

**Table 19.9.** Effect of staking, not staking and weed control on *Dioscorea rotundata* and *D. alata* yields (t/ha).

| | | | *D. alata* | | | *D. rotundata* | | |
|---|---|---|---|---|---|---|---|---|
| Treatment | Rate a.i. kg/ha | Time | Unstaked | Staked | Mean | Unstaked | Staked | Mean |
| Fluro + metolachlor | 2.0 + 2.0 | PE | 4.54 | 18.21 | 11.38 | 14.73 | 13.23 | 13.98 |
| Primextra™ | 3.0 | PE | 7.30 | 17.17 | 12.24 | 14.17 | 13.00 | 18.58 |
| Gramuron™ | 3.0 | Post | 6.00 | 18.38 | 12.19 | 14.20 | 11.57 | 12.88 |
| Hoe weeding | 3 + 8 + 12 | WAP | 7.71 | 20.13 | 13.92 | 12.60 | 10.67 | 11.63 |
| Weed-free control | | | 14.17 | 24.34 | 19.25 | 16.23 | 14.33 | 15.28 |
| Weedy control | | | 3.29 | 15.61 | 9.45 | 4.63 | 7.10 | 5.87 |
| Mean | | | 7.17 | 18.97 | | 12.76 | 11.65 | |

Source: adapted from Akoroda (1995). PE, pre-emergence; post, post-emergence; WAP, weeks after planting.

**Table 19.10.** Major constraints to yam production in Nigeria (% of farmers reporting the constraint).

| Constraint | High intensity areas (eastern Nigeria) | Low intensity areas (south-western Nigeria) |
|---|---|---|
| Weeds | 9.0 | 6.8 |
| Soil fertility decline | 52.0 | 9.2 |
| Soilborne pests and diseases | 12.0 | 54.0 |
| Leaf pests and diseases | 5.0 | 11.3 |
| Storing | 1.5 | 10.8 |
| Marketing of produce | 0.0 | 0.3 |
| Mound making | 0.3 | 3.1 |
| Planting materials | 1.3 | 0.8 |
| Staking materials | 0.6 | 1.4 |

Source: adapted from IITA (2000).

to N and K fertilizers, while their response to P is slight. This could be due to very efficient P uptake, possibly as a result of the contributions of mycorrhizae (Onwueme and Charles, 1994).

In central Côte d'Ivoire, the response of *D. alata* to NPK-Ca fertilization was studied to see the impact of weather conditions in two growing seasons. The application of a NPK-Ca dose of 160-10-180-110 kg/ha was compared to no fertilizer. It appeared that fertilization increased the tuber yield in both seasons. The increase in above-ground organ yield (leaves and stems) was not reflected in tuber yield increase, suggesting that fertilizer favoured top growth over the tubers. The leaf area index (LAI) and the fresh tuber yield were similar between the two growing seasons under non-fertilization, indicating a good adaptation of *D. alata* to low soil fertility (Hgaza *et al.*, 2010).

It has been hypothesized that the poor response of *D. alata* to fertilizers may be due to the development of a root system that would not allow the plant to capture the nutrients. To test this hypothesis, growth of the *D. alata* root system in relation to plant growth as affected by fertilizer input was studied. The horizontal and vertical distribution of the roots was also described and three types of roots (seminal, adventitious and tubercular) were identified. Roots grew within the mound until 100 days after planting (DAP) and then they extended radially in the soil in the first soil horizon (15 cm depth) with a maximum root extension observed at 160 DAP. It was observed that tuber yield formation was independent from root growth and therefore that the root system did not limit tuber productivity (Hgaza *et al.*, 2011).

Cornet *et al.* (2014) observed that only 22% of 200 field experiments dealing with yam fertilization showed an increase in yield. One of the problems encountered by agronomists conducting such experiments is that high plant size inequality leads to high experimental error and it is, therefore, impossible to detect any positive effect of the agronomic practices being tested. The variation within

statistical treatments is often greater than the variation between treatments. Experiments conducted to clarify this complex problem indicate no differences in the coefficient of variation of plant size and plant tuber yield between plants established at high and low plant density. This implies that competition is not the driving factor controlling plant variability (expressed as CV% between plants of the same genotype). Uneven emergence appears the primary cause. Yam emergence takes place over a long period, creating an early inter-plant size hierarchy which later affects tuber production (Cornet *et al.*, 2015). Further experiments have confirmed that emergence date was the only direct cause of plant yield variability common to *D. alata* and *D. rotundata*. However, it is suggested that some uncontrolled latent variables such as seed-tuber physiological age and reserves may also contribute to this intraclonal variation. Ultimately, the uncontrolled wide range of physiological ages and reserves in seed-tuber lots impacts the plant size hierarchy and the marketable yield (Cornet *et al.*, 2016).

Within uniform planting material, the time to sprouting and number and vigour of sprouts vary greatly. It is quite clear that optimum methods of fertilizer placement for yam have not yet been established. There is an obvious need for more information on fertilizer application methods and timing. Delaying N applications until after the crop is established has already been shown to increase the chances of a yield response.

Spot placement of fertilizers in the planting hole, or banding in the planting furrow on the ridge, may not provide efficient access. A commonly used method involves a side dressing in a furrow around the mound, but this may damage primary roots which radiate from the corm and are very close to the soil surface at the base of these mounds. Broadcasting before planting may be preferable. Lining the fertilizers between the ridges to avoid P fixation in P-fixing soils is another practical solution. Surface application just before rain, or at frequent intervals, may be preferable to furrows for side dressing.

In the West Indies it is recommended the fertilizer applications presented in Table 19.11 be applied.

**Table 19.11.** Fertilizer rates and time of application for solid fertilizers (S) and fertilizers diluted in the irrigation system (I).

| Fertilizers | Weight kg | N | P | K | Time |
|---|---|---|---|---|---|
| 19-9-28 (S) | 200 | 38 | 18 | 56 | Planting |
| | 400 | 76 | 36 | 112 | 45 DAP |
| 15-12-24 (S) | 400 | 60 | 48 | 96 | Planting |
| | 400 | 60 | 48 | 96 | 45 DAP |
| 8-20-20 (I) | 300 | 24 | 60 | 60 | Planting |
| Potassium chloride (KCl 60%) (I) | 160 | 0 | 0 | 96 | Every 2 weeks for 4 months |
| Ammonium nitrate (33%) (I) | 240 | 79 | 0 | 0 | Diluted in 450 l |

Source: adapted from Joachim *et al.* (2003). DAP, days after planting

It is, however, possible to formulate some basic recommendations regarding the fertilization of yams. It appears that the application of more than 40 kg N, 40 kg P and 40 kg K is not justified from an economical point of view. The return on investment will be close to nil because the largest effect of fertilizer occurs with the first increments. Hence, when there is a poor response to fertilizers, the application of smaller doses will result in less waste. If the yam yield potential is low because of late planting, small mounds or ridges or small sett size, then it is difficult to recommend high fertilizer application and the above NPK recommendations (40-40-40) can be considered a maximum. Varieties favoured for pounded yam are those that most require high levels of organic matter. If farmers can get a premium price for these varieties, they may be able to invest in the high labour cost of transporting organic matter; occupying the field for 1 year with a cover crop; or the reduction of planting density and the increased labour involved in using the live staking agroforestry system (Carsky *et al.*, 2010).

For the development of sustainable yam cropping systems, soil fertility restoration and crop performance rely on fallow duration and management. Yam growth and yield have been simulated with the EPIC model (erosion productivity impact calculator) to test its usefulness. This mathematical model has been developed to determine the relationship between soil erosion and soil productivity. In Benin, as in other tropical countries, farmers prefer to plant yam mainly on virgin savannah land and as the first crop in the rotation after fallow. The results obtained from the EPIC model applications emphasize the need for more research to better understand and quantify fallow duration and management practices (Srivastava *et al.*, 2012b).

## HARVESTING

In most countries, farmers start their harvest when foliage senesces. This is usually a little too late, as a senescing foliage has already stopped functioning and does not contribute to tuber bulking. In some regions, planters start excavating before the foliage wilts but, in this case, attention is given to making sure that yams have reached maturity. Yams are usually harvested at the end of the rainy season and it is easier to uplift the tubers when the soil has dried. The soil around the tubers is removed and farmers gauge their size and look at the colour of their distal end to decide if they are sufficiently mature. Harvests are spread over several months, depending on the early and late maturing varieties the farmer is cultivating. For a given species, the harvest period is still insufficient to cover the whole year but, in some countries (in Melanesia for example), the cultivation of different *Dioscorea* spp. allows for consumption almost all year round.

The more irregular in shape is the tuber, the longer is the harvest and cracks decrease its commercial value. The tools used are the same as those for

making the mounds. The dried stems and foliage are first of all removed with machetes and put aside. For compact tubers, a fork with flat blades, similar to that used to harvest potatoes, is placed under the tubers and then uplifted by pressing on it with a foot. This is appropriate for species producing a large number of small tubers, such as *D. esculenta* and *D. trifida*, or for *D. alata* cultivars (e.g. 'Florido') (Fig. 19.4). For larger tubers, the soil is removed gently, starting from the base of the stem and going down towards the distal end of the tuber, which is then uplifted when free.

If the tubers are immature, they tend to be very watery and have a poor taste; and, if they are left in the ground for too long, they are exposed to factors that can cause deterioration in quality. Local knowledge of the agroecological conditions is often the only guide for farmers. In Nigeria, the effect of the time of harvest on *D. rotundata* quality was investigated to determine when the tuber was mature. Setts were planted at the beginning of the rainy season and harvesting was done at monthly intervals from 3 to 7 months after stem emergence. Fresh and dry tuber yields increased steadily over the harvesting period until the 6th month and decreased thereafter. Varieties differed in the number of tubers they produced per plant, but time of harvest did not influence this attribute. The mean sensory evaluation of boiled and pounded yam showed little variation from 4 until 7 months. The best scores of the sensory evaluation, however, were obtained at 6 months, before final foliage senescence occurred, which coincided with the time of highest tuber yield (Akinwande *et al.*, 2007).

In some countries (West Indies, Ivory Coast, New Caledonia), mechanized harvesters have been developed for varieties with a very compact and even tuber shape. In Loir-et-Cher, France, the harvest of *D. oppositifolia* planted at high density and producing, on ridges, tubers of an average 60 cm long is

**Fig. 19.4.** Varieties with compact tuber shape are easily harvested without skin damage (photo: V. Lebot).

fully mechanized thanks to the very sandy and light soil where it is cultivated. Mechanization requires that the setts planted are small so the tubers that will be harvested mechanically are also small and uplifted easily. The staking system, if any, should be removed completely so that stakes do not interfere with the machines.

Depending on species, there is generally only one harvest per year but, in West Africa, *D. cayenensis* and *D. rotundata* cultivars are harvested twice a year. In Nigeria, the first harvest is called 'milking' and consists of cautiously excavating a tuber on a live plant, which remains in the soil until it reaches full maturity. The tuber is cut just under the corm with a machete or a bush knife and the soil is pushed back into place. A new tuber will then develop and will be harvested. This practice provides tubers as early as possible in the year but also helps to obtain seed tubers from varieties which normally produce only one tuber. The largest tubers, however, are always those obtained from plants that are not 'milked'.

The harvesting of *D. bulbifera* bulbils should be left until the foliage has disappeared completely and the stems are well dried before harvest. Their quality deteriorates with an early harvest.

# 20

# Pests and Diseases

Numerous pests and diseases can cause serious yield losses in the field or in storage, but their incidence is very variable, depending on country, region, species, variety and the cropping system used. Generally, when yams are intercropped in traditional agroforestry systems, they tend to be fairly exempt from attack, whereas when they are monocropped on larger, open fields, they are much more vulnerable.

## PESTS

Surveys conducted in Nigeria indicate that farmers consider insects to be the most important pests in high-intensity yam-growing areas (IITA, 2000) (Table 20.1).

In Africa, yam beetles are the most important pests. They are: *Heteroligus meles*, *H. appius*, *Heteronychus licas*, *Prionoryctes rufopiceus*, *P. caniculus* (all Dynastidae spp.) and *Lepidota reichei* (Melolonthidae). *Heterolligus meles* is by far the most important from Sierra Leone to Angola. The eggs are laid in moist soil and the larvae start consuming organic matter. After pupation, the adult beetles appear at the beginning of the rainy season and colonize the yam fields. They start burrowing into the soil at the base of the stem and feed on the tubers, which are still young and developing at that time of year. Their feeding causes lesions of 1–2 cm in diameter and each lesion represents the removal of approximately 4 g tissue. The appearance of the tuber, and consequently its market value, are seriously affected. The use of any contact insecticides, applied either on the setts or on the ground at planting, is very efficient. The best results seem to be obtained with aldrin. Little information is available on cultural control measures against yam beetles. The effect of natural enemies in their biological control is not known, but a number of tachinid and sarcophagid flies have been bred in an attempt to initiate biological control (Kumar, 1990).

In the Pacific, the rose beetle *Adoretus versutus* can consume up to 50% of the leaf lamina and, in some islands (e.g. on Efaté, Vanuatu), damage is very

**Table 20.1.** Major pests and diseases of *Dioscorea cayenensis* and *D. rotundata* in Nigeria (% of farmers reporting the case).

| Pests | Farmers' responses (%) |
|---|---|
| Nematodes | 1.0 |
| Insects | 6.0 |
| Yam tuber beetles | 46.0 |
| Scale insects | 18.0 |
| Termites and ants | 25.0 |
| Anthracnose | 0.0 |
| Others | 4.0 |

Source: adapted from IITA (2000).

severe owing to reduction of the total photosynthetic area. Its control with insecticides is somewhat difficult as this beetle is nocturnal and hides in the litter during the day, where it is well protected. In some cases, Papuana beetles (*Papuana* spp.), which are responsible for considerable losses on taro (*Colocasia esculenta*), also attack *Dioscorea* spp.

Scale insects and mealy bugs (Coccidae, Diaspididae) can have an important economic impact. Three species have been reported in Ivory Coast (*Gonaspidiotus hartii* or *Aspidiella hartii*, *Aspidiotus destructor* and *Planococcus citri*). Infestation occurs very early on the stored tubers and attacks result in their commercial depreciation. Their coating cannot be removed easily and necessitates hand brushing (Degras, 1993).

A world review of insects associated with *Dioscorea* spp. listed a total of 73 species, including 48 species when the crop is in the field, and 27 species after harvest, in storage. Most insects belong to the order Coleoptera (35 spp.), Hemiptera (15 spp.), Lepidoptera (13 spp.), Isoptera (5 spp.), Hymenoptera (2 spp.), Diptera (1 spp.) and Thysanoptera (1 sp.). Yam scales, mealybugs and a few beetles cause significant losses to tubers both in the field and in storage (Korada *et al.*, 2010). In Nigeria, 13 insect species have been identified on *D. alata* and *D. rotundata*. Insects in the order Hymenoptera were most prevalent, follow by those in order Coleoptera. The orders Heteroptera and Hemiptera were found in low numbers (Asala *et al.*, 2016) (Table 20.2).

## NEMATODES

Various species of nematode attack *Dioscorea* spp. by puncturing plant cells and causing cell breakdown and malfunction in the plant tissues. Three species are considered to be of economic importance: *Scutellonema bradys*, *Pratylenchus coffeae* and *Meloidogyne incognita* (Quénéhérvé, 1998).

*Scutellonema bradys* is known as the yam nematode and has been recorded in West Africa, the Pacific and the West Indies. This species is found in the soil around

**Table 20.2.** Insect species collected on *Dioscorea alata* and *D. rotundata* in Abuja (Nigeria).

| Scientific name | Family | Common name |
|---|---|---|
| Coleoptera: | | |
| *Scarabaeus* spp. | Scarabaeidae | Scarab beetle |
| *Tetragonoderus* spp. | Carabidae | Ground beetle |
| *Monolepta nigeriaebryant* | Chrysomelidae | Leaf beetle |
| Orthoptera: | | |
| *Zonocerus varvegate* | Pyrgomorphodae | Variegated grasshopper |
| *Catantops melanostictus* | Acrididae | Shorthorned grasshopper |
| Hymenoptera: | | |
| *Gryllu bimaculatus* | Gryllidae | Field cricket |
| *Camponotus vestitus* | Formicidae | Big-headed ants |
| *Ammophila tenuis* | Sphecidae | Black and yellow bug |
| *Apis mellifera* | Apidae | Honey bee |
| Heteroptera: | | |
| *Plautra* sp. *brunnipennis* | Petatomidae | Sting bug |
| *Gracnethust* spp. | Cynidae | Black sting bug |
| *Dieuches albostriatus* | Lygaeidae | Seed bug |
| Hemiptera: | | |
| *Aphis* spp. | Aphididae | Aphid |

Source: adapted from Asala *et al.*, 2016.

the yams and is an endoparasite of the roots and tubers. The eggs are laid in the plant tissues, where they hatch and produce very large populations in the tubers (as many as 62,000 nematodes/10 g fresh tuber). The nematodes cause the breakdown of cell walls and destruction of the cell contents, and produce cavities within the tissues. In the field, *S. bradys* is usually found in the periderm and rarely penetrates deeper than 1 or 2 cm into the tuber. However, during tuber storage, penetration goes deeper and causes the development of small lesions, easily observed when the tuber skin is removed. They turn black and form a dry-rot layer, which can invade the whole tuber (Bridge, 1982). This nematode does not cause a reduction in yam growth, but can spoil a considerable part of the edible portion and reduce its commercial value. In West Africa, most species (*D. alata*, *D. bulbifera*, *D. cayenensis*, *D. rotundata* and *D. esculenta*) are attacked, but some varieties are much more resistant than others.

Several experiments have been conducted in the West Indies to attempt to control and reduce the incidence of *S. bradys* attacks. Nematicide treatments applied at harvest are efficient, but chemicals need to be applied at each cycle, as the nematodes are not eliminated completely and reproduce quickly. The use of healthy planting material, either from bulbils or from *in vitro* plantlets, is an attractive but very expensive alternative. A high proportion of nematode-free seed tubers can be produced by coating with Cadusafos. However, this toxic

product should be used only to counter a serious attack of great economic impact (Cadet and Daly, 1996).

In Costa Rica, the most frequent nematodes are *Scutellonema* and *Aphelenchoides*, followed by *Meloidogyne*, *Tylenchus*, *Pratylenchus* and *Helicotylenchus*. *M. javanica* and *M. incognita* are found concomitantly in white yam (*D. rotundata*) and *M. incognita* in *D. trifida*. *P. coffeae* and *P. brachyurus* are found in *D. cayenensis* and *D. trifida*. *P. coffeae* was found in the three regions of Costa Rica (Humphreys-Pereira *et al.*, 2017).

In Benin, the pathogenicity of three populations of *S. bradys* from different geographical areas was assessed on seven cultivars: one *D. rotundata* and six *D. alata*. *S. bradys* does not affect the plant vine circumference, vine dry weight or the number of tubers per plant across cultivars, but affects tuber weight. The greatest weight loss is recorded in fertilized tubers infected with *S. bradys*. Nematode multiplication rates are higher in tubers during the first 3 months of storage, but decrease in the 4th and 5th months (Baimey, 2005). Galled tubers collected from farmers' stores and markets in Nigeria and Ghana have been shown to be infested with *M. incognita* (69% of the samples collected), *M. javanica* (13%), *M. enterolobii* (2%) and *M. arenaria* (2%) (Kolombia *et al.*, 2017).

The lesion nematode *P. coffeae* is present in the West Indies and the Pacific Islands. The symptoms are similar to those of *S. bradys*. The nematodes are found in the tuber skin and cause severe necrosis and deep cracks in the outer tissue layers. This is associated with a subsequent deterioration of tuber quality and, finally, a significant loss in market value.

Root-knot nematodes, *Meloidogyne* spp., are present in most countries and different species (*M. arenaria*, *M. hapla*, *M. incognita* and *M. javanica*) are found. The juveniles infest the roots and tubers and establish themselves on a feeding site in vascular tissues. The feeding of the females produces galls, or so-called knots, typical of *Meloidogyne* spp. In the south-eastern region of Nigeria, these nematodes are widespread pests on *D. rotundata* and *D. alata*. It has been shown that when setts are inoculated artificially with *Meloidogyne* spp. they geminate normally but plant yield is reduced significantly (Bridge, 1982). If young seedlings are parasitized by these nematodes, the plants become stunted and severe infestation can kill young plants. In the state of Orissa, India, the popular *D. alata* cultivar called 'Hinjilicut' is highly susceptible to the root-knot nematode. Tubers are deformed with an irregular surface, which contains many females, along with egg masses. A local screening of 27 accessions of *D. alata* germplasm has led to the identification of a highly resistant and high-yielding cultivar ('Sree Keerthi') (Mohandas and Misra, 2005).

Cultural practices directly determine the extent of nematode damage. Fallow is not sufficient as the presence of wild hosts makes at least 4 years fallow necessary in order to have some effect on the nematode population. Intercropping with maize, ginger, cocoyam, taro and sweet potato gives some control results, but not all farmers can afford to do this. Some cover crops, such as *Tagetes* spp. (African marigold), *Aeschynomene histrix*, *M. pruriens* and *Pueraria*

*phaseoloides* are promising. In West Africa, *Helicotylenchus* spp. are the most frequently encountered and prominent nematodes followed by *Pratylenchus* spp., *Scutellonema* spp. and *Meloidogyne* spp. The most effective cover crops used to control these nematodes are: *T. erecta*, *Aeschynomene histrix*, *Mucuna pruriens* and *Pueraria phaseoloides* (Claudius-Cole *et al*., 2015).

Plots which have been cultivated recently with vegetables should be avoided. Production of nematode-free planting material by using stem cuttings is effective, but is a laborious solution and not all farmers are willing to adopt it. The treatment of planting material by immersion in hot water prior to planting is more effective than field treatments. Hot water treatment involves immersing the tubers in preheated water for a time sufficient to kill the nematodes without damaging the tissues. The immersion of tubers at 50–53°C for 25 min is recommended. This may eliminate *S. bradys* and *Meloidogyne* spp. but it depends on numerous factors, including tuber age, species, varieties, dormancy, nematode densities and depth of infestation.

In Jamaica, household disinfectants such as Dettol, bleach and Jeyes fluid are relatively effective against *M. incognita*, *R. reniformis*, *Helicotylenchys* spp. and other nematodes (Hutton, 1998).

## BACTERIA

A few bacteria have been suspected of being responsible for losses due to tuber rot during storage. A *Corynebacterium* sp. has been found to cause a dry rot of the tuber. *Serratia* spp. have been identified in tubers from Nigeria and Puerto Rico, as well as *Erwinia* spp., but it is suggested that these bacteria may be a secondary infection rather than the cause of the tuber rot (Zohouri, 1998).

## FUNGI

Numerous fungus species have been isolated from the foliage and tubers of *Dioscorea* spp. (Table 20.3).

Depending on species and varieties, *Phyllosticta* spp. can cause large necrotic spots on the lamina, which enlarge and spread to all the foliage. *Rhizoctonia solani* may cause the lamina to turn completely brown but the damage varies significantly according to the weather. *Corticium rolfsii* attacks all levels of the plant and, when severe, its development at the stem base can cause the whole plant to wilt. In Nigeria, *Fusarium oxysporum* has been reported as causing serious losses in fields which have been cultivated for too long.

None of these species, however, has an economic impact comparable to the yam anthracnose, caused by the fungus *Colletotrichum gloeosporioides* (incomplete state and conidean form of *G. cingulata*). Anthracnose has been reported in all yam-producing regions of the world and is characterized by blackening

**Table 20.3.** Fungi species isolated on *Dioscorea* spp. foliage and tubers.

| Species | West Indies | Africa | Oceania |
|---|---|---|---|
| Foliage: | | | |
| *Alternaria* sp. | × | | |
| *Ascochyta* sp. | × | × | |
| *Botryodiplodia theobromae* | × | × | |
| *Cercospora* sp. | × | × | × |
| *Choanephora cucurbitarum* | × | | |
| *Cladosporium* sp. | × | | × |
| *Colletotrichum capsici* | × | × | |
| *C. gloeosporioides* | × | × | × |
| *Corticium rolfsii* | × | × | |
| *Corynespora cassiicola* | × | × | |
| *Curvularia* sp. | × | × | |
| *Diplodia* sp. | × | | |
| *Fusarium* sp. | × | × | |
| *F. oxysporum* | × | | × |
| *Glomerella cingulata* | × | × | × |
| *Goplana dioscoreae* | | | × |
| *Helminthosporium* | × | | |
| *Heterosporium luci* | × | × | |
| *Illosporium* sp. | × | | |
| *Lasiodiplodia theobromae* | | | × |
| *Macrophomina phaseoli* | × | | |
| *Monochaetia* sp. | × | | |
| *Mychosphaerella dioscoreicola* | × | | |
| *Oidium* sp. | | | × |
| *Periconia* sp. | × | × | |
| *Pestalotia* sp. | | | × |
| *Pestalotiopsis cruenta* | × | × | |
| *Phoma* sp. | × | | |
| *Phomopsis* sp. | × | | |
| *Phyllosticta* sp. | × | × | × |
| *Pythium* sp. | × | | |
| *Rhizoctonia* sp. | × | × | × |
| *Sphaeropsis* sp. | × | × | |
| *Sphaerostilbe repens* | | | × |
| *Stachybotrys* sp. | × | × | |
| *Stemphyllium* sp. | × | | |
| *Vermicularia* sp. | × | | |
| Tubers: | | | |
| *Aspergillus niger* | | × | × |
| *A. tamarii* | | × | |
| *Botryodiplodia theobromae* | | × | |
| *Fusarium monoliforme* | | × | × |
| *Penicillium cyclopium* | | × | |

**Table 20.3.** Continued.

| Species | West Indies | Africa | Oceania |
|---|---|---|---|
| *P. gladioli* | × | | |
| *P. oxalicum* | | × | |
| *P. sclerotigenum* | | × | |
| *Rhizopus nodosus* | | × | |

Source: adapted from Zohouri (1998), Lebot (2003).

and dieback of the leaves and shoots, giving a burnt appearance to the vines and foliage. In some regions, the damage done to the crop is so rapid and severe that farmers believe it is the result of thunder. *C. gloeosporioides* exudes phytotoxic products that are a water-soluble, host-selective glycoprotein-type of toxic compound composed of large polysaccharides, of which 80%–85% are mannose and galactose (Alleyne, 1996). Necrotic lesions on the leaves are always associated with the area in close contact with the exuded toxin. Leaf necrosis and death of stems lead to a reduction of the photosynthetic potential of the plant foliage, which generally occurs before tuber bulking. It is extremely damaging on *D. alata*. In the Caribbean, for instance, yield losses of 50%–100% are recorded on favoured varieties during epidemics (Degras, 1993; Green, 1994; Sweetmore *et al.*, 1994). The causal organism, *C. gloeosporioides*, is also found on many other crops, as well as on weeds.

Incidence of the disease is related closely with rainfall and atmospheric humidity. Apparently, it is not too severe in the drier areas of India, or in the West African yam belt. In the Pacific, losses are high and control is difficult (Jackson *et al.*, 1980; Winch *et al.*, 1984). Fungicides have been recommended, but are unsuitable for smallholder production and even in commercial plantings, often give only temporary relief. Benlate (containing active ingredient (a.i.) Benomyl) was an efficient systemic before being declared illegal. Dithane is effective, but has to be used regularly. Methods of cultural control have assumed that alternative hosts are the main source of inoculum for seasonal epidemics (Jackson *et al.*, 1980) and infection of setts has been overlooked or mistaken for lesions caused by the nematode *P. coffeae* (Bridge, 1996).

Unfortunately, the most popular cultivars, or those which are particularly adapted to commercial production, are also those which are the most susceptible. In Barbados, West Indies, anthracnose severely reduced the production of 'White Lisbon' (McDonald *et al.*, 1998). In Puerto Rico, an evaluation of the marketable yield and the natural reaction to anthracnose of four *D. alata* cultivars ('Florido', 'Diamantes', 'Forastero' and 'Kabusah') reveals no significant yield differences among the last three. Their average marketable yields of 26.2, 25.6 and 24.8 t/ha, respectively, are significantly higher than that obtained for the widely used 'Florido' (2.9 t/ha). This popular cultivar shows the highest disease severity (Gonzalez, 2006).

Variation within *C. gloeosporioides* is still poorly defined and hinders breeding for resistance. In the Pacific, the South Pacific Yam Network (SPYN) (Lebot, 2003) has attempted to identify the numerous co-factors involved in the epidemy. In five different Melanesian countries, more than 80 isolates were collected of *Dioscorea* spp. and crop species or weeds present in the same cultivated plots. The objective was to assess the variability existing within these isolates and to attempt to locate the source of the inoculum and the origin of the epidemy using inter simple sequence repeat with polymerase chain reaction (ISSR-PCR) markers to fingerprint isolates of *C. gloeosporioides*. There are significant differences in pathogenicity among *C. gloeosporioides* isolates, but there is a lack of a clear association between morphological data and pathogenicity among isolates. Although the occurrence of *G. cingulata* on yam has been reported widely, there is still a paucity of information on its importance in the epidemiology of yam anthracnose. The fact that almost half of the isolates tested produce sexual structures on yam host tissue reveals that *G. cingulata* occurs more frequently than previously thought. There is, however, no clear link between pathogenicity and the production of the teleomorph form and, hence, it is most likely that the teleomorph stage plays a role in genetic variability, as well as acting as a means for vegetative propagation from season to season (Lebot, 2003).

Isolates of *C. gloeosporioides* from both yam and non-yam species are able to infect *D. alata*, as well as a number of other non-yam hosts. From a practical point of view, this means that *C. gloeosporioides* from yam is a potential pathogen of a number of crops. The associated natural flora found in, or around, fields acts as an inoculum reservoir posing a serious threat to yam production from one season to another. Hence, in yam-growing areas, practices such as intercropping (or mixed cropping) with known *C. gloeosporioides* hosts should be minimized and the destruction of species known to host the fungus and other sanitization measures should be recommended.

*C. gloeosporioides* has also been detected in yam tubers from Vanuatu and Papua New Guinea (PNG), confirming that the fungus is able to infect and survive in tuber tissues from season to season. Infected tubers used as planting material may act as a primary source of inoculum, playing an important role in the epidemiology of the pathogen in the field. The disease has also been shown to be tuber-borne in both West Africa and the West Indies (Green and Simons, 1994). Infection starts in the field and develops in storage. Tuber-borne infections could have severe implications for production, both as a source of infection and as a means of dispersal. However, the mechanism of spread of *C. gloeosporioides* from tuber to canopy is yet to be understood fully. The pathogen has not been re-isolated or detected from shoot parts of plants raised from heavily infected tubers, ruling out any systemic spread of this fungus.

Spread may well start from the rotting seed sett once the plant has reached the autotrophic stage. The high incidence of soil-borne pathogens such as *Fusarium* spp. and *R. solani*, as well as tuber-rotting agents such as *Rhizopus*

spp., *Penicillium* spp. and *Aspergillus* spp., confirms that these pathogens are nuisances, both in the field and in storage. Further studies to determine whether they also play a role in predisposing tuber infection by *C. gloeosporioides* are still required. Moreover, the high degree of contamination by these fungi, particularly *Rhizopus* and *Rhizoctonia*, may inhibit the growth of *C. gloeosporioides* on agar, hence leading to an underestimation of its frequency in tuber tissues when detection studies are being conducted. In addition, detection of *B. theobromeae*, *Phoma* spp., *Phomopsis* spp., *C. capsici* and *Curvularia* spp., which also cause a number of leaf spot diseases on yam, gives an indication of the potential risk these pathogens, including *Colletotrichum gloeosporioides*, may pose to tuber quality (Lebot, 2003).

In the Pacific, the heterogeneity exhibited at the molecular level by isolates of *C. gloeosporioides* indicates the existence of a complex population structure in which sexual recombination probably plays a major role in generating variation. In all countries, there is little or no evidence of clonality. This is due probably to the nature of yam cultivation in small plots within agroforestry systems, rather than in large fields of monocrops like those of West Africa. The lack of clear relationships between molecular groups and geographical origins, coupled with the evidence that very similar strains are present in widely separated localities, probably reflects the historic movement of clonal germplasm between the Pacific Islands. The most appropriate approach to control the spread of this disease is to breed new varieties with parents originating from different genepools, which are resistant or tolerant to anthrachnose. In Vanuatu a breeding programme combining parents from India and local varieties has been successfully implemented (Fig. 20.1a, b).

In Nigeria, molecular markers have shown that sexual recombinations of *C. gloeosporioides* may play an important role in anthracnose epidemics (Abang *et al.*, 2006). Two distinct morphotypes are associated with anthracnose disease. Molecular differentiation clearly separates isolates of the aggressive defoliating morphotype from the moderately virulent, non-defoliating strain (Abang *et al.*, 2002, 2005).

Identification of the levels of resistance to yam anthracnose is laborious and cumbersome. A tissue culture-derived, whole-plant inoculation assay may be an alternative method, faster and more cost-efficient than conventional field techniques. The use of the spray inoculation method has been shown to be reliable. The whole-plant area scoring method conducted in two assessments (5 and 7 days after inoculation) provides the best conditions for evaluating yam genotypes. The tissue culture-derived whole-plant assay has been used to test 60 *D. alata* cultivars for their reactions to three isolates of *C. gloeosporioides*. As in field conditions, a wide range of variation in cultivar resistance and the significant effects of pathogen isolate and interactions, are observed. The potential of the tissue culture-derived whole-plant assay for anthracnose resistance breeding programmes appears promising and could speed up the improvement process (Onyeka *et al.*, 2006a, b).


**Fig. 20.1a.** Anthracnose-susceptible variety of *D. alata* attacked by *Colletotrichum gloeosporioides;* **b**. Improved hybrid resistant to anthracnose (photo: V. Lebot).

Screening yam germplasm in the field for anthracnose resistance can be a complex exercise. The reliability of anthracnose severity rating parameters has been compared and it appears that all evaluated parameters (detached-leaf severity, whole-plant severity, lesion size and spore production) can be successfully scored and used for assessing severity of the disease. However, detached-leaf and whole-plant evaluation have a positive agreement with the field evaluation while data from other ratings need to be transformed (Nwadili *et al.*, 2017).

In Guadeloupe, recurrent anthracnose epidemics since the 1970s did not alter varietal dynamics strongly, but sometimes forced farmers to adopt species less susceptible than *D. alata*, such as *D. cayenensis* and *D. rotundata*. It appears, however, that the main factors affecting changes in diversity are not related to agronomy and there are different processes differentiating short-term from long-term varietal dynamics, independently of the anthracnose risk (Penet *et al.*, 2016).

## VIRUSES

About 15 different viruses have been described as infecting members of the *Dioscorea* genus. Although the effects of the virus diseases on yield are difficult

to quantify accurately, it is quite clear that infection reduces vegetative growth and tuber size (Thouvenel and Dumont, 1990).

Detection of viruses is done by different techniques ranging from serological tests (enzyme-linked immunosorbent assay, ELISA), electron microscopy and deoxyribonucleic acid (DNA) techniques such as cDNA (complementary DNA) probes and PCR. ELISA tests are used on leaf or tuber samples to detect accurately the identification of the virus involved. There are no techniques available for controlling viruses in the field. One of the solutions is the development of a sanitation programme to produce virus-free *in vitro* plantlets, but more data are needed to document their re-infection rate once established in the field (Table 20.4).

Two viruses of the family Potyviridae (YMV and DAV = YMMV) are reported to be the most widespread and economically important viruses worldwide, and are a major constraint to the international movement of germplasm, as very few laboratories have the means to produce virus-free yam germplasm (Lebas, 2002).

Yam mosaic potyvirus (YMV) is the most important virus infecting yams in the tropics. It causes symptoms ranging from mild mosaic on leaves to stunted growth. YMV is transmitted mechanically from plant to plant by *Aphis gossypii*, *A. craccivora*, *Rhopalosiphum maidis* and *Toxoptera citricidus* (Odu *et al.*, 2004a, b). In West Africa the virus is present in all cultivated species, while in Guadeloupe, it is detected mostly from *D. trifida*, *D. cayenensis* and *D. rotundata* (Urbino *et al.*, 1998). YMV has not been demonstrated conclusively to be present in the Pacific region.

Dioscorea alata virus (DAV) (syn. yam mild mosaic virus, YMMV) is transmissible from *D. alata*, the host plant, only by the aphids *A. craccivora* and *R. maidis*. It induces mild mottling, veinal chlorosis, occasional vein banding,

**Table 20.4.** The main viruses known to infect yams. Source: author's own

| Virus | Acronym | Genus |
|---|---|---|
| *Dioscorea* latent virus | DLV | Potexvirus |
| *Dioscorea alata* virus (syn. yam mild mosaic virus) | DAV (YMMV) | Potyvirus |
| Cucumber mosaic virus | CMV | Cucumovirus |
| *Dioscorea dumetorum* virus | DdV | Potyvirus |
| *Dioscorea bulbifera* bacilliform virus | DbBV | Badnavirus |
| *Dioscorea alata* bacilliform virus | DaBV | Badnavirus |
| Yam mosaic virus | YMV | Potyvirus |
| Chinese yam necrotic mosaic virus | ChYNMV | Macluravirus |
| *Dioscorea esculenta* virus | DEV | Potyvirus |
| *Dioscorea* mottle virus | DMoV | Comovirus |
| *Dioscorea trifida* virus | DTV | Potyvirus |
| Japanese yam mosaic virus | JYMV | Potyvirus |
| Internal brown spot virus | IBSV | – |

leaf distortion and, in some cases, severe chlorosis. DAV (potyvirus) is the virus detected most commonly by serology (ELISA) in *D. alata*, *D. esculenta* and *D. bulbifera*. The molecular technique RT-PCR is generally more sensitive than ELISA for detecting DAV. Sequence analysis suggests that there are many different strains of DAV present in the Pacific region, but there is no strong association between particular sequence types (strains) and geographic or host origin. Many samples from the Pacific also test positive by ELISA for *D. dumetorum* potyvirus (DdV), another potyvirus (Lebot, 2003).

Cucumber mosaic virus (CMV) is a widespread virus found mostly on vegetables and is transmitted both mechanically and by aphids in a non-persistent manner. It causes mild mottle-leaf chlorosis on most cultivars of *D. alata*. However, the genetic variability of CMV strains probably means that, as yet, no single antiserum can be used with certainty to detect all the strains that may be present in yams. The susceptibility of some genotypes of *D. alata* to CMV is a serious constraint to yam breeders as a great number of different sources are omnipresent in the field. In Nigeria, CMV has been reported as causing only mild vein chlorosis symptoms in *D. rotundata* (Odu *et al.*, 2004a). Studies conducted in the field under natural infection and in four locations allowed the identification of resistant varieties of *D. cayenensis* and *D. rotundata*, but it will take more time to find out if they are acceptable to growers. *D. rotundata* genotypes were evaluated for their response to three mechanical and vector-transmitted viruses (DAV, DaBV and CMV). A landrace from Nigeria developed symptoms of infection with CMV and DaBV following mechanical and vector transmission (Odu *et al.*, 2004b).

The relative importance of potyviruses may be distorted, as they are detected more easily than other viruses (such as badnaviruses, cucumoviruses, potexviruses and comoviruses). Badnaviruses, owing to their very low virus titres and ability not to produce any clear symptoms, often go undetected. *D. alata* bacilliform virus (DaBV) is transmitted mechanically and by mealy bugs (*P. citri*) from *D. alata* to other *Dioscorea* spp. It causes severe leaf distortion, crinkling and mottling in infected plants. In Nigeria, YMV, DAV, CMV and DaBV can be found together infecting *D. alata* varieties, which are natural hosts of these viruses (Odu *et al.*, 2006). Badnavirus particles were first reported in yam in association with a flexuous virus, causing internal brown spot (IBS) disease in *D. alata* and *D. cayenensis* in the Caribbean. The presence of another yam bacilliform virus has been indicated by DaBV being related serologically to a badnavirus from *D. bulbifera*, named *D. bulbifera* bacilliform (DbBV). The possible integration of badnavirus sequences in the yam host genomes, together with their high genetic variability, complicates the development of reliable indexing tests (Lebot, 2003). Badnaviruses are highly diverse and prevalent in *Dioscorea* spp. of the Pacific and have been reported in *D. alata*, *D. bulbifera*, *D. esculenta*, *D. nummularia*, *D. pentaphylla*, *D. rotundata and D. trifida* (Kenyon *et al.*, 2008).

Powerful analytical tools are now allowing virologists to progress rapidly in the detection and identification of badnaviruses. In West Africa and the West

Indies, the genomes of five yam badnaviruses have been elucidated: *Dioscorea* bacilliform *alata* virus (DBALV), *Dioscorea* bacilliform *sansibarensis* virus (DBSNV), *Dioscorea* bacilliform *rotundata* virus 1 (DBRTV1), *Dioscorea* bacilliform *rotundata* virus 2 (DBRTV2) and *Dioscorea* bacilliform *trifida* virus (DBTRV) (Umber *et al.*, 2016). The complete genome sequences of three new yam badnaviruses from Fiji, PNG and Samoa have been determined. Phylogenetic analysis revealed the sequences to be closely related to other yam badnaviruses. However, two isolates appear to be new virus species, named *Dioscorea* bacilliform ES virus (DBESV) and *Dioscorea* bacilliform AL virus 2 (DBALV2), respectively while another isolate has been identified as *Dioscorea* bacilliform RT virus 2 and is described as *Dioscorea* bacilliform RT virus 2-[4RT] (DBRTV2-[4RT]) (Sukal *et al.*, 2017).

Tissue culture and virus elimination can be done by chemotherapy and thermotherapy. Plants derived from therapy can be indexed using serological methods for several yam viruses (YMV, YMMV (DAV), DaBV, DbBV, DLV and CMV) by ELISA or immunosorbent electron microscopy (ISEM). If necessary, more sensitive, molecular methods can also be used. Degenerate, non-specific, potyvirus PCR primers have been used to detect a number of different potyviruses in yam, and primer pairs specific for YMV and YMMV (DAV) have been developed (Mumford and Seal, 1997). Similarly, degenerate primers to the aspartic protease gene and reverse transcriptase genes of badnaviruses have been used to detect badnavirus in several yam cultivars and to develop specific primers and probes (Hull *et al.*, 1996).

All virus elimination methods are based on regenerating plantlets in tissue culture from treated nodes or meristems taken from infected plants. Thermotherapy, whereby plants are grown at an elevated temperature (> 34°C) in controlled conditions prior to young nodes or meristems being transferred to tissue culture, is an effective means of eliminating DAV from infected yam accessions. Up to 40% of nodes that regenerate in tissue culture following this treatment test negative for DAV. A procedure whereby lengths of yam vine are heated by passing an electric current through them, known as electrotherapy, has also been investigated. Some nodes reach temperatures of up to 39°C during this treatment. Preliminary results using DAV-infected plants indicate that electrotherapy also increases the rate of virus elimination. However, much more work is required to substantiate these findings, since indexing of the plantlets was done while they were still very young and it is well recognized that virus titres are often very low in newly established tissue culture plantlets. It is often only after the plantlets have been grown in soil for several months that the titre increases again to detectable levels (Lebot, 2003).

Filloux and Girard (2006) have developed an efficient elimination system for badnaviruses, potexviruses and potyviruses. After a 2-month tissue culture, about 35% of the meristems regenerate into plantlets and all the accessions regenerate at least one plantlet. Well-developed plants are then grown in glasshouses, controlled visually for viral symptoms and tested again with RT-PCR. Thermotherapy combined with meristem culture leads to the elimination of

badnaviruses, potexviruses and two potyviruses (DAV and YMV). However, badnavirus elimination seems to be problematic on *D. rotundata* with the same protocol, especially if badnavirus-like sequences are integrated in the yam genome. Therefore, at present, no *D. rotundata* accession can be considered free of badnavirus. Virus-free accessions are maintained *in vitro* or in insect-proof glasshouses in the Centre de Coopération Internationale en Recherche Agronomique pour le Développement (CIRAD) yam germplasm transit centre in Montpellier, France. The international distribution of these accessions has been achieved *in vitro* and about 50 accessions have been sent safely to five countries in West Africa and in the Caribbean (Table 20.5).

The high prevalence of badnaviruses in *D. cayenensis* and *D. rotundata* cultivars in West Africa suggests that the introduction of sanitized yam propagules (mini-setts or full tubers) may have an impact in reducing the incidence of virus disease. However, it has been shown that there are integrated badnavirus sequences called eDBVs *(endogenous Dioscorea bacilliform virus)* in yam. Unfortunately, PCR diagnostic techniques are not reliable enough to enable decisions on germplasm distribution. The existing serological techniques are thought to be inadequate in failing to react sufficiently to badnaviruses. A proposal has been made to determine if the eDBVs are infectious and if these sequences act as sources of infection, or if they provide resistance to homologous badnavirus through gene-silencing mechanisms. It is recommended that the use of ELISA tests, with existing antisera as well as PCR, could allow the confirmation of their presence. PCR-positive but ELISA-negative results can then be studied in more detail to determine whether viral particles are present or not. Careful management will be required to prevent virus-free clones from becoming infected rapidly as soon as they are planted (Seal *et al.*, 2014).

Third-generation sequencing techniques, capable of generating much longer reads from individual ribonucleic acid (RNA) or DNA, are promising. Among these techniques is that implemented in the Oxford Nanopore MinION which has been used to determine the full genome sequences of a range of plant virus genomes. This technique has been transferred successfully for the detection of yam viruses (Filloux *et al.*, 2018).

**Table 20.5.** Regeneration efficiency after chemotherapy.

| Species | No. of accessions | No. of meristems cultivated | No. of plantlets regenerated | Regeneration ratio (%) |
|---|---|---|---|---|
| *D. alata* | 41 | 820 | 325 | 39.6 |
| *D. nummularia* | 4 | 140 | 28 | 20.1 |
| *D. praehensilis* | 1 | 20 | 17 | 84.6 |
| *D. rotundata* | 26 | 520 | 174 | 33.5 |
| *D. trifida* | 3 | 60 | 9 | 14.6 |
| Total | 75 | 1560 | 553 | 35.4 |

Source: adapted from Filloux and Girard (2006).

## INTEGRATED PEST AND DISEASE MANAGEMENT

Intensification of yam cultivation can benefit from breeding for host plant resistance, but the modification of unsuitable cultural practices also forms an important component of integrated control. In most countries, the practice of growing yam first in the rotation and avoiding continuous cultivation on the same field has much to do with avoidance of pest and pathogen pressure, as well as loss in soil fertility. Integrated management of yam pests and diseases consists of the appropriate selection of planting material and the use of control measures that provide positive impact. It starts with phytosanitary measures to prevent the introduction of pathogens into the cropping system. Ideally, this starts at harvest, and plants exhibiting viral symptoms should not be harvested for use as seed setts. Unfortunately, farmers tend to bulk together their harvest and cannot tell which tubers come from which plants. In practice, tubers from diseased plants should be harvested first and put aside so that they are not kept as planting material. An accurate examination of the tubers available for propagation, fungicide treatment of their pieces and the rogueing of those suspected to host a pathogen or pest is a necessary step.

Data on successful integrated pest management (IPM) projects for yams are scarce but some practical measures can slow down epidemics. For example, some weed species (e.g. *Mikania micrantha*) are a potential source of anthracnose inoculum and it is often observed that the epidemy strikes faster and more severely in plots which are not cleaned properly. In traditional agroforestry systems, farmers are generally aware of the anthracnose-resistant and susceptible varieties they have and interplant them, so that when the epidemy strikes its movement across the field is slowed down.

In Nigeria, intercropping is seen as a possible alternative to control pests as it suppresses weeds, pests and diseases. It is also observed that timely harvesting of fresh tubers in the field should be done to avoid termite infestation, a serious threat in this region. Lima bean and African yam bean are being used in most traditional cropping systems in south-eastern Nigeria as intercrops with significant advantages for farmers (Ibeawuchi *et al.*, 2007), especially with cowpea (Osundare, 2014). As they are not hosts of yam pest and diseases, they act as buffers and are efficient filters to prevent the spread of pathogen populations.

# 21

# Postharvest Quality and Marketing

Yam is a crop with potential for increased commercial exploitation. Tubers are increasingly sold at local urban markets and they are also being exported, returning much-needed cash to rural communities. Yam, alone among the tropical root crops, can be stored for long periods and, because of this and its robust nature, it can be transported to processing units with relative ease. Its processing potential is now strengthened by the rapid development of small machines adapted to village level.

## CHEMICAL COMPOSITION

Chemical composition depends mainly on the species, cultivar or wild form. Considering their high moisture content, yams are comparatively less able to satisfy energy requirements than other root crop species, but their protein, mineral and vitamin content is higher. When processed into flour, yams have a nutritional value comparable to cereals (Trèche, 1998). The food value is composed of carbohydrates (starch, sugars, fibres), proteins, minerals, vitamins and a negligible amount of lipids.

Analyses have been done but not all species were represented and varietal differences were not evaluated in detail (Bradbury and Holloway, 1988). However, there is sufficient indication that the differences between varieties are important, as they are in other root crop species (Table 21.1).

The African species have been investigated thoroughly, revealing significant genetic variation within *Dioscorea cayenensis* and *D. rotundata* for the major components of their food value (Trèche, 1998). Some varieties have a chemical composition well suited to some traditional uses (e.g. *fufu*), while others do not. For *D. alata*, different cultivars from New Caledonia present highly variable tuber characteristics but no correlations could be connected to taste or specific palatability (Lebot *et al.*, 1998). Indigenous knowledge, however, claims that there is tremendous variation between the culinary and palatability properties of *D. alata* cultivars, some being suitable for certain types of preparation while

 

**Table 21.1.** Fresh weight composition of *Dioscorea* spp. (values are means of different samples).

| Species: | *alata* | *esculenta* | *bulbifera* | *nummularia* | *pentaphylla* | *rotundata* | *trifida* |
|---|---|---|---|---|---|---|---|
| Samples (*n*): | (16) | (99) | (25) | (12) | (9) | (3) | (3) |
| Moisture % | 77.3 | 74.2 | 71.9 | 81.7 | 82.5 | 65.7 | 80.7 |
| Energy (kJ/100 g) | 406 | 443 | 258 | 266 | 550 | 284 | 580 |
| Protein % | 2.06 | 2.04 | 1.94 | 1.65 | 1.42 | 1.52 | 0.53 |
| Starch % | 16.7 | 19.3 | 23.2 | 11.7 | 13.9 | 30.2 | 14.2 |
| Sugars % | 1.03 | 0.55 | 0.22 | 0.20 | 0.12 | 0.32 | 0.23 |
| Dietary fibre % | 1.88 | 1.15 | 1.84 | 1.42 | 0.66 | 0.63 | 1.02 |
| Fat % | 0.08 | 0.06 | 0.06 | 0.05 | 0.03 | 0.09 | 0.04 |
| Ash % | 0.81 | 0.82 | 0.95 | 0.69 | 0.76 | 0.73 | 0.70 |
| *Minerals (mg/100 g):* | | | | | | | |
| Ca | 8.2 | 7.5 | 6.5 | 8.4 | 13 | 4.6 | 8 |
| P | 38 | 39 | 40 | 27 | 26 | 28 | 38 |
| Mg | 17 | 26 | 30 | 19 | 23 | 17 | 15 |
| Na | 3.3 | 3.1 | 8.6 | 2.7 | 6.1 | 4.7 | 2.9 |
| K | 318 | 303 | 448 | 346 | 374 | 361 | 350 |
| S | 12 | 16 | 15 | 9.0 | 13 | 12 | 8.2 |
| Fe | 0.60 | 0.75 | 0.38 | 0.56 | 0.44 | 0.60 | 0.54 |
| Cu | 0.15 | 0.17 | 0.34 | 0.21 | 0.25 | 0.12 | 0.13 |
| Zn | 0.39 | 0.46 | 0.50 | 0.31 | 0.36 | 0.30 | 0.35 |
| Mn | 0.04 | 0.24 | 0.04 | 0.13 | 0.05 | 0.03 | 0.03 |
| Al | 0.64 | 0.51 | 0.29 | 0.49 | 0.62 | 0.63 | 0.41 |
| B | 0.09 | 0.07 | 0.05 | 0.10 | 0.17 | 0.08 | 0.11 |

*Continued*

**Table 21.1.** Continued.

| Species: | *alata* | *esculenta* | *bulbifera* | *nummularia* | *pentaphylla* | *rotundata* | *trifida* |
|---|---|---|---|---|---|---|---|
| Samples (*n*): | (16) | (99) | (25) | (12) | (9) | (3) | (3) |
| *Vitamins (mg/100 g):* | | | | | | | |
| Vitamin A | 0.018 | 0.017 | – | – | – | 0.8 | – |
| Thiamin | 0.047 | 0.045 | – | – | 0.036 | – | – |
| Riboflavin | 0.030 | 0.028 | – | – | 0.018 | – | – |
| Nicotinic acid | 0.38 | 0.41 | – | – | 0.33 | – | – |
| Total vitamin C | 28 | 20 | – | – | – | – | – |
| Total oxalate (Ox) | 18 | 13 | – | – | – | – | – |
| Malate | 105 | 83 | – | – | – | – | – |
| Citrate | 142 | 123 | – | – | – | – | – |
| Trypsin inhibitor (TIU/g) | 0.56 | – | – | – | – | – | – |

Source: adapted from Bradbury and Holloway (1988).

others are not, and some cooking much more quickly than others. Varieties from Papua New Guinea (PNG), Vanuatu and Fiji have been analysed for their physico-chemical characteristics in an attempt to relate those characteristics with eating quality, and to assess the possibility of selecting varieties according to their chemotype. Varieties with good eating quality are characterized by high dry matter (DM), starch and amylose content. Chemotypes appear to be controlled genetically (Lebot *et al.*, 2006).

The amylose (A) versus starch (S) ratio is an important palatability trait in Vanuatu. Preferred varieties seem to have a high A/S ratio (> 0.18) and all varieties that have tubers with poor eating quality are characterized by low A/S ratio (< 0.16), high mineral and high protein content. The total sugar content is another important characteristic and some varieties are appreciated because of their sweet taste, which is confirmed analytically by the high sugar content (up to 5.71% for cv. 'Maligni'). However, sugar content alone cannot determine quality. Starch, amylose and total sugar content are correlated positively with DM. Mineral, lipid and protein content are correlated positively to each other, but correlated negatively with DM, starch and amylose. Total sugar content is correlated negatively with mineral and protein content (Lebot *et al.*, 2006) (Table 21.2). Some of these correlations confirm previous results obtained with cultivars grown in New Caledonia (Lebot *et al.*, 1998). For recommended varieties, this often corresponds to a white flesh which is not susceptible to oxidation when exposed to air. Chemotypes being controlled genetically, breeding *D. alata* for improved chemical composition of the tubers may be possible.

In West Africa, *D. alata* is popular for producing boiled yam but, so far, the varieties cultivated are unsuitable for pounded yam. *D. alata* has a high yield, high multiplication ratio and better tuber storability than *D. rotundata*, but the texture of its flesh is usually not as firm and less suitable for pounded yam. In Ghana, *D. alata* varieties have significantly higher moisture and protein contents with higher peak time and pasting temperature as compared with *D. rotundata*. The DM and starch content, swelling power and pasting viscosities are lower than *D. rotundata* (variety 'Pona') (Wireko-Manu *et al.*, 2011). The 'Pona' variety is also recommended for flour production because of its high DM and starch contents (Polycarp *et al.*, 2012).

Nutritional qualities have been investigated for the major species, but less work has been done on minor *Dioscorea* species. The latter are considered solely as subsistence or famine relief foods, not as vegetables for urban centres. To date, value-added product development has not been tried for the minor *Dioscorea* species, although it is considered essential. *D. esculenta* is also cultivated widely but is not popular in West Africa because the physico-chemical properties of the tubers are not well adapted to African culinary processes; its flour, however, has potential for bread making (Ukpabi, 2010).

High-quality yam flour is produced from fresh tubers, is odourless, white and free from foreign material. It is suitable for the baking and confectionery industries and can be easily stored for a longer period (12–18 months) if the flour

**Table 21.2.** Physico-chemical characteristics of 48 *D. alata* accessions from Vanuatu (values are in % dry weight). Source: author's own

| Acc. no. | DM % | Starch % | Amylose % | Ratio A/S | Minerals % | Lipids % | Proteins % | Sugars % | T°C – | T°C + |
|---|---|---|---|---|---|---|---|---|---|---|
| Max. | 31.42 | 78.6 | 20.7 | 0.21 | 4.9 | 0.5 | 17.0 | 5.71 | 81.5 | 91.6 |
| Min. | 13.68 | 63.6 | 13.4 | 0.13 | 2.5 | 0.2 | 8.8 | 0.6 | 78.8 | 87.6 |
| Mean | 23.44 | 73.1 | 17.2 | 0.17 | 3.3 | 0.3 | 11.95 | 1.85 | 74.9 | 84.2 |
| Std | 4.02 | 3.67 | 2 | 0.02 | 0.5 | 0.1 | 2.13 | 1.37 | | |
| CV% (coefficient of variation) | 17.2 | 9.1 | 11.6 | 11.6 | 15.2 | 33.3 | 17.8 | 91.3 | | |

DM, dry matter.

has a low moisture content. A wide variation is observed in functional characteristics between species and varieties. The pastes of flour from *D. dumetorum* are stable and hence have a lower tendency to undergo retrogradation during freeze and thaw cycles than flour from other species (Wahab *et al.*, 2016).

The chemical analysis of yam tubers is often a necessary prerequisite to proper germplasm evaluation, but is a cumbersome and expensive exercise when several hundreds of accessions need to be analysed. To develop a user-friendly analytical tool, near infra-red spectroscopy (NIRS) calibrations have been developed. Accessions belonging to seven different *Dioscorea* spp. were analysed for starch, amylose, sugars, proteins, minerals and cellulose, and the comparison of the NIR spectra and the chemical values allowed the establishment of equations of calibration. The $R^2$ values (coefficient of determination) for starch, sugars and proteins were high enough to allow good estimates of their contents, but amylose, cellulose and minerals could not be predicted precisely. It is thought that NIRS could be used in yam breeding programmes to characterize the numerous accessions and breeding lines rapidly and at low cost, but there is a need to improve the equations with larger sets of data (Lebot and Malapa, 2012).

A first attempt to predict the dioscin content in yam tubers using NIRS concluded that the accuracy was average ($R^2$ value = 0.72) because of the low concentration of dioscin (Kwon *et al.*, 2015). Most yam consumers are looking for a non-oxidizing white flesh with low or no sweetness and no bitterness. DM and starch contents are determinants for fresh tuber flesh quality and the texture and elasticity in the mouth; while sugars are responsible for sweetness and the browning of the fried yam. The reducing-sugar content also determines the formation of acrylamide during high-temperature cooking. With the processing of yam into fried products, low reducing-sugar content is another quality trait. When yams are processed into flours, there is variation between and within yam species: some are non-oxidizing, while others turn brown a few seconds after the tuber is peeled and cut. Browning in raw and processed tubers results from the activities of enzymes (polyphenol oxidase and peroxidase) and is a major limitation to value addition. The total phenolic content has been found to be highest in the proximal and mid-sections of the tuber than in the distal section of the tuber. Browning correlates with total phenol and DM contents of tubers (Graham-Acquaah *et al.*, 2014).

The analysis of individual sugars in eight *Dioscorea* spp. revealed that maltose was detected only in *D. esculenta* accessions (1.75% DW). This species, also known as 'sweet yam', presented the highest fructose content (0.65%), a sugar perceived as sweeter than other sugars. The tubers of *D. esculenta* presented the highest total sugars (5.04%) and the highest reducing sugars (RS = 3.15%). *D. alata* hybrids, selected on their taste after boiling, present low sugars, and this tends to indicate that consumers prefer low sugars (Table 21.3).

Yams are also rich in useful and healthy secondary metabolites: phenolics, flavonoids, anthocyanins and saponins. A preliminary screening of different

**Table 21.3.** *Dioscorea* spp. individual sugar contents. Species mean values are in % dry weight

| Species | acc. n | % DM | maltose | sucrose | glucose | fructose | Total sugars | RS[1] | S/RS[2] |
|---|---|---|---|---|---|---|---|---|---|
| *D. alata* (VU)* | 216 | 33.38 | – | 1.66 | 0.36 | 0.51 | 2.53 | 0.87 | 1.92 |
| *D. alata* (IN) | 40 | 28.54 | – | 1.58 | 0.27 | 0.51 | 2.35 | 0.77 | 2.05 |
| *D. alata* (hyb) | 128 | 36.56 | – | 0.70 | 0.27 | 0.36 | 1.33 | 0.63 | 1.11 |
| *D. bulbifera* (tub) | 26 | 26.48 | – | 2.14 | 0.45 | 0.07 | 2.67 | 0.53 | 4.06 |
| *D. bulbifera* (bulb) | 26 | 26.40 | – | 5.10 | 1.93 | 0.25 | 7.28 | 2.18 | 2.34 |
| *D. cayenensis* | 22 | 31.33 | – | 2.88 | 0.62 | 0.73 | 4.25 | 1.35 | 2.14 |
| *D. dumetorum* | 2 | 44.25 | – | 1.01 | 0.11 | 0.05 | 1.17 | 0.16 | 6.13 |
| *D. esculenta* | 46 | 29.02 | 1.75 | 1.89 | 0.75 | 0.65 | 5.04 | 3.15 | 0.60 |
| *D. nummularia* | 36 | 37.49 | – | 1.06 | 0.31 | 0.15 | 1.52 | 0.46 | 2.30 |
| *D. pentaphylla* | 2 | 18.75 | – | 1.36 | 0.19 | 0.16 | 1.71 | 0.36 | 3.82 |
| *D. trifida* | 4 | 29.53 | – | 1.44 | 0.42 | 0.41 | 2.27 | 0.81 | 1.77 |

Source: adapted from Lebot *et al.*, 2018a. *VU = Vanuatu, IN = India, hyb = hybrids, tub = tubers, bulb = bulbils.
[1]total reducing sugars (= maltose + glucose + fructose).
[2]sucrose/total reducing sugars.

species and varieties within species revealed significant variation. *D. bulbifera* bulbils and *D. nummularia* tubers present high total phenolic acid concentrations (Fig. 21.1).

*D. bulbifera* bulbils and tubers have a very high catechin content (6.96 mg/g), although the content is lower in *D. alata* and *D. nummularia*; catechins were not detected in the few accessions of *D. dumetorum* and *D. trifida* analysed. Steroidal saponins (dioscin and gracillin) were detected in *D. cayenensis* and *D. esculenta* (Lebot *et al.*, 2018a) (Table 21.4).

Allantoin (a hydantoin) protects tissues in the stomach, inhibits tumour growth (Liu *et al.*, 2016), reduces plasma glucose and has an anti-diabetic effect (Go *et al.*, 2015).

Yam steroidal saponins have blood pressure-lowering, anti-inflammation and antifungal activities. The major yam saponins are dioscin, gracillin, protodioscin and protogracillin. After hydrolysis, these yam steroids produce a steroidal aglycone known as diosgenin, which is used as a source of steroid hormones by the pharmaceutical industry (Jesus *et al.*, 2016). The worldwide market for diosgenin is approximately 1500 t/year with sources being mostly wild *Dioscorea* spp. In China, wild *D. zingiberensis* plants are being endangered (Zhang *et al.*, 2018). The most traded medicinal wild yam is *D. villosa*, which is currently found in over two-thirds of the USA, but it is also endangered because of habitat loss and over-harvesting. Cultivated yams have been analysed to see if they could be used as an alternative source of secondary metabolites. It appears that *D. cayenensis*, *D. esculenta* and *D. rotundata* are good sources of allantoin and total saponins. Within *D. rotundata*, some accessions present high levels of allantoin (40.61 mg/g) and total saponins (69.65 mg/g). Cultivated varieties or breeding lines, rich in total saponins (dioscin, gracillin, protodioscin, protogracillin and other non-identified saponins) may represent a potentially interesting source of raw material for diosgenin production via acid hydrolysis, and a sustainable alternative to wild yam species (Lebot *et al.*, 2019b).

The analysis of carotenoids in different yams has shown that there is significant variation between varieties for $\beta$-carotene content, but that the yellow

**Fig. 21.1.** *Dioscorea bulbifera* aerial bulbils are very rich in useful secondary metabolites (phenolics, flavonoids, anthocyanins) (photo: V. Lebot).

**Table 21.4.** *Dioscorea* spp. mean values for phenolic acids, catechins and saponins. Values are in mg/g dry weight (source: adapted from Lebot *et al*., 2018a).

| Species | Acc. no. | Total phenolic | Catechin | Epi-catechin | Total catechins | Gracillin | Dioscin | Total saponins |
|---|---|---|---|---|---|---|---|---|
| *D. alata* (VU)* | 216 | 4.87 | 0.14 | 0.45 | 0.66 | – | – | – |
| *D. alata* (IN) | 40 | 5.07 | 1.61 | 2.14 | 5.31 | – | – | – |
| *D. alata* (hyb) | 128 | 5.69 | 0.91 | 1.00 | 3.11 | – | – | – |
| *D. bulbifera* (tub) | 26 | 4.33 | 2.14 | 2.75 | 6.96 | – | – | – |
| *D. bulbifera* (bulb) | 26 | 9.96 | 4.92 | 10.71 | 25.18 | – | – | – |
| *D. cayenensis* | 22 | – | – | 0.31 | 0.65 | 6.41 | 5.94 | 26.38 |
| *D. dumetorum* | 2 | – | – | – | – | – | – | – |
| *D. esculenta* | 46 | – | – | 0.32 | 0.32 | 4.51 | 3.74 | 11.66 |
| *D. nummularia* | 36 | 9.55 | 0.53 | 1.25 | 3.61 | – | – | – |
| *D. pentaphylla* | 2 | – | – | 0.41 | 0.41 | – | – | – |
| *D. trifida* | 4 | – | – | – | – | – | – | – |

*VU = Vanuatu, IN = India, hyb = hybrids, tub = tubers, bulb = bulbils.

Guinea yam (*D. cayennensis*) has no higher *β*-carotene content than that of white Guinea yam (*D. rotundata*) (Price *et al.*, 2018).

Yams are, therefore, a good source of antioxidants but most often they are consumed after boiling and this cooking method impacts the chemical composition of the food product. The total phenol, total flavonoid, anthocyanin and tannin contents have been measured before and after boiling. The results reveal that the total phenol and anthocyanin contents of the yam are significantly lower after boiling. As most antioxidants are water-soluble compounds, the discarding of the water used for boiling the yam results in significant losses. Hence, processing of yam with minimal water and without discarding should be recommended to get the maximum benefit (Abeynayake and Sivakanesan, 2014).

## PHYSIOLOGICAL DISORDERS IN FRESHLY STORED TUBERS

The dormancy period directly determines the number of months tubers can be stored at ambient temperatures. Once dormancy ends, sprouting starts and the tubers deteriorate rapidly due to pathogenic invasion, and storage is no longer possible. Several attempts to extend the dormancy period by physical or chemical means have resulted in limited practical applications for producers and traders. The dormancy length depends on the species and the variety. *D. alata* and *D. rotundata* tubers can remain dormant for 3–5 months on average, while *D. cayenensis* and *D. trifida* are dormant for 1–2 months.

Tubers respire actively at harvest and during sprouting but, while they are in dormancy, their respiratory activity is reduced. Respiration accounts for a significant loss in DM weight in stored tubers which, when stored for up to 5 months at ambient temperature, may lose between 10% and 30% of weight. The reduction in DM during storage is probably caused by both the respiratory process and the activity of microorganisms within the tuber tissues. Following an injury, such as a cut in the periderm, there is a rapid increase in tuber respiration rate. Reduction of storage temperature can extend dormancy and reduce storage loss but yams are susceptible to low-temperature injury as soon as they reach 10–12°C (Passam, 1982; Ravi and Aked, 1996) (Table 21.5).

Several modern techniques, including cold storage, freezing, chemical treatments, wax coating and irradiation, have been applied to the major species (*D. alata*, *D. cayenensis* and *D. rotundata*), but their applicability to the minor *Dioscorea* species (*D. bulbifera*, *D. dumetorum*, *D. esculenta*, *D. nummularia*, *D. oppositifolia*, *D. japonica*, *D. transversa* and *D. trifida*) is unknown. Factors that might impinge on satisfactory storage remain to be studied.

When *D. oppositifolia* (syn. *D. opposita*) is stored at ambient conditions, the moisture content decreases during storage from 68% to 57%, and total sugars, reducing sugars and protein increase by 6.5%–9.8%, 1.7%–2.3% and 13.0%–14.6 %, respectively. Starch and enzyme activities also increase during the early days of storage and decrease progressively. However, changes during

**Table 21.5.** Respiration and weight loss of *Dioscorea rotundata* tubers during storage.

| | Total % weight loss/day | | Percentage of total weight loss due to respiration | |
|---|---|---|---|---|
| Age of tubers | 25°C | 35°C | 25°C | 35°C |
| After harvest | 0.22 | 0.36 | 27 | 30 |
| Dormant | 0.15 | 0.28 | 7 | 10 |
| Sprouting | 0.21 | 0.34 | 35 | 20 |

Source: adapted from Passam (1982).

storage are more significant at cold temperatures and in packaged conditions than at ambient conditions. It is suggested that when changes occur in the early stages of storage, they positively affect the nutritional potential of the tubers by a marked increase in nutrients. Also, low-temperature sweetening greatly affects the nutritional potential of yam tubers by a series of interactions between starch and sugars when they are stored at 4°C (Zhang *et al.*, 2014).

## MARKETING AND QUALITY STANDARDS

Throughout the world, the largest proportion of the yam harvest is marketed locally as fresh tubers, although dried chips or the resulting flours are gaining rapidly in popularity in West African urban markets. In most of these towns, the marketing of yams is very volatile, with supplies arriving from rural areas in truckloads at the convenience of the transporters. In West African countries, the most important constraints faced by yam traders are transport costs, seasonality of production, poor market infrastructure, lack of credit and damage to and rotting of tubers. Significant quality depreciation can be associated with pest and disease infestations, harvesting damage and overexposure to sunlight in the marketplace. A combination of all these factors can lead to a price discount of between 25% and 40% (Bancroft *et al.*, 1998).

Yam tubers are fragile and bruise easily. They do not, therefore, withstand any form of rough treatment and require careful handling to avoid skin bruising and tuber breakage. At harvest, the soil and rootlets are removed gently by hand and the small tubers are placed in wooden or plastic boxes (80 × 50 × 40 cm). These boxes should not be left in full sunlight and should be stored in cool, shaded, dry storage areas with good aeration as soon as possible. Tubers are normally cured just after harvest to heal any cuts or abrasions that harvest operations may have caused. Curing is done by spreading the tubers in the shade to allow wounds to heal, to toughen their skin (especially at the distal end) and to reduce the moisture content slightly. This operation improves their storability and extends their shelf life. Curing can last for 1–7 days with an ambient atmosphere

of 90%–100% relative humidity and is done at temperatures of between 32 and 40°C. The most effective treatment is 24 h at 40°C (Ravi and Aked, 1996).

In practice, temperature is very difficult to control accurately, so farmers have to find the most suitable location on their farms by trial and error. If intended to be shipped to distant export markets, the tubers should be packed tightly in strong, waxed, corrugated cartons or – eventually – in wooden crates. It is, however, beneficial to wrap each individual tuber in old newspaper or in coconut fibres. The packaging system depends on the quarantine requirements of the importing country.

There are lucrative ethnic markets in the USA, Europe, Australia and New Zealand. Yams are also popular in growing Asian markets. Consumer preference varies greatly, depending on cultural background, and producers must be aware of ethnocultural differences pertaining to tuber size, shape, flesh colour and skin smoothness. In the USA, the majority of imports (*D. alata*) are from Costa Rica and the Caribbean, while in the EU, the imports (*D. cayenensis* and *D. rotundata*) come mostly from Ghana and Ivory Coast. Yam supplies being seasonal, there are large price fluctuations.

There are no strict grade standards set by the importing countries but it is essential that the tubers are sent clean and in an undamaged condition. The tubers must be consistent in colour and varietal characteristics; mature (dormant, with firm skin and properly healed, corked, distal end); firm; unsprouted; and free from decay, pests and diseases, mechanical injuries (cuts) and soil. The export markets usually demand smaller tubers of compact and uniform shape with an average weight of 1–3 kg. Different species should not be mixed when packed and only tubers of the same size should be packed together in the same carton. Calibration is important and traders often pay lower prices where there is none, arguing that labour is expensive in the importing countries. The geographic origin, species and variety should be indicated clearly on the carton. A clean, light-brown colour of the skin with a bright, non-oxidizing, white flesh is preferred by most consumers, but there are niche markets for attractive purple-fleshed varieties. Finally, in all cases, the texture has to be free of fibres when cooked.

A survey conducted in Guadeloupe (West Indies) to understand consumers' preferences revealed that among the 'purchasing criteria', the retail price for fresh yam is considered to be more important than the other criteria. It is followed by external damage (bruises), geographical origin of the tuber and its size. The most frequently cited 'consumption criteria' are the taste, texture and colour of flesh after cooking. Taste is considered more important than the other criteria (Barlagne *et al.*, 2017).

## STORAGE METHODS

There are a few basic requirements for good on-farm storage of tubers. The area must be well ventilated so that moisture does not remain on the tuber

surface, where it will promote a variety of microorganism infestations. The temperature should be as low as possible, but not below 12°C. At ambient temperatures, between 25 and 35°C, tuber respiration is high and this decreases DM and accelerates sprouting. Unfortunately, in most countries, farmers do not have the financial means and technology to reduce the temperature, and shading is the only practical way of cooling down the tubers. Finally, tubers should be inspected on a regular basis and any rotting ones should be removed as soon as located. Sprouts may arise and should also be removed on a regular basis, until the planting period.

The yam barn is the most common storage system in West Africa. The tubers are tied with strings perpendicularly to vertical poles fixed in the ground and shaded by palm fronds, but the barn itself may be located under a tree. The structure remains in place only for the season and is not permanent. The main poles can be tall, live cuttings which will actually take root and sprout, giving rise to live poles which are more resistant to termite attack. The crossbars can be made of a lighter wood, such as bamboo. Tubers can also be stored on raised platforms called 'beds' and this is the most common system in the Pacific. These structures can be fairly permanent and quite elaborate (e.g. the yam houses of the Trobriand archipelago villages in south-eastern PNG). Their geographical orientation is important as they have to be placed in the direction of the prevailing winds and perpendicular to the sun's radiation movement for maximum shade and temperature reduction. In the same region, tubers may be hung individually from horizontal bamboo poles which are supported by forked hardwood sticks. This systems aims to prevent rodent attacks, as well as favouring excellent ventilation.

On agricultural research stations, tubers are kept in buildings of approximately 9 × 9 × 11 m with a concrete floor and half walls; wooden racks; insect screens instead of windows; and roofed with insulated corrugated iron. These structures can hold more than 10,000 tubers for 5 months with minimum microbial decay. The incidence of scale insects may be serious over such a long period and experiments have shown that *D. alata* tubers, buried in sand contained in wooden boxes, can remain free of scale insect attacks.

Quality changes occur during storage and have been documented for *D. alata*, *D. esculenta* and *D. rotundata* stored under ambient conditions (25–33°C and 75%–80% relative humidity) for up to 4 months. Starch content decreases, while sugars remain almost constant. The polyphenol content shows no variation in *D. rotundata* but increases significantly in *D. alata* and *D. esculenta*. On the other hand, a rapid loss of moisture is significant for *D. rotundata* but is slow for *D. alata* and *D. esculenta*. In fact, farmers are well aware that some of their varieties keep better than others. Different varieties of the same species vary markedly in their storage life and tolerance to storage pests and diseases.

At 16°C, the dormancy and storage life of *D. alata* tubers can be extended easily to 4–5 months if the tubers are cured before storage to reduce pathogen infestations (Passam, 1982). Though theoretically attractive, cold storage is

not practical owing to the cost and the natural bulkiness of yams. Gamma irradiation at 7.5 krad has been applied successfully and safely to *D. alata* tubers to inhibit sprouting, but nor is this technique applied on a commercial scale. Sprout-suppressing chemicals have been tested, such as those used commercially for Irish potatoes, as well as plant hormones applied in the form of postharvest immersion in a solution, but all have shown little application to yam storage (Table 21.6).

Natural or synthetic hormones have also been tried to extend dormancy (Table 21.7). Gibberellic acid ($GA_3$) can prolong dormancy of *D. alata* tubers

**Table 21.6.** Sprout-suppressant chemical effects on the length of yam tuber storage.

| Species | Chemical | Effects on storage | Other effects |
|---|---|---|---|
| *D. alata* | TCNB | None | |
| | PCNB | None | |
| | IPPC | None | |
| | Maleic hydrazide | Reduced sprouting | Weight loss |
| | CIPC | Less than 1 month | Phytotoxic |
| *D. rotundata* | TCNB | None | |
| | Maleic hydrazide | Slightly delayed sprouting | |
| *D. esculenta* | Maleic hydrazide | None | |

TCNB = tetrachloronitrobenzene; PCNB = pentachloronitrobenzene; IPPC = isopropylphenylcarbamate; CIPC = isopropyl-N-(3-chlorophenyl) carbamate.
Source: adapted from Passam (1982).

**Table 21.7.** Growth-regulating chemical effects on yam tuber storage life.

| Species | Compound | Storage life | Other effects |
|---|---|---|---|
| *D. alata* | Methyl-α-NAA | + 1.5–2 months | Phytotoxic |
| | Chlorethanol + thiourea | Up to 3 months | |
| | Chlorethanol | Promoted sprouting | |
| | Ethylene chlorhydrin | Promoted sprouting | |
| | Gibberellic acid | + 7 weeks | |
| | Gibberellic acid | Up to 4 weeks | |
| *D. rotundata* | Methyl-α-NAA | None | |
| | B-NAA | None | |
| | Gibberellic acid | None | |
| | IAA | None | |
| | Kinetin | None | |
| *D. esculenta* | Gibberellic acid | + 6 weeks | |

IAA = Indole-3-acetic acid, NAA = Naphthaleneacetic acid
Source: adapted from Passam (1982).

but its effect is critically dependent on its time of application. When applied just after harvest, it delays sprouting; but, when applied later in storage, it has virtually no effect. GA is a natural plant hormone manufactured on a commercial scale, which might be useful, considering the low expertise needed for the treatment and the absence of toxicity (Passam, 1982). It is, however, somewhat expensive for smallholders and therefore its adoption is low, although the treatment is easy and efficient.

Numerous other compounds have been tried (Degras, 1993), with limited results or poor application. Waxing the tubers is not recommended as wax coating impairs oxygen circulation.

## TRADITIONAL PROCESSING TECHNIQUES

Tubers of all species are consumed mostly as boiled yam. They are peeled, cut into pieces and cooked for 10–20 min, depending on species, variety and DM content. Most of the time, they are accompanied by sauces and other vegetables. Pounded yam is prepared from pieces of boiled yam, pounded in a wooden mortar until it forms a thick paste. This paste is then eaten in the form of balls, with sauce and/or meat. The consistency is a matter of taste and, depending on the consumer, can be more or less watery, but most West Africans prefer it viscous and elastic in the mouth. The exact consistency depends on the variety and most likely on the relative proportions of amylose, starch and fibres. The pounding process has been modernized for urban dwellers and small electric machines can pound tubers in silence in a few minutes (Onwueme and Charles, 1994).

In Vanuatu *laplap*, the national dish, is made from finely grated fresh tubers that produce a slimy and sticky paste which is spread on and covered with *Heliconia indica* leaves and steam cooked in a ground oven. The result is a sort of yam pudding with a very pleasant texture and aroma. Species rich in DM (*D. nummularia* and *D. rotundata*) are usually preferred for this preparation.

There are many other recipes, including mashed yams (similar to mashed Irish potatoes) and fried, roasted and baked yams. Yam chips, similar to potato chips, are also produced by frying thin slices of tubers.

Yam flour is prepared from dehydrated tubers. The fresh tubers are peeled and, after a hot water treatment generally conducted in the field and aimed at surface sterilization, they are then sun-dried for several days until they are completely dry. Varieties of *D. rotundata* producing numerous smaller tubers are preferred for this market (e.g. the 'Kokoro' cultivar in Benin). This raw material can be stored easily, transported and sold directly to consumers, who will process it into flour themselves or at local mills. Producers usually pay the mill owner in kind and give him a share of their flour. The dried tuber pieces are then pulverized into flour with electrical or mechanical hammer mills. The resulting flour can be stored in bags for months and is quite convenient for the

growing cities of West Africa. The yam flour is stirred over boiling water and cooked for a few minutes to obtain a thick viscous *fufu*, which resembles the one obtained with pounded, boiled yam. Consumers prefer yam tubers with low sweetness (Baah *et al.*, 2009). This product is developing very rapidly and farmers have to adapt by adopting the right varieties, but are also facing new problems such as the high labour requirements for on-farm processing, as well as the control of pests in sun-dried yam (tuber borers).

The browning of fresh tubers is attributed to phenolic compounds, most likely catechins (Akissoe *et al.*, 2005; Lebot *et al.*, 2018b). This is a problem as drying is the traditional process in West Africa to extend the shelf life of yam tubers. The flesh of the fresh tuber is usually white but *amala* (a popular paste in Benin), made from dried flour, turns brown during processing and the quality of the final product deteriorates. There is a relationship between the *amala* browning and the total phenol (TP) content of the flour: the higher the phenol content, the darker the product. In Benin, yams traditionally are blanched at an intermediate temperature (60–75°C) before drying. No significant variation is observed in phenol content during blanching, whereas it increases during drying. Polyphenoloxidase, peroxidase and phenolic compounds drop sharply to less than 20% of the initial activity after only 10 min of blanching at 65°C (Akissoe *et al.*, 2005).

## INDUSTRIAL PROCESSING

Yam flakes are produced by drum-drying cooked and mashed yam, or by hot-air drying diced and cooked yam. The former system produces flakes and the latter a powder form. Both are cooked in less than 5 min with boiling water. For hot-air drying, the diced yams are dried in hot chambers just after cooking, and then milled into powder. Both products are packaged hermetically to extend product life. The microbial load is close to nil and the moisture content around 7%, and shelf life can be almost 1 year. The final product, sold commercially in supermarkets and urban foodstores, has all the characteristics of pounded yam and is of a creamy white colour. The level of elasticity is controlled by adding more or less water during the cooking process and depends on consumers' taste.

For export markets, frozen slices are prepared in sealed plastic bags. The portions are sliced into pieces 1–2 cm thick and dipped in a solution of 1% metabisulfite to prevent oxidation. The slices are then precooked at 40°C for 15 min and frozen at −40°C for 30 min. The frozen slices can then be stored in a freezer at −3 to −5°C. This is an acceptable product, ready to cook and eat. The use of antioxidant improves the colour greatly and avoids discoloration for up to 3 months of storage.

The varied texture characteristics of yam flours have been shown to be of industrial interest in the Philippines (Salda *et al.*, 1998). Their similarities to

other commercial starches or flours are useful for product development of noodles, snacks and baby food products. In Taiwan, the incorporation of *D. alata* flour in bread has been shown to increase the antioxidant capacity of the blended bread markedly (25% yam flour/75% wheat flour). It is suggested that breads containing yam flour may be regarded as potential health-promoting foods as the incorporation of yam flour markedly increases its antioxidant capacity. Apparently, substituting yam flour in a bread formulation does not interfere with bread acceptability (Hsu *et al.*, 2004).

The shapes of the starch granules are round to oval or angular, and the size of the starch granule increases with growth, ranging from 10 to 40 mm. The chemical composition, thermal and material properties of the starches vary considerably among species but yam starch has some properties useful for the food industry. It is stable at high temperatures and within a low pH and, when pregelatinized, yam starch can be combined with cassava starch to improve its functionality (Alves and Grossmann, 1998). Yam starches with low amylose content can be used to develop gels with very good acid resistance after cooking. These starches have good potential as substitutes for modified starches in acid solutions such as tomato products, dressings and sauces. *D. alata*, *D. cayenensis* and *D. rotundata* starches have a very high viscosity after cooking and a good resistance to high-temperature treatments. They could be used as substitutes for chemically modified starches in ultra-high-temperature (UHT) foods, and in canned baby foods, for the development of natural products (Amani *et al.*, 2002).

The starch paste shows a lower breakdown at an early harvest time and appears to be thermostable during heating, but has a high setback after cooling. Pasting behaviours show that higher amylose content is associated with a lower pasting temperature and a higher peak viscosity (Huang *et al.*, 2006). Variations between species and varieties are observed in the solubility, phosphorus and crude fat content, and gelatinization temperatures of the different yam starches. The properties of the different *D. alata* starches may prove useful in nutritional applications (Riley *et al.*, 2006).

The tablet formation properties of starches from *D. rotundata*, *D. dumetorum*, *D. opposita* and *D. alata* have been evaluated to determine their applicability as a direct compression excipient. The amylose content, size and shape of the starch granules and specific surface area appear to play a significant role in compressibility. *D. rotundata* and *D. alata* (which have larger granules and high amylose content) exhibit poor compressibility and do not form compacts, while *D. dumetorum* and *D. opposita* (which have polygonal grains, small particle size and high specific surface area) are more compressible and form tablets of acceptable crushing force, and could thus be useful as an excipient in direct compression (Odeku *et al.*, 2007).

The purple-fleshed tubers of some varieties of *D. alata*, *D. esculenta*, *D. nummularia* and *D. trifida* contain substantial amounts of anthocyanins. These substances are natural colorants which can be extracted from the tubers at

reasonable cost, considering the average tuber yield of yam, per unit of area and time. In the Philippines, the cultivar 'Ubi' (*D. alata*) is grown to satisfy the colorant needs of the ice cream industry. In China, the analysis of a purple-fleshed *D. alata* variety allowed the separation of eight compounds including cyanidin3-gentiobioside, alatanin C, cyanidin 3-ferulyl gentiobioside, cyanidin3-sinapylgentianoside, peonidin 3-gentiobioside and alatanin 2. The dominant anthocyanin in this variety is alatanin C which accounts for about 46.3% of the total anthocyanins (He *et al.*, 2015).

The future of processed yam products will depend on the adaptability of peeling to mechanization, as most products require peeled yams as the starting raw material. Hand peeling is labour-intensive and often wasteful, while mechanical peeling is difficult to apply to tubers irregular in shape. Lye peeling, using chemical and thermal actions on the tuber skin, may be useful and flesh losses are reduced compared to hand peeling, with insignificant free lye retention after peeling. In most species and varieties, the proximal end of the tuber shows greater resistance than the distal end.

# Section IV
# Aroids

Taro, *Colocasia esculenta* (L.) Schott (*Araceae*, Monocotyledons), is an ancient root crop and there are about half a billion people who include taro in their diets. In many areas of the tropics, it is closely associated with people's culture and traditions. There are four other aroid root crops: giant taro (*Alocasia macrorrhizos* (L.) Schott), swamp taro (*Cyrtosperma merkusii* (Hassk.) Schott), cocoyam (*Xanthosoma sagittifolium* (L.) Schott) and elephant foot yam (*Amorphophallus paeoniifolius* (Roxb.) Blume). All five species may also be grown as ornamentals (see table below).

Geographic origin of the most important aroids.

| Aroid species | Common names | Geographical origin |
|---|---|---|
| *Alocasia macrorrhizos* | Giant taro | Asia, South-east Asia |
| *Amorphophallus paeoniifolius* | Elephant foot yam | Asia, South-east Asia, Melanesia |
| *Colocasia esculenta* | Taro, dasheen | Asia, South-east Asia, Melanesia |
| *Cyrtosperma merkusii* | Swamp taro | Northern Melanesia |
| *Xanthosoma sagittifolium* | Cocoyam, tannia | Central & South America |

Cocoyam is probably the most similar to taro, with relatively large sagittate leaves, but the side cormels rather than the central corm are consumed. Giant taro is a large succulent perennial herb with thick elongated corms and large sagittate leaves. Swamp taro is also a large perennial herb with sagittate leaves, usually larger than those of giant taro, adapted to freshwater swamps. Elephant foot yam has complex-compound leaves and a round and flat corm.

# 22

# Origin and History

## DOMESTICATION

Taro is probably the oldest crop on earth and has been grown on irrigated terraces in tropical Asia for more than 10,000 years. One hypothesis is that rice may have first been noticed as a weed in flooded taro patches (Plucknett, 1984). Four species are related to taro (*Colocasia fallax*, *C. affinis*, *C. indica* and *C. gigantea*) and, because they are all confined to north-eastern India and South-east Asia, it has been suggested that *C. esculenta* originated in this area. These related species have a much narrower range of distribution than wild *C. esculenta*, which extends to India, South-east Asia, South China, Melanesia and Australia; it could also, therefore, be argued that they are derived locally from *C. esculenta*. The problems associated with the origin, domestication and spread of taro have been studied by different teams, who have concluded that it is not possible to determine a single centre of origin (Yen and Wheeler, 1968; Plucknett, 1984; Lebot, 1999; Matthews, 2014).

Taro was most likely domesticated several times in different locations in a vast zone from India to South China, Melanesia and northern Australia. Wild populations were isolated for a long period of time and the effect of insular isolation, combined with human and natural selection pressures, has induced genetic diversity within a single, highly polymorphic species, *C. esculenta* (Fig. 22.1).

The Asian origin of taro has been well documented (Matthews, 2014) and the question of its domestication in the Pacific has been clarified. On the very ancient site of Kila cave, located on the small island of Buka, north of Bougainville island, Northern Solomon Islands, taro and *Alocasia macrorrhizos* and *Amorphophalus paeoniifolius* starch granules have been identified on stone artefacts dated to be 28,000 years old (Loy *et al.*, 1992). An independent emergence of agriculture, during the early and mid-Holocene at Kuk Swamp in the highlands of New Guinea, has been documented. Analysis of prehistoric use of stone tools for processing starchy food has been conducted and reveals the presence of taro starch granules. Residues and starch granule analyses also indicate that taro was processed during the early and mid-Holocene. Although

**Fig. 22.1.** Taro (*Colocasia esculenta*) corms of dasheen-type variety (cv. 'Alkat') (photo: V. Lebot).

the taro starch granules do not permit differentiation between wild or cultivated forms, it is argued that taro processing was active by at least 10,000 years ago. However, from at least 6950 to 6440 years ago the processing of taro indicates that it is likely to have been domesticated and integrated into cultivation practices (Fullagar *et al.*, 2006).

*C. esculenta* was cultivated in the Pacific Islands by early settlers, as revealed by the dating of starch grains from Bourewa, south-west Viti Levu, Fiji, to 3050–2500 years ago (Horrocks and Nunn, 2006). Taro was probably introduced by Austronesian sailors who settled the islands of Melanesia, between the Bismarck Archipelago in Eastern New Guinea and Vanuatu, and later Fiji, from 3500 to 3000 BP. It was probably already being cultivated by the indigenous people in New Guinea and the Austronesians distributed cultivars into the Pacific Islands, along with other crops (Yen, 1991). Fossil evidence shows that Polynesians introduced taro to the northern part of New Zealand after 1200 where it was replaced by intensive cultivation of sweet potato after 1500 (Prebble *et al.*, 2019).

Diploids and triploids exist in Asia but all traditional Australian and New Guinea taros are diploids. Cytological studies indicate that Australian genotypes have chromosome numbers and karyotype identical with Papua New Guinea (PNG) wild forms and cultivars (Coates *et al.*, 1988). In PNG, wild taros often produce seeds and it is known that birds disperse these seeds. In Java, seeds of *C. gigantea* are eaten and spread by palm civets (Hambali, 1980). Birds may have been responsible for the spread of wild *C. esculenta* populations from Sunda to Sahul before human migrations, allowing human settlers to domesticate the local gene pool.

Another problem is the origin of wild taro in the Solomon Islands, Vanuatu and New Caledonia. If taro was brought to these countries, it was probably brought in cultivated and not wild form, as it is most unlikely that the migrating people collected and distributed non-edible wild genotypes. The typical wild genotypes have a very high concentration of oxalates and extremely small corms. Many Melanesian cultivars flower naturally, insect pollinators are very active and natural hybridization occurs regularly. As a result, in PNG, the Solomons and Vanuatu, naturally set seed is not uncommon in farmers' fields. The Melanesian germplasm contains primitive types, with stolons and abundant flowering.

The study of isozyme variation in more than 1400 cultivars and wild forms of taro collected in Asia and Oceania reveals greater variation in Asia than in Oceania, with Indonesia hosting the greatest diversity. The great genetic diversity of the Indonesian cultivars may reflect the lack of improvement made to this crop. Morphotypes often exhibit several 'wild' characters, including frequent flowering and stolon production. Oceanian cultivars have originated from a common, narrow genetic base and were probably domesticated in Melanesia. The genetic (isozymic) variation is nil in Hawaii and in most islands of Polynesia, suggesting that the genetic base is extremely narrow. The variegated forms found frequently in Polynesian fields are due to a long period of vegetative propagation. Accumulated somatic mutations and the cultivars existing in Polynesia are probably clones of a common Melanesian source (Lebot and Aradhya, 1991). Amplified fragment length polymorphism (AFLP) markers have confirmed the isozyme results, and two independent domestications of taro in South-east Asia and Melanesia have been confirmed (Kreike *et al.*, 2004) (Fig. 22.2).

The American *X. sagittifolium* is most likely to have been domesticated on the northern side of the Amazon basin (Fig. 22.3). There are no accurate archaeological records for *C. merkusii* but the overall picture is the same: the wild population is distributed widely, so local domestication may have come from local sources. *Cyrtosperma merkusii* is unknown in the South-east Asian islands and may have been domesticated by the occupants of coastal New Guinea, where it is endemic and grows wild (Fig. 22.4). The same is probably true for *A. macrorrhizos* (Fig. 22.5). The elephant foot yam (*Amorphophalus paeoniifolius*) (Fig. 22.6) originates from the Gulf of Bengal and South-east Asia (Lebot, 1999).

## DISCOVERY OF THE CROP BY WESTERN EXPLORERS

*Colocasia esculenta* was already cultivated throughout the tropics, but also in temperate latitudes, for instance China, Nepal, Japan, Korea, the Mediterranean and New Zealand, when the European navigators documented its presence. It was a very ancient crop in Cyprus, Turkey and Lebanon (Matthews, 1991,

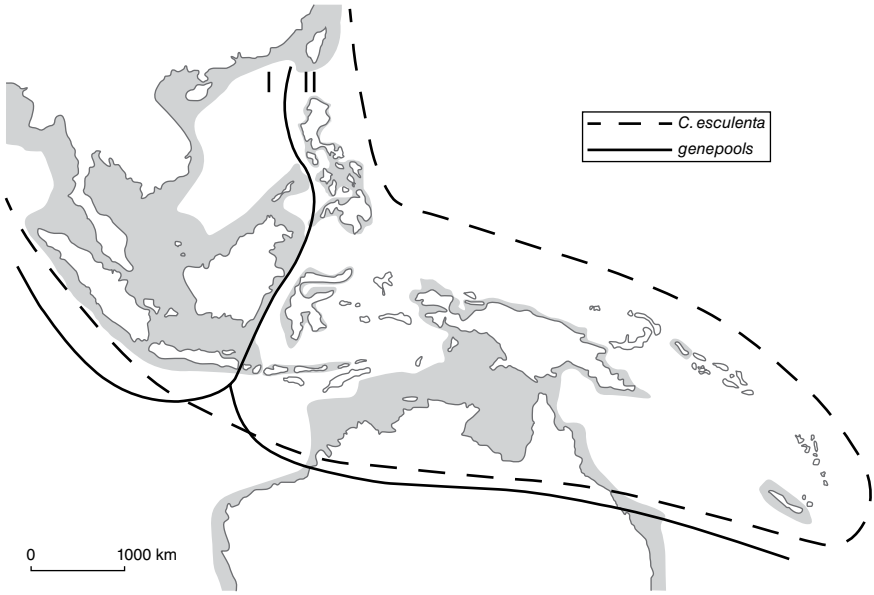


**Fig. 22.2.** Area of origin of cultivated taro, South-east Asia and Pacific gene pools.

**Fig. 22.3.** *Xanthosoma sagittifolium* cormels (photo: V. Lebot).

2014) and was also introduced into Africa very early, perhaps entering from Asia via the Nile, or most likely via Madagascar with Austronesian colonizers. It reached Egypt about 2000 years ago.

Taro was transferred to the West Indies with the slave trade. Introduction routes to Cuba during the 18th century probably came from West Africa, the Canary Islands and Madeira (where it is still cultivated) by the slave trade. Another source could have been the Philippines, on Spanish galleons trading between Manila, Acapulco and Havana. It was most likely reintroduced into

**Fig. 22.4.** *Cyrtosperma merkusii* plants (photo: V. Tuia).

Cuba, after the Spaniards, with Chinese immigrants during the 19th century and by the Japanese just before the Second World War. It has been suggested that taro was introduced into North America from Asia by European shipping.

Two different routes for the introduction of taro into Japan have been suggested, based on isozyme and rDNA (ribosomal DNA) variation in eastern Asia. One route comes directly from China and the other from South-east Asia, via Taiwan and the Ryukyu Islands. Several distribution waves have introduced genetic material from different origins into different locations (Matsuda, 2002).

*Xanthosoma* was introduced to Central and West Africa, between the 16th and 17th centuries, when it was brought by Portuguese slavers into São Tomé

**Fig. 22.5.** *Alocasia macrorrhizos* corm (photo: V. Lebot).

and Principe, where they had important trading bases (Bown, 2000). Cocoyam introduction in Asia and Oceania occurred in the 19th century and was the result of the intervention of missionaries (Wilson, 1984).

## PRESENT GEOGRAPHICAL DISTRIBUTION

According to FAO databases (www.fao.org, 2017), taro and cocoyam (*X. sagittifolium*) produce the lowest yields of all root crops, with an average of 5.9 t/ha. World production in 2017 was approximately 10 million fresh tonnes from 1.7 million ha. However, these statistics clearly underestimate the importance of aroids, because many countries that are significant producers do not supply their figures (India, Bangladesh, Burma, Malaysia, Indonesia, Vietnam, Cambodia, Brazil and Cuba, to cite a few) (Table 22.1). In most countries, aroids are considered as minor, in backyard and home gardens, and their acreage and production are not recorded although they are omnipresent.


**Fig. 22.6.** *Amorphophallys paeoniifolius* corms (photo: V. Lebot).

Statistics demonstrate that aroid cultivation is stable, or even growing. World production was around 4 million t in 1961, which indicates that the global trend follows demographic growth. There is a consensual assessment that aroids are orphan crops of utmost importance to the poor, essential for food security and that they represent an untapped potential for further economic development. In most countries, taro is cultivated within a shifting agroforestry system with very limited input, such as machinery or fertilizers, by smallholders. Such cropping systems are prevalent in the Pacific Island countries where production is comparable to the average world yield. In Africa, *X. sagittifolium* is replacing *C. esculenta* because the local cultivars are thought to be more adapted to the preparation of *fufu*. It is also more robust and drought tolerant, although taro is now cultivated in Sahelian countries such as Burkina Faso. Unfortunately, in many countries of Africa, taro leaf blight (TLB) is now spreading rapidly and very few landraces are tolerant to it (Grimaldi *et al.*, 2018). New improved hybrids have been introduced recently but their evaluation and distribution will be a slow process. As taro and other aroids are orphan crops of the international agricultural research system, there is no institution in charge of germplasm preservation and distribution, and farmers are left to themselves (Lebot *et al.*, 2018c).

In Cuba, annual production is around 97,000 t (over 160,000 ha) and is fairly stable, but restrictions imposed on irrigation have reduced its importance considerably. This situation also affects *Xanthosoma*, but *Colocasia* is more

**Table 22.1.** Major aroid-producing countries in 2017.

| Region | Country | Production (thousand t) | Area (thousand ha) | Average yield (t/ha) |
|---|---|---|---|---|
| Africa | Nigeria | 3250 | 831 | 3.9 |
| | Cameroon | 1847 | 227 | 8.1 |
| | Ghana | 1200 | 184 | 6.5 |
| | Madagascar | 243 | 40 | 6.0 |
| | Rwanda | 215 | 55 | 3.8 |
| | Guinea | 142 | 23 | 6.3 |
| | Central African Rep. | 130 | 39 | 3.9 |
| | Côte d'Ivoire | 83 | 67 | 1.2 |
| | Egypt | 76 | 2.2 | 34.0 |
| | Congo | 69 | 18 | 3.9 |
| | Gabon | 68 | 11.1 | 6.1 |
| | Burundi | 45 | 6.2 | 7.3 |
| | Chad | 28 | 12.6 | 2.3 |
| | Liberia | 28 | 3.1 | 9.0 |
| America | Nicaragua | 43 | 4.4 | 9.8 |
| | Dominica | 12.3 | 1.2 | 9.8 |
| | Guyana | 8.6 | 0.1 | 9.0 |
| | Trinidad and Tobago | 2.8 | 0.3 | 9.0 |
| | USA | 1.7 | 0.1 | 11.9 |
| Asia | China | 1865 | 95 | 19.6 |
| | Papua New Guinea | 274 | 37 | 7.5 |
| | Japan | 150 | 37 | 12.5 |
| | Philippines | 109 | 15.0 | 7.2 |
| | Thailand | 102 | 10.7 | 9.6 |
| | Solomon Islands | 46 | 2.6 | 17.3 |
| | Fiji Islands | 43 | 2.1 | 20.0 |

Source: adapted from FAO (2017).

sensitive to irrigation, although it is preferred and produces very high yields (36 t/ha in 8–10 months) under intensive cultivation in comparison with the 20 t/ha in 12 months for the traditional Cuban taro cropping system (Rodriguez-Manzano *et al.*, 2004).

In countries where crop management techniques are relatively elaborate and sophisticated (i.e. Hawaii and Egypt for taro and Florida for cocoyam), it is observed that yields per unit of area and time are clearly too low, and improving the crop genetically is now urgent to allow farmers to capture new markets and attract interest from processors. In Egypt, Thailand, China, Japan and Hawaii cropping systems are fairly intensive and occasionally mechanized,

especially on the island of Kauai, Hawaii. Taro is an important crop in Yunnan Province, south China. It is an important staple in the Yangtse River Valley but is scarce in northern China. Taro is cultivated extensively in the Jiaodong district in Shandong Province, where rainfall is abundant. In Laiyang and in the Jiaodong Peninsula, taro is cultivated as an export cash crop (3000 t frozen cormels/year), accounting for 50% of the total Chinese exports of frozen taro. According to Japanese statistics, however, Japan imports 40,000 t fresh corms annually from south China.

In New Zealand, the interest is in maintaining a regular supply of high-quality pink taro for the large Samoan population. There is also a desire to increase the quantity of locally grown fresh taro leaves to be used as a local vegetable. Because of the temperate climate, the commercial production of introduced Japanese cultivars is likely to develop gradually. Production systems, however, have to be improved for weed control and the agronomic management of high-quality corms (Bussell *et al.*, 2004).

In Fiji, South Pacific, the volume of taro sold annually on the local market is around 50,000 t and this market is expected to grow following the demand driven by the urban population. Approximately 40,000 households grow taro, and there is a well-developed marketing chain supplying the numerous domestic market outlets. The volume of taro exported to New Zealand is around 7000 t annually. Fiji is competing with Samoa in this ethnic market.

# 23

# Taxonomy and Botany

## CLASSIFICATION

The *Araceae* family consists of about 110 genera with over 2500 species. It is divided into seven subfamilies: *Acoroideae*, *Aroideae*, *Calloideae*, *Lasioideae*, *Monsteroideae*, *Pothoideae* and *Pistioideae* (Mayo *et al.*, 1997; Bown, 2000). Members of the aroid family can be found in almost every climatic region except deserts and polar regions. Species adapted for areas with cool or dry periods are characterized by dormancy of their corms, underground rhizomes or seeds, which allows them to survive unfavourable periods. The two main centres of origin are considered to be tropical America and Asia, but some species are also endemic of the Mediterranean, Africa and Australia–Papua New Guinea (PNG). The majority of aroids are climbers and epiphytes of tropical rainforests. Many of these species are associated with aquatic or semi-aquatic environments.

A common characteristic of all aroid species is the spathe and spadix type of inflorescence. The spathe is a large bract subtending and unsheathing the inflorescence (Bown, 2000). A spadix is a spike of flowers on a swollen, fleshy axis. Individual flowers are very small, bisexual or unisexual. Bisexual flowers usually have a special type of perianth consisting of tepals, floral structures that are not clearly distinguishable as being either sepals or petals. A spadix with unisexual flowers is usually divided into distinct zones. The female zone is at the base and the male zone is above. The two zones are usually separated by one of the sterile flowers. The spadix often ends with an appendix also composed of sterile flowers. The main purpose of this appendix is the dispersal of odorous substances.

The aroid family is characterized by protogyny, in which the female flowers become receptive before pollen is shed. Protogyny induces cross-pollination and most aroid inflorescences are adapted specifically to insect pollination. Some inflorescences (e.g. *Colocasia esculenta* and *Xanthosoma sagittifolium*) are characterized by a specific shape and size of the spathe. The space between the spathe and the spadix can serve as a shelter for insects during rain or at night,

as a mating place or as a place for feeding and growth. The commencement of flowering is characterized by the release of an attractive fragrance or, in some species, an unpleasant odour that attracts only certain insects. This is the case for the inflorescence of *A. paeoniifolius* (syn. *A. campanulatus*), which imitates putrefied flesh and attracts flies.

The leaf structure and shape of aroids are extremely variable. Leaves are frequently adapted to specific environments such as shade, continuous flooding or drought. The size of aroid leaves varies from species to species, from variety to variety and from very small to gigantic. Extremely large leaves are characteristic of some genotypes of giant swamp taro, *C. merkusii*.

The determination of the genera is sometimes complex. *Alocasia*, *Amorphophallus*, *Colocasia* and *Xanthosoma* species are monoecious, while *Cyrtosperma* species have hermaphrodite flowers. Further determination of the genera with hermaphrodite species may include the presence or absence of a sterile appendix on the spadix. Inflorescences of all, except *Xanthosoma*, are appendaged. The appendix on *Xanthosoma* inflorescences either is absent or cannot be distinguished clearly.

Leaf shape is a useful characteristic for determining genera. The genus *Amorphophallus* can be separated easily from others because of compound laminas. The majority of *Colocasia* species have peltate leaves, while most of *Xanthosoma* and *Alocasia* species have sagittate leaves. However, there is also great morphological variability, especially among *Alocasia* species.

## MORPHOLOGICAL DESCRIPTIONS OF MAJOR AROIDS

The genus *Colocasia* belongs to the subfamily *Aroideae*. The main characteristics of this subfamily are unisexual flowers on inflorescences usually clustered, with relatively simple spathes constricted at the interface between male and female zones on the spadix. Vegetative parts often exude a coloured sap. The leaves have a reticulate venation, simple to pedate. The genus includes herbs characterized by stout underground rhizomes bearing stolons and forming colonies in their natural habitats.

*C. esculenta* leaves are peltate, somewhat glaucous, with blades hanging. Secondary venation is reticulate and collective veins are present. Inflorescences are appendaged. The ovules are orthotropous and are numerous in two series on three to five parietal placentae. Some authors consider *C. esculenta* as one polymorphic species with two botanical varieties:

**1**. *C. esculenta* var. *esculenta*, named taro or dasheen; and
**2**. *C. esculenta* var. *antiquorum*, named eddoe.

The main difference between the *esculenta* and *antiquorum* varieties is in the shape and size of the main corm and cormels. Var. *esculenta* genotypes are characterized by a larger main corm and smaller side cormels. Var. *antiquorum*

genotypes usually have a relatively smaller central corm and well-developed side cormels. Taxonomists claim that another difference is in the length of the sterile appendix of the spadix: that of var. *antiquorum* is usually much longer in comparison with that of var. *esculenta*. However, the differences in this character are far from obvious because of wide variation within each group (Hiromichi, 2002).

Several studies based on morphological and cytological investigations (Yen and Wheeler, 1968; Kuruvilla and Singh, 1981; Tanimoto and Matsumoto, 1986; Coates *et al*., 1988) found genetic diversity between var. *esculenta* and var. *antiquorum*. Several authors asserted that the former was diploid and the latter was triploid (Kuruvilla and Singh, 1981; Irwin *et al*., 1998). This classification is, however, controversial and it has not been demonstrated that all diploids are dasheen types and belong to var. *esculenta* and that all triploids are eddoe types and belong to var. *antiquorum*. It is generally accepted that the majority of triploids are of Asian origin, and that they are abundant in areas of high altitude and latitude, and rare in other areas.

In practice, there are two morphological groups: dasheen (corm is consumed) and eddoe (side cormels are consumed), which do not match taxonomic and cytological groups and are not differentiated by molecular markers. From an agronomic point of view, eddoe types can be considered as genetically less improved and lower yielding than dasheen-type cultivars. Eddoe types have plant architecture similar to wild forms of taro and their non-edible corms (very fibrous) compete with cormels for photosynthates. *C. esculenta* is a herbaceous plant, usually 0.5–1.5 m tall. Leaves of almost all genotypes are peltate. The most typical exception is the *piko* group of cultivars from Hawaii, which have hastate leaves. Laminas can be from 30 cm to more than 80 cm long and from 20 cm to more than 50 cm wide. Leaf petioles are stout, clasping at the base. Petiole length varies, depending on genotype, from less than 30 cm to more than 1.5 m. Leaf size is influenced strongly by the environment. Maximal dimensions of taro leaves are usually associated with the beginning of flowering. With approaching maturity, leaf petioles become shorter and leaf blades smaller. Their colour varies from a very light green to a very dark purple, depending on genotype. It can be uniform or have variations such as lines, spots or blotches of different pigmentations. Leaf petioles and leaf laminas do not always have the same colour (Fig. 23.1).

The fruit of *C. esculenta* is a berry and one berry can contain over 50 seeds. The actual number of seeds per berry depends on pollination efficiency, type of pollination (cross-pollination, self-pollination), self-compatibility, fertilization and environment. The berries are packed together densely and form a fruit head. The highest number of seeds per fruit head has been estimated at more than 22,000 seeds with a thousand-seed weight of 0.2 g (Ivancic *et al*., 1996). The berry is usually green in colour but may be orange or purple. When the berries are mature, the peduncula wilts and the fruit head falls to the ground. In Vanuatu, birds called *nambilak* in Bislama ('road runners' or *Gallirallus philippensis*) eat the fruits

**Fig. 23.1.** *Colocasia esculenta,* taro.

and disperse the seeds. Some fall in cultivated plots, where they germinate spontaneously and produce new taro plants, which eventually can be selected by farmers if their morphotypes are attractive (Fig. 23.2).

Taro is characterized by enlarged, starchy corms. Corms vary in size and shape, depending on type of planting material and ecological factors, particularly soil characteristics. Corms of typical upland varieties are usually round or slightly elongated, while extremely elongated corms are more characteristic of paddy genotypes. The corm consists of three main parts: skin, cortex and core. The skin may be smooth, fibrous and covered with scales. The cortex is the region between the skin and the root initials. The cortex and the core consist mainly of parenchymatic tissues. The core also includes fibres. There is large variation in fibre content among genotypes and it is highly influenced by the environment and age of the plant. The pigmentation observed in corm cross section varies from white, light yellow, dark yellow and orange to pink, red

**Fig. 23.2.** Inflorescences, spathe, spadix, fruits.

and purple. There can be combinations of white with purple or red blotches or white parenchyma with darker pigmented fibres. The root system is superficial and fibrous (Figs 23.3 and 23.4). Eddoe-type varieties present an interesting commercial potential, especially for export towards urban markets, as they are

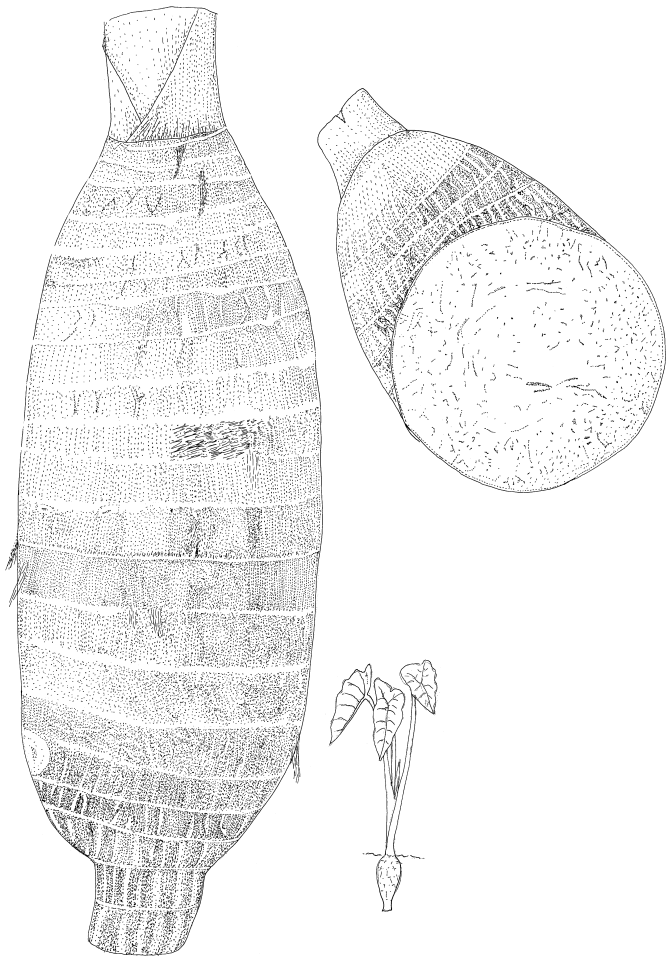

**Fig. 23.3.** Corm and cross section.

**Fig. 23.4.** Taro (*Colocasia esculenta*) corm of dashen-type variety with different layers of cells presenting anthocyanin pigmentation with darker pigmented fibres (photo: V. Lebot).

easier to transport, store and handle. The cormels have a thinner skin which is easier to peel (Fig. 23.5).

*Xanthosoma sagittifolium* is an important food for some 400 million people and has overtaken taro as the main edible aroid in many tropical areas (Onokpise *et al.*, 1999; Matthews, 2014). The genus, originating in northern South America (Giacometti and León, 1994), has about 40 species grown as ornamentals and food crops. The taxonomic position of cultivated *Xanthosoma* spp. is unclear and there is a tendency to call all cultivated *Xanthosoma* spp. by the name *X. sagittifolium*. New species are being described and there is a need for a review of the taxonomy (Gonçalves, 2011).

The genus includes three important food species: *X. sagittifolium*, *X. atrovirens* and *X. violaceum*. Another species, *X. brasiliense*, is grown for its edible leaves. *X. sagittifolium* is a robust plant reaching heights of 2 m or more. The major difference between it and taro is in leaf shape. *Xanthosoma* spp. have sagittate leaves, while *Colocasia* spp. have peltate leaves. Leaves are thick and long-petioled, with the main vein at the lower side of either basal lobe being marginal as it joins the petiole. The leaves are arrow-shaped with sharp tips and deep, wide basal lobes and a prominent marginal vein. Leaf petioles can be more than 2 m long, with blades more than 1 m long and up to 0.7 m wide.

Inflorescences are large, usually two to three together in a cluster, sometimes up to ten, and appearing one after another. They appear when the plants are well developed, generally after at least 6 months of growth. Each inflorescence consists of a spadix covered by a spathe. The spadix, which is about 15–20 cm long, is divided into the female lower part, the male upper part and the sterile part between the two. The spathe has an ovoid or oblong convolute tube and a narrow, trough-shaped blade longer than the spadix. The spathe is large, mostly light green, silver-green, yellow-green or purple. Inflorescences appear in groups or clusters, usually from two to five, depending on the genotype and the environment. Within a cluster, the youngest inflorescence is closest to the leaf petiole. Each female flower consists of a relatively small ovary, a short

**Fig. 23.5.** Taro (*Colocasia esculenta*) cormels of eddoe-type variety (photo: V. Lebot).

style and a disc-like stigma. Male flowers usually consist of four or six anthers, united into an angular column. Ovules are anatropous or semi-anatropous. Pollen is white or pale yellow and sticky. Seed set is rare, perhaps because of the narrow genetic base of the cultivars combined with incompatibility systems and female or male sterility.

The main corm is usually very acrid and is not eaten. The optimal environment is soil that is fertile and well drained. The plants can tolerate a certain level of shade. Cultivars are differentiated mainly by leaf pigmentation, plant size, cormel shape and number, cormel tip shape and pigmentation, spatial arrangement of cormels and cormel flesh pigmentation. Young leaves of some cultivars can be used as a vegetable (Figs 23.6, 23.7 and 23.8).

**Fig. 23.6.** *Xanthosoma sagittifolium*, cocoyam, macabo, tannia.

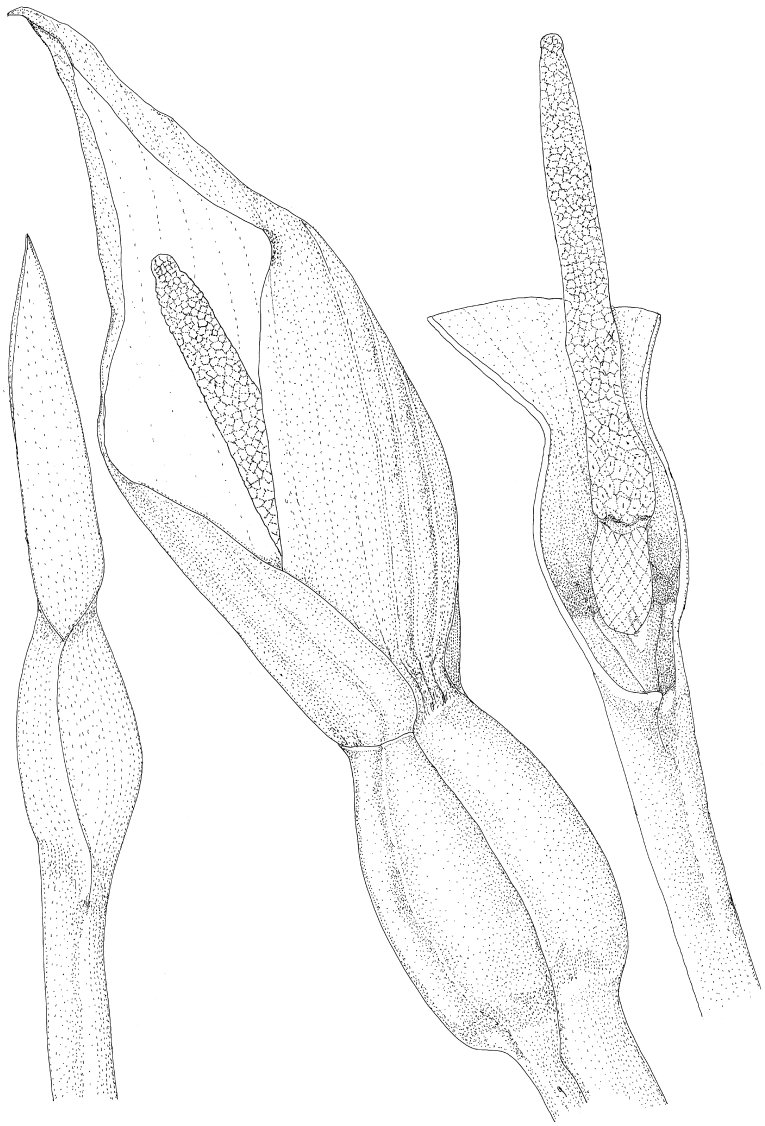

**Fig. 23.7.** Inflorescences, spathe and spadix.

*Alocasia macrorrhizos* (syn. *A. macrorrhiza*) probably originated in the Philippines. It has been suggested that the ancestor of *Alocasia* diverged from its mainland sister group about 24 million years ago. Borneo then played a central role in the expansion of *Alocasia* and the Philippines were reached from Borneo in the Late Miocene and Early Pliocene (Nauheimer *et al.*, 2012). Its seeds were probably spread naturally eastwards to Melanesia, where wild forms were

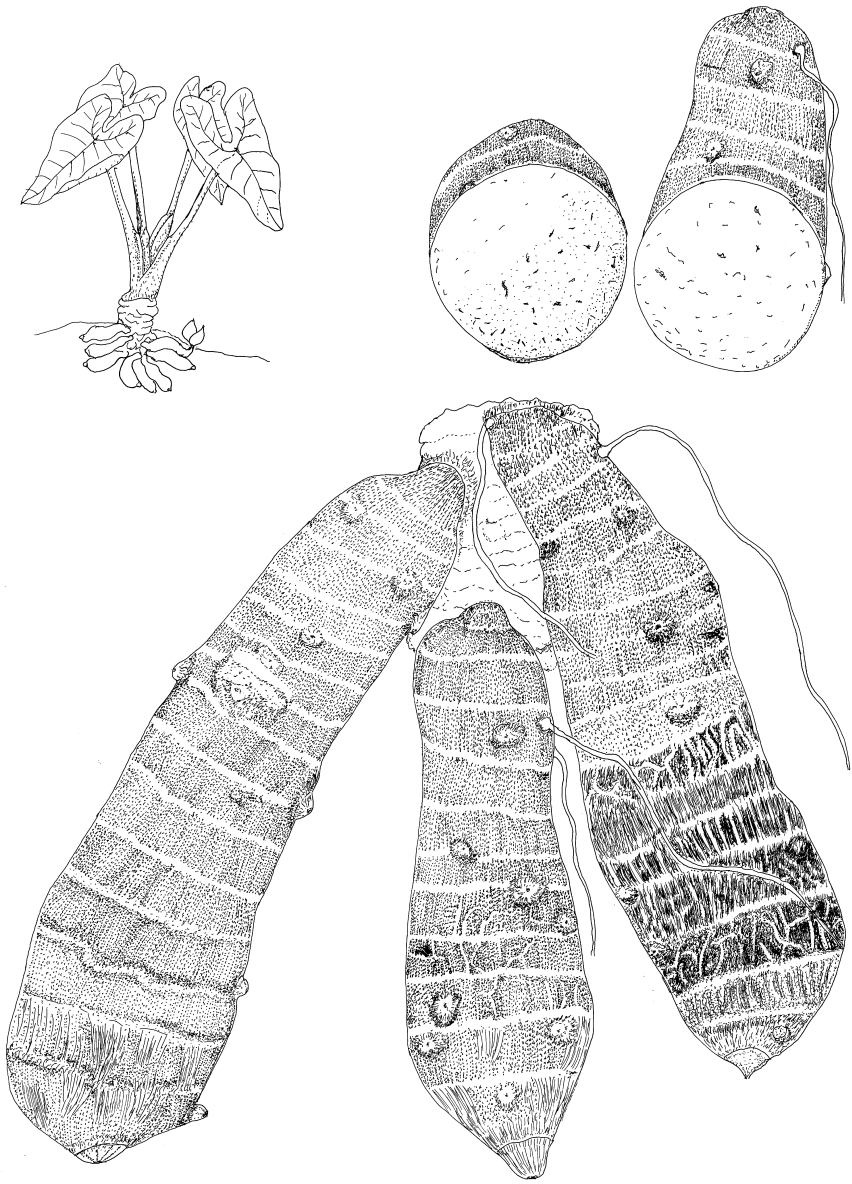

**Fig. 23.8.** Cormels and cross section.

also found in natural habitats. The genus contains about 65 species occurring through Sri Lanka and India, through Indochina to China and southern Japan, Malaysia, Indonesia, New Guinea and Australia (Hay and Wise, 1991). The main centre of diversity of the genus is the island of Borneo, where there

are 23 species. Cultivated *A. macrorrhizos* is distributed throughout the Pacific, where it is grown extensively in Western Samoa, Tonga, Wallis and Futuna and the Lau group of Fiji, but only in parts of Vanuatu. It is also cultivated in tropical America and in some parts of Africa, where it is a minor crop. It is presumed that the few edible cultivars have a narrow genetic base (Lebot, 1992).

The genus *Alocasia* is characterized by herbs or short monocaulous trees with simple, mostly hastate or sagittate leaves. Leaf margins are entire to deeply lobed. Venation is reticulate with intramarginal veins. *Alocasia* spp. are monoecious. Inflorescences are two to several together, with spathes constricted and the upper part persistent or deciduous. The spadix consists of four parts: a lower or female portion, a sterile zone, a male zone and a large sterile appendix. Female flowers are globose with button-like to stellate sessile or stalked stigmas (Hay and Wise, 1991). The ovules are few, basal and orthotropous. Male flowers consist of hexagonal or, rarely, distinctly irregular synandria.

*A. macrorrhizos* is a large, succulent perennial herb with large, elongated stems. The height depends on plant age, genotype and environmental conditions. The plant has several broadly sagittate leaves, bluntly triangular in outline, indistinctly leathery, with the secondary venation prominent.

Inflorescences are relatively large and usually appear in clusters. It is predominantly a cross-fertilizing species. The main pollinators are insects, mostly flies and small beetles, which are attracted by a strong odour. Wind may also be a pollinating agent. Rain usually causes self-pollination and self-fertilization of self-compatible genotypes, which can produce numerous seeds. Self-fertilization can be prevented by self-incompatibility, protogyny and the constriction of the spathe in the sterile region between the female and male parts of the spadix. In an optimal climate, flowering of *A. macrorrhizos* is profuse. In wild populations, it is usually synchronized, enabling cross-fertilization. The upper part of the spathe is pale yellow, membranous, oblong, hood-forming and falling soon after anthesis (Hay and Wise, 1991).

The fruits of *A. macrorrhizos* are berries which may contain several, but not many, seeds. The colour of ripe berries appears to be controlled genetically and can be red, orange or yellow. The number of seeds per fruit head varies from 10 to 50.

Corms of *A. macrorrhizos* are long, thick, woody-appearing cylinders or trunks, which are peeled and then baked or boiled. Corms sometimes can reach a length of more than 2 m, depending primarily on the length of the growth period, which can be extended over several years. Cultivars are distinguished by their corm characteristics (flesh pigmentation, quality traits, yield, corm size and corm surface shape), leaf pigmentation, variegation and leaf size (Figs 23.9, 23.10 and 23.11). Wild genotypes are characterized by an extremely high concentration of calcium oxalate (Quero-García *et al*., 2008).

*Amorphophallus* spp. are deciduous herbs with large underground, usually hemispherical corms producing a single large compound, umbrella-like leaf. There are about 100 species of *Amorphophallus* in Africa, India, Malaysia and Australia. *A. konjac* is cultivated and used in Japan and the warmer parts of

**Fig. 23.9.** *Alocasia macrorrhizos*, giant taro.

China. Traditionally, it is made into noodles and is now grown for the nutraceutical industries, which use its unusual carbohydrate (mannose) in the preparation of calorie-free gels. *A. oncophyllus* and *A. variabilis* are used in Indonesia. There appears to be a high degree of endemism, with only *A. paeoniifolius*, *A. muelleri* and *A. abyssinicus* having a wide geographic range. The most spectacular and the largest inflorescences are produced by *A. titanum* (Bown, 2000).

The most important species is *A. paeoniifolius*, elephant-foot yam. The cultivated form is grown as a root crop in several parts of the Pacific and Asia

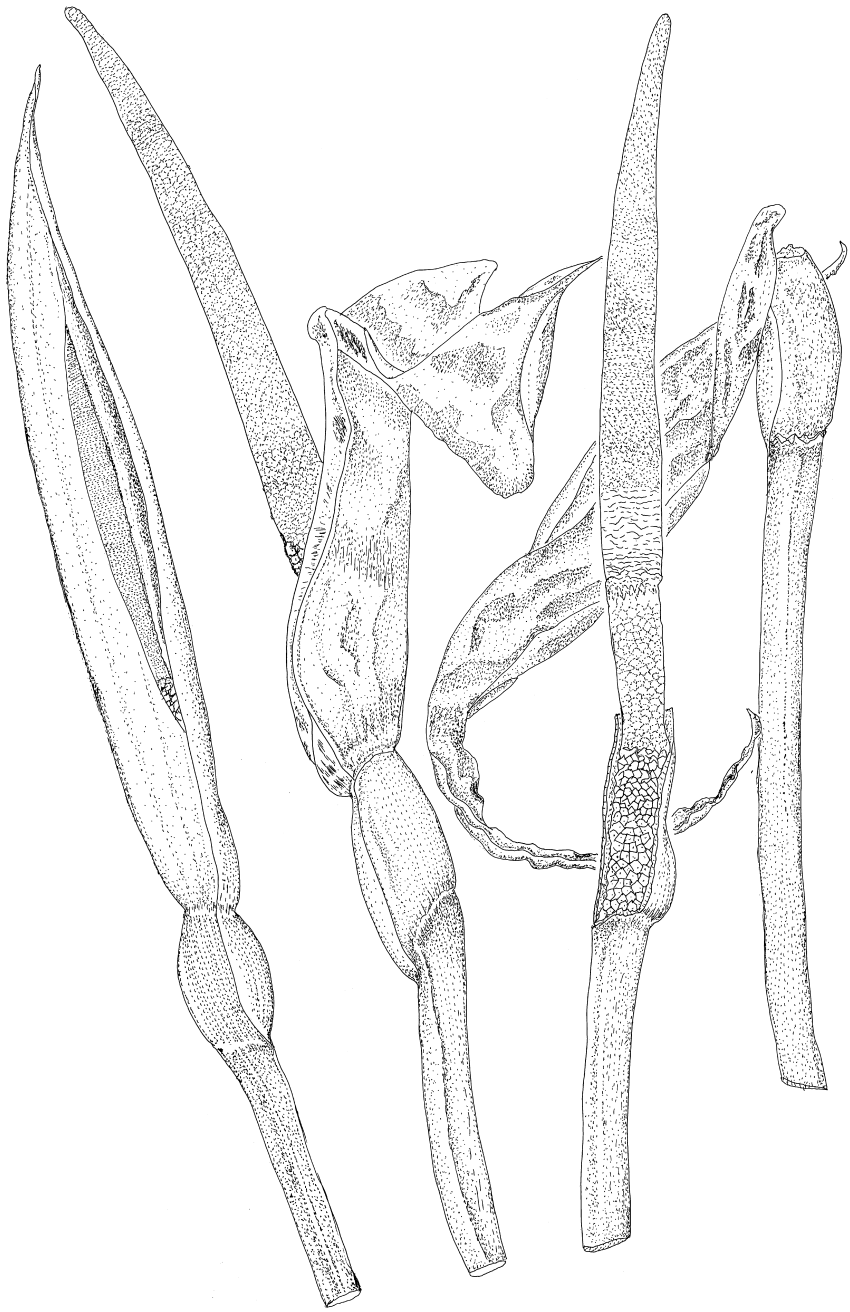

**Fig. 23.10.** Inflorescences, spathe and spadix.

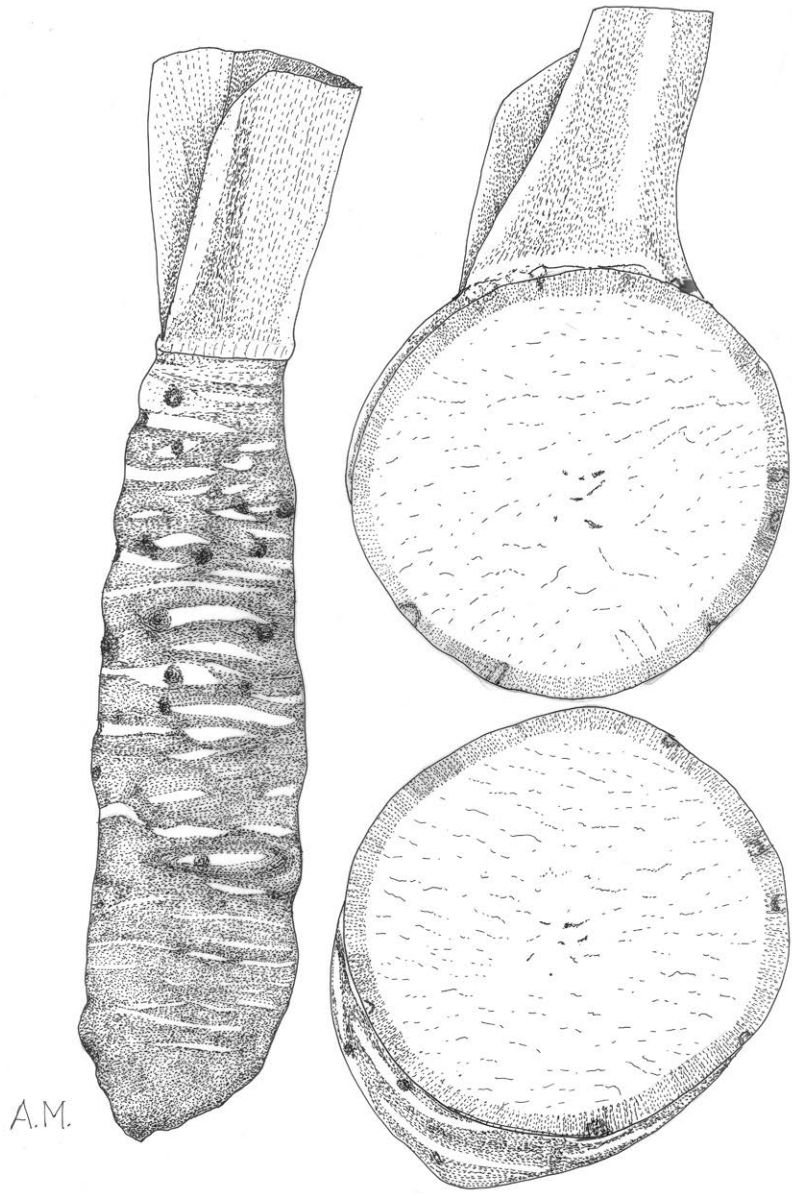


**Fig. 23.11.** Corm and cross section.

and is used as a vegetable for curries in Kerala, India (Hay and Wise, 1991). In Melanesia, it is still the practice to leave the plants that are found when land is cleared of forest for cultivation. It is in India where the greatest diversity of edible forms exists. In the north-eastern states, wild forms are used as vegetables

and for medicine (Jackson *et al.*, 2007). In Indonesia, two different forms are recognized: forma *sylvestris* and forma *hortensis* (Bown, 2000). Forma *sylvestris* is characterized by very scabrous petioles, and forma *hortensis* with more or less smooth petioles. The smooth petioles are considered to be associated with edible corms. Cultivars vary in corm surface shape and colour, flesh pigmentation, petiole size and pigmentation, yield and quality. The petiole is postular and maculate and has a reticulate venation.

The plants, when they flower, develop large and attractive inflorescences, produced without a leaf on thick peduncles. The spathe is large and has the shape of an elongated bell. The colour varies, depending on genotype, from purple to yellow and green, or green blotched. The spadix is thick and terminates with a large appendix. Flowers are unisexual. Female flowers have elongated styles. The female zone is not separated from the male by a sterile zone. Stamens are yellow and numerous, crowded beneath an enlarged appendix.

The complete life cycle of *A. paeoniifolius* usually lasts several years. The plants may be propagated vegetatively or by seed. In the tropics, the inflorescence will open fully and release pollen after 15–25 days, depending on genotype, environmental conditions and the size of the inflorescence. The plants are characterized by protogyny and are predominantly cross-pollinated. The periods of stigma receptivity and pollen shed usually overlap in the same inflorescence. Self-fertilization is prevented mainly by strong mechanisms of self-incompatibility. The release of odour is associated with the beginning of stigma receptivity, occurring in the afternoon before the spathe opens. The strong odour attracts flies that bring pollen and distribute it on the stigmas of the female flowers, which are at that time already receptive. The odour remains intense for several days, and sometimes for more than 1 week (Fig. 23.12).

The genus *Cyrtosperma* is characterized by robust, usually solitary herbs with underground rhizomes. Leaves are simple, hastate or sagittate, usually coriaceous with the anterior lobe never longer than the posterior one, on long, tough, stiff, blotched, spiny petioles with sharp apices. Venation is reticulate throughout and prominent on the leaf underside. Among the 11 species in the genus (Hay and Wise, 1991; Iese, 2005), the giant swamp taro or *C. merkusii* is the most important crop species, especially for some of the Pacific atolls where it is a major food.

The plants are often very tall and can reach 3 m or more high. The large leaves are arrow-shaped, pointing upwards to form a more or less straight line with the axis of the petioles, similar to *Alocasia*. The leaf blades have deep and sharply pointed basal lobes. The lower portions of the petioles are sometimes spiny. The inflorescence is a solitary spadix on a long peduncle that closely resembles a petiole. The spathe is usually hard, deep purple, often with yellowish stripes, or sometimes green to white. The spadix is sessile with hermaphrodite flowers throughout its length, each with four to five free tepals. Fruits are small and globose, orange to scarlet berries ripening from the tip of the spadix downwards. Seeds are kidney to helical shaped, often ornamented.

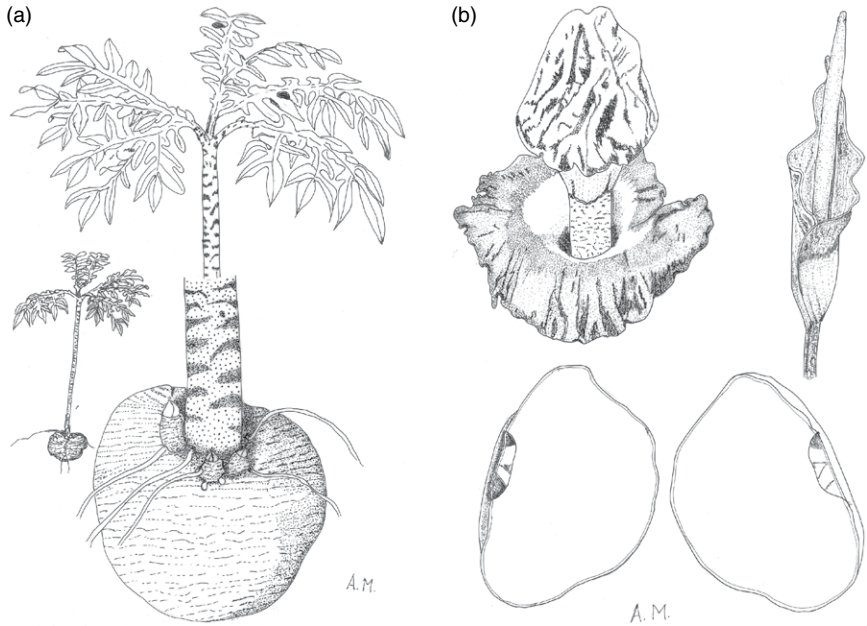


**Fig. 23.12.** *Amorphophallus* paeoniifolius, elephant-foot yam; **a** plant; **b** corm cross section, inflorescences of *A. paeoniifolius* and of *A. konjac*.

The growth period of *C. merkusii* or giant swamp taro can be very long, usually 4 years but sometimes as much as 10–15 years, and corms may reach 40–80 kg. The crop is grown mainly in atolls and freshwater swamps, or along creeks and rivers. Some of the cultivars are reasonably tolerant of salinity. Cultivars can be differentiated by leaf shape, leaf pigmentation, leaf size, spininess, spathe colour and size, quality and yield parameters, maturity period and salinity tolerance (Fig. 23.13).

## RELATED SPECIES

There are seven species in the genus *Colocasia*: *C. affinis*, *C. fallax*, *C. esculenta*, *C. gigantea*, *C. gracilis*, *C. mannii* and *C. virosa*. *C. fallax* and *C. affinis* are little used. *C. fallax* is used as a vegetable in Yunnan, southern China, where the species is found in dense valley forest and shrublands. *C. affinis* is a rare ornamental outside Asia. *C. gigantea* is distributed more widely than the other minor *Colocasia* species. It is regarded as a lesser food crop of South-east Asia, mainly as a leafy vegetable (Fig. 23.14). *C. gracilis*, *C. mannii* and *C. virosa* are poorly known species and it is not yet clear if they are truly distinct (Matthews, 2014).

Wild *Colocasia* spp. with large corms and no stolons (*C. oresbia*) and lower acridity (*C. lihengiae*) have been identified as candidate sources of traits

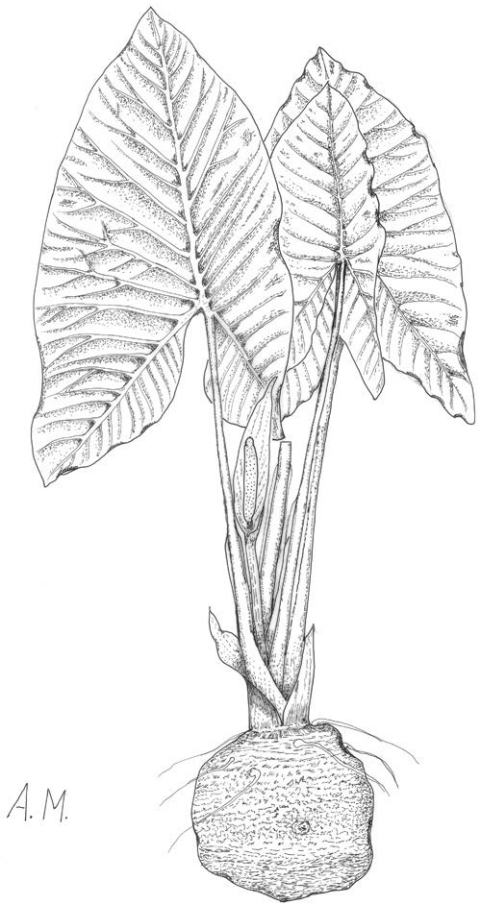


**Fig. 23.13.** *Cyrtosperma merkusii*, swamp taro.

favourable for the domestication of taro through natural hybridization in areas where these species are sympatric. It is thought that *C. esculenta* may have been domesticated with a selection pressure on starch bulking and stolon reduction through hybridization with *C. oresbia* or with a drastic reduction in acridity through hybridization with *C. lihengiae*. Natural populations of wild *C. esculenta* display long stolons, small corms and strong acridity (Matthews, 2014). In Yunnan Province (Yingjiang county), China, new species of *Colocasia* are being described. *C. bicolor* has unisexual flowers without a perianth (Cai *et al.*, 2005). *C. yunnanensis* is another new species distinguished from the morphologically fairly similar *C. bicolor* because its leaves have five to nine pairs of large purple spots, a sterile zone with white hairs in the inflorescence and a spadix without an appendix (Cai *et al.*, 2006). This type of botanical determination of new species illustrates the confusion that could be created within the *Colocasia* genus by enthusiastic taxonomists who are sometimes


**Fig. 23.14.** *Colocasia gigantea*.

prone to 'discover' a new species when there is only some variation within the existing ones.

For example, on morphological grounds it seems difficult to support *C. formosana* as a species separate from *C. esculenta*. It has been suggested that since *C. esculenta* is poorly defined, it remains difficult to reject *C. formosana*. It is hoped that in the future, when wild populations of *C. esculenta* are better documented, it may be possible to split *C. esculenta* into multiple species or subspecies (Matthews *et al.*, 2015). However, if these different morphotypes are able to cross-pollinate successfully and to produce viable seeds, the usefulness of such a taxonomic undertaking remains questionable.

The white-fleshed *X. caracu* is grown in Florida and Puerto Rico. *Xanthosoma belophyllum* is eaten in Venezuela. The leaves of *X. undipes* cormels

are boiled and fermented in Mexico to produce *chicha*, an alcoholic beverage (Bown, 2000). In Nigeria, *X. mafaffa* does not hybridize with *X. sagittifolium* and is therefore thought to be truly distinct (Okeke, 1992). Some species, such as *X. auriculatum*, *X. helleborifolium*, *X. mexicanum*, *X. pentaphyllum* and *X. robustum*, are used as medicinal plants.

## CYTOLOGY

For counting chromosome numbers, fresh root tips are pretreated with 0.2% colchicine or 2 mM 8-hydroxyquinoline for 4 h and fixed in a mixture of ethanol and acetic acid (3:1 v/v). The sample is then hydrolysed in 1 N HCl for 4 min at 60°C and stained with Schiff's reagent. Each stained root tip is squashed in 45% acetic acid and examined with a microscope (Coates *et al.*, 1988; Matsuda, 2002).

In Nigeria, mitotic index studies were carried out on cultivars of *Xanthosoma* and *Colocasia* using young healthy roots (about 15 mm) which were collected at 2-h intervals from 06:00 to 20:00. Root tips were fixed in 1:3 ethanol:acetic acid for 24 h and stored in 70% ethanol prior to squashing in orcein. Microscopic counts showed that the dynamics of mitosis varies between cultivars. The peak of metaphase is between 12:00 and 14:00 for most cultivars, but one has its metaphase rising to a peak between 14:00 and 16:00. This suggests that the best time to harvest root samples for optimum metaphase is immediately before 12:00 (Ekanem and Osuji, 2006).

It is generally believed that the *C. esculenta* basic chromosome number is $x = 14$. However, if $x = 14$, then there is a theoretical possibility that the basic number may also be $x = 7$. Sreekumari (1997) believes that $x = 14$ is too high to be assumed as the original basic number of chromosomes. In the absence of any established form of taro with a chromosome number $2n = 14$, the present $2n = 28$ condition may be considered as a functional diploid number of alloploid origin evolved from the ancestral $2n = 14$ taxa. Meiotic and karyomorphological data favour the contention of $x = 7$ as the original basic number of chromosomes (Sreekumari, 1997). Lebot and Aradhya (1991) studied zymograms of the progenies resulting from a cross between genotypes with 28 chromosomes. They came to the conclusion that the zymograms of the offspring generation were not the zymograms of normal diploids. The segregation indicated that the individuals may be tetraploids with $4n = 28$ ($x = 7$). However, recent investigations using fluorescent *in situ* hybridization with ribosomal DNA probe (Kokubugata and Konishi, 1999) showed evidence for the basic number $x = 14$.

The genotypes with $2n = 28$ chromosomes then are diploids, $3n = 42$ are triploids and those with $4n = 56$ are tetraploids. The majority of cultivated and wild genotypes are diploids; they flower and produce seed. Triploids have been documented in Australia, India, Japan, New Caledonia, New Zealand, Nepal, the Philippines and Timor (Yen and Wheeler, 1968; Coates *et al.*, 1988; Kreike

**Table 23.1.** Chromosome numbers in the aroids.

| Species | Reported somatic numbers of chromosomes |
|---|---|
| *Acorus calamus* L. | 18, 24, 36, 44, 45, 48, 54 |
| *A. gramineus* Aiton | 18, 22, 24 |
| *Alocasia fornicata* Schott | 42 |
| *A. indica* (Lour.) Spach | 28 |
| *A. montana* Schott | 28 |
| *Amorphophallus bulbifer* Bl. | 36, 39 |
| *A. campanulatus* (Roxb.) Bl. | 26, 28 |
| *A. dubius* Bl. | 28 |
| *A. rivieri* Durieu | 26, 32, 39 |
| *A. titanum* Becc. | 26 |
| *Anaphyllum wightii* Schott | 26 |
| *Ariopsis peltata* Nimmo. | 28, 42, 80 |
| *Arisaema leschenaultii* Schott | 28 |
| *A. neglectum* Schott | 28 |
| *A. wightii* Bl. | 28 |
| *Arum maculatum* L. | 28, 56 |
| *A. italicum* Miller | 64, 84 |
| *Caladium bicolor* (Ait.) Vent. | 30, 48 |
| *Calla palustris* L. | 36, 72 |
| *Colocasia esculenta* (L.) Schott | 14, 24, 28, 42, 56 |
| *C. affinis* Schott | 28 |
| *C. fallax* Schott | 28 |
| *C. indica* Lour. (Hassk.) | 28 |
| *C. bicolor* C.L. Long & L.M. Cao | 28 |
| *C. gigantea* (Blume) J. D. Hooker | 28 |
| *C. yunnanensis* C.L. Long & X.Z. Cai | 28 |
| *Cryptocoryne spiralis* Fischer | 12 |
| *Dieffenbachia picta* Schott | 34 |
| *Dracunculus vulgaris* Schott | 28 |
| *Lagenandra meeboldii* Fischer | 36 |
| *L. ovata* Thw. | 36 |
| *Lasia spinosa* Thw. | 26 |
| *Pistia stratiotes* L. | 28 |
| *Remusatia vivipara* Schott | 28 |
| *Steudnera discolor* Hort. | 56 |
| *Theriophonum indicum* Engl. | 16 |
| *T. minutum* Engl. | 16 |
| *Typhonium bulbiferum* Dalz. | 20 |
| *T. cuspidatum* Decaisne | 16 |
| *T. trilobatum* Schott | 18, 26, 36 |
| *Xanthosoma sagittifolium* (L.) Schott | 26 |
| *X. violaceum* Schott | 26 |

Source: Ivancic and Lebot (2000).

*et al.*, 2004). Triploids may have originated from sexual recombination between diploid and tetraploid individuals (fusion of haploid $n = 14$ and diploid $n = 2x = 28$ gametes). The offspring individuals theoretically will have $3n = 42$ chromosomes. Another possibility is irregularity in gametogenesis in normal diploids, resulting in one or more gametes with an unreduced number of chromosomes. If such a gamete fuses successfully with a normal haploid one, the resulting embryo becomes triploid, although this development is extremely rare.

A global study on taro diversity has inferred the ploidy level of accessions from the maximum number of alleles at all loci investigated using simple sequence repeats (SSRs). The number of cultivars showing three alleles at least at one locus differed among countries but, interestingly in South Africa, 56 cultivars showed three alleles at least at one locus. It is thought that many triploids were introduced into Africa from India at the beginning of the 20th century by Indian traders and settlers. Some African triploids, however, seem to be related to the Japanese cultivars. The 42 cultivars from the Pacific region did not show more than two alleles, confirming Yen and Wheeler (1968) chromosome counts. Also, cultivars from Caribbean Islands and the Philippines did not present more than two alleles per locus (Chaïr *et al.*, 2016b).

Tetraploids ($4n = 56$) are considered to be important for the formation of triploids ($3n = 42$) (Matthews, 2014) but it is not known whether they exist in wild populations, and Yen and Wheeler (1968), and Coates *et al.* (1988) did not mention them. They may be produced spontaneously in nature owing to the doubling of the chromosome number in a shoot tip cell, which in further cell division results in tetraploid somatic tissue and, finally, in a tetraploid individual. Tetraploids are produced artificially by treating young tissue with a solution of colchicine. Mitotic division of tetraploid tissues may result in a tetraploid plant (Sreekumari *et al.*, 2004). The *Araceae* family is extremely heterogeneous and there is tremendous variation in chromosome numbers (Table 23.1).

# 24

# Breeding and Genetics

Modern aroid production is becoming intensive and oriented to the market, which requires cheap, healthy and high-quality products. The aim of taro breeding is to create genotypes that are high yielding, with corms of good eating quality, resistant to diseases, tolerant to pests and well adapted to specific environments (paddy or dryland conditions).

One of the first taro breeding programmes was initiated in the Solomon Islands in the early 1970s. Its main objective was to create taro genotypes resistant to the taro leaf blight (TLB) caused by *P. colocasiae* (Patel *et al.*, 1984). In the early 1980s, breeding programmes started in Hawaii and Samoa, focusing on yields. Breeders followed these footsteps in Papua New Guinea (PNG), India (Central Tuber Crops Research Institute (CTCRI) in Kerala), the Philippines (PhilRootcrops in Baybay, Leyte), Fiji and Vanuatu (Ivancic and Lebot, 2000; Sreekumari *et al.*, 2004). However, not much was achieved and this was thought to be due to the narrow genetic bases involved. In some cases, it was also due to the introduction of wild stock which introduced, along with resistance to *P. colocasiae*, acridity and other deleterious traits (i.e. stolons), which required several cycles to eliminate. Progress was slow and somewhat unconvincing and, if heterosis occurred, it was far from obvious. Following the introduction in 1993 of TLB into Samoa, a breeding programme was initiated, which was based on the introduction of Asian varieties tolerant to TLB. This programme has since been very successful: numerous improved hybrids have been distributed and the export industry of taro has been restored and is developing in Samoa. Other breeding programmes have been established in the Pacific, Asia and Africa following the introduction of TLB to Europe.

## OBJECTIVES AND SELECTION CRITERIA

A new cultivar has to be high yielding, have good postharvest shelf life and be resistant to major pests (mostly *Papuana* spp. beetles) and diseases (especially to *P. colocasiae*). Yield improvement is a complex, quantitative trait which depends

on genotype, environmental factors and genotype × environment (G × E) interactions. For aroids these are, however, difficult to measure accurately. A high-yielding taro variety may produce low yields because the planting material is weak. The use of different types of planting materials from the same clone generally results in significant differences in yield. Calibration of propagules is, therefore, a necessary (but time-consuming) preliminary step before any evaluation process. Plant height and leaf area (LA) are associated closely with growth vigour, health and photosynthesis, and are important factors influencing taro yield (Simin *et al.*, 1995).

Markets require a constant supply of uniform, healthy, fresh corms of an adequate size (approximately 2 kg). This can be achieved with early maturing cultivars with a growth period of 5–7 months. Corm yield and corm quality appear to be correlated negatively. Typical high-quality cultivars such as 'Akalomamale' in the Solomons, 'Numkowec' in PNG, 'Tarapatan' in Vanuatu or 'Bunlong' in Hawaii are relatively low yielding and susceptible to leaf blight. Soft corms with high water content generally characterize very high-yielding cultivars.

## SEXUAL REPRODUCTION AND STERILITY

Edible aroids have basically the same structure of inflorescences as *Colocasia*. However, there are enormous differences in the size, pigmentation and proportions of the female, male and sterile parts of the spadix. In most species, however, female flowers are usually mixed with sterile ones, which can be distinguished by their light colour. Fertile female flowers are always green and with well-developed stigmas. The seed productivity of the taro inflorescence depends on the number of parietal placentae and the associated number of ovules per ovary. The number of placentae per ovary varies from two to four, while the number of ovules per ovary varies from 10 to more than 80, depending on cultivar (Ivancic and Lebot, 2000).

During the flowering process, the spathe opens and curves away from the opening. The whole portion of the inflorescence is then released and pollen can be spread by pollinating agents. Aroids produce heat and thermogenesis. The heat produced by the inflorescence creates a microclimate, which makes insects more active. The significant thermogenic activity of taro inflorescences (6.8°C above the ambient temperature) is synchronized with protogyny and insect pollination, offsetting variations in ambient air temperature during the most critical period of flowering and promoting cross-pollination (Ivancic *et al.*, 2004a). Studies conducted on *A. macrorrhizos* (Ivancic *et al.*, 2005) indicate that the highest temperatures are produced by the sterile appendix of the inflorescence and are more than 20°C above the ambient air temperature. For *C. gigantea*, the average maximum temperature of inflorescences is 9.8°C above the ambient temperature (Ivancic *et al.*, 2008).

One day before pollen is released, the spathe slowly starts opening. The odour becomes intense and starts attracting insects, some of which come from inflorescences that flowered 1 day earlier and have already released pollen. In this way, they may pollinate the female flowers. At this time the stigmas are already receptive and pollen grains that come from a compatible genotype can start germinating. Inflorescences within the same cluster never flower at the same time. They start flowering in the order in which they developed, the time intervals between them varying from 2 days to more than 1 week. Fertile taro genotypes usually start flowering about 3 weeks after replanting, but small material takes much longer. In some cases, plants can start flowering immediately after replanting the headsets or suckers. The early appearance of inflorescences is a normal and frequent event when the well-developed top parts of nearly flowering plants are used for planting. Inflorescences that appear early can be fertile and used in crossing.

Poor flowering of cultivars is the main factor limiting hybridization. Dry winds and high temperatures often cause seed set failure. To eliminate negative environmental effects, the crossing plots should be well irrigated, fertilized and protected from dry winds with trees such as *Gliricidia sepium*. There are several possibilities for promoting flowering if plants are diploids:

- Treatment with gibberellic acid ($GA_3$) (0.3–0.5 g/l).
- Removal of leaves (very effective for *Alocasia* and *Xanthosoma*).
- Stress induced by drought and high temperature.
- Removal of cormels, suckers and stolons.

Treated plants usually start flowering 3–5 weeks after the $GA_3$ treatment, but the inflorescences remain sterile. Breeders should then combine two or more flower-inducing treatments. Environmental stress or flowering hormones used as promoters have to be followed by a period which is optimal for growth. If not, the induced flower development will be stopped or the inflorescences will be sterile.

## CROSSING TECHNIQUES AND TRUE SEED PRODUCTION

The first visible indication of the approaching flowering process is the appearance of the flag leaf. Once the flag leaf is exposed, the first inflorescences usually appear within 1–3 weeks. The spathe will unfold slowly and enable pollinators to enter. The majority of insects will remain inside the inflorescence until the next morning. At that time, the inflorescence will be completely opened and the pollen released. The odour will disappear but the same attraction will come from another inflorescence, which will release pollen 1 day later. This mechanism is essential for efficient insect cross-pollination based on protogyny.

Pollination is done by different insects, wind or water, though insects are the main vectors. In PNG, the insects found in *Colocasia* inflorescences are

*Drosophilella pisticola* and *D. stamenicola*, belonging to the dipterous family, Drosophilidae. The names of these species are associated with the larval stage which occupies the pistillate or staminate portion of the taro spadix. The insects enter the fresh inflorescence when it starts opening (Matthews, 2014). In Malaysia, 30–40 dipteran flies, *Dacus dorsalis*, have been recorded per inflorescence. Other visitors of taro inflorescences are bees, small solitary wasps, small Coleoptera insects, mosquitoes and ants (Ivancic and Lebot, 2000).

Wind pollination is significant for genotypes with open flowering and a fully exposed male part of the spadix. Rain results mostly in self-fertilization by washing pollen grains from the male part of the spadix to the female part. For controlled pollination, the stigma becomes receptive at the time when the inflorescence emerges from the petiole sheath; this is about 5 days before the odour is released or 6 days before pollen is shed, and the stigma remains in this condition for up to 10 days. The procedure for hybridization has four steps:

**1**. Preventing insect pollination before hand pollination.
**2.** Emasculation.
**3.** Pollination.
**4**. Preventing insect pollination after hand pollination.

To avoid undesired insect pollination and self-pollination, the female parent has to be emasculated at an early stage. Emasculation must be completed before pollen can be shed and also before insects penetrate the inflorescence. Penetration of insects can be prevented by isolation with rain-resistant paper bags. One of the best solutions, however, is to cut off the inflorescences on a 30–40 cm length of the peduncle 2 days before pollen is released and to keep them in a container with some water, in an isolated, moderately cool and dry room until pollen is released.

Emasculation is conducted 2 days before the inflorescence opens and pollen is shed. The upper part of the spathe is cut, together with the male portion of the spadix. The lower part of the spathe is then removed carefully using a small knife. The spathe should not be removed completely; rather, a ring of the spathe about 8–10 mm high should be left to protect the lower part of the inflorescence. The emasculation procedure for other aroids (*Alocasia*, *Amorphophallus* and *Xanthosoma*) is similar (Fig. 24.1).

One of the exceptions is *C. merkusii*, which has inflorescences with dense bisexual flowers. The mechanisms of protogyny and self-incompatibility are, in most cases, sufficient for obtaining hybrid seed. Emasculation is also not needed for *A. paeoniifolius* because of its strong self-incompatibility system.

Pollination is done immediately after emasculation and fresh pollen can be stored successfully for at least 1 week without losing its viability. Pollen can also be stored frozen in dry conditions. One male inflorescence can pollinate several females, depending on the quantity of pollen available. An attempt has been made to tackle asynchronous behaviour in taro by preserving cryostored pollen, ranging from 1 week to 2 months, and to use this cryostored pollen

**Fig. 24.1.** *Xanthosoma sagittifolium* inflorescence. Female flowers (yellow part) located at the bottom of the spadix are isolated by sterile flowers (pink zone) from the male flowers (white zone) located in the upper part (photo: V. Lebot).

for hybridization. Fruit setting was observed within 1 week of hybridizing taro with cryopreserved pollen. Seed germination *in vitro* was recorded in the range of 60%–90%. It is possible to improve planned hybridization in asynchronous flowering taro with the aid of cryopreservation tools (Mukherjee *et al.*, 2016). There are several possible ways to distribute pollen on stigmas: brush, fingers or directly by the male portion of the spadix.

After pollination, female flowers are protected with small bags made of paper, cloth, cotton or other material, or with the green part of the spathe that was removed during emasculation (Fig. 24.2). The best and the cheapest material is probably cotton. Protection is needed for about 1 week. The cloth and paper bags have to be removed to enable normal development of fruit heads. Growing fruits may have to be protected against attacks by different insects, with small elongated bags made from fly screen, or simply with cotton wool. Protection measures may not be needed if regular spraying with insecticides is done (Wilson, 1989).

In most cases, the fruit heads are ready to be harvested 30–35 days after fertilization (Fig. 24.3). Seeds can be stored for at least 2 years in a desiccator inside a refrigerator. Seeds sealed in small plastic bags and stored in a moderately

**Fig. 24.2.** Controlled pollination of *Xanthosoma sagittifolium* is done after emasculation (removal of the male upper part of the spadix) by gently applying pollen on the female flowers and covering them with the green bottom part of the spathe to prevent other pollinations (photo: V. Lebot).

**Fig. 24.3.** Fully mature fruit heads of *Colocasia esculenta* are collected for seed extraction (photo: V. Lebot).

cool and dry room remain viable for more than 1 year. Seeds have no specific dormancy period and can be planted soon after harvesting. Fresh seeds have to be dried and then planted (Fig. 24.4).

Taro seeds are very small and have to be planted in small pots placed into 'water beds'. In such nurseries, germination is simple and cheap. They usually start to germinate 2–3 weeks after planting. Soil may be treated with a low concentration of fungicide, or sometimes with sterile water, to avoid infection.

**Fig. 24.4.** Seeds of *Colocasia esculenta* (photo: V. Lebot).

**Fig. 24.5.** Seedlings of *Xanthosoma sagittifolium* (photo: V. Lebot).

The germination rate can be improved by covering the pots with transparent plastic sheets immediately after planting the seeds. Once a day, the sheet has to be removed and the pots sprayed with sterile water, using a hand sprayer. After seed germination, the emphasis has to be put on aeration. For this reason, the transparent plastic sheet has to be raised to allow the air to circulate. The relative humidity, however, has to be kept high.

Seeds start germinating about 10 days after sowing. An average germination rate between 60% and 70% is considered satisfactory. Tiny seedlings are extracted from trays with tweezers 1 month after germination and are replanted directly in Jiffy® pots, where the young plants can stay for 2 months before establishment in the field (Fig. 24.5). Before field planting, the abundant root system and the leaves are cut back and $C_1$ plants are installed at high densities (20 × 20 cm) and replanted again 4 months later ($C_2$ at 50 × 50 cm). It is necessary to test several thousand individuals, even when the parents are the best existing genotypes. In more advanced cycles, the chances of getting superior genotypes will

probably increase because of the accumulation of positive genes, but chances will still remain relatively low because of highly heterozygous progenies.

The flowering ability of the taro genotypes is usually restored in the hybrids, even those resulting from crosses between two parents which had to be sprayed with $GA_3$ to force them to flower. Most of the hybrids flower profusely and this is a serious problem as the inflorescences produce 'shoulders' and deform the shape of the corms. Flowering genotypes cannot produce perfect shapes, only sterile ones can.

*Xanthosoma* improvement has been done in Cameroon. Hybridization resulted in the production of more than 10,000 seeds from some crosses but few viable seeds from others, perhaps due to ploidy differences (Goenaga and Hepperly, 1990; Agueguia *et al*., 1994; Tambong *et al*., 1997; Onokpise *et al*., 1999), and some attempts have been made to produce new forms through *in vitro* culture (Tambong *et al*., 1998).

No intensive and systematic breeding work has been done on *A. macrorrhizos*. The main characteristics which have to be improved are quality of corms, growth cycle (the growth period is extremely long), environmental adaptability and disease resistance.

*Amorphophallus* spp. is being improved in India by CTCRI. The germplasm collection has 195 accessions, selections have been made for different regions and hybrids have been released. Some 1670 seeds comprising 1280 hybrids ('Sree Padma' × Am 40) and 390 inbreds ('Sree Padma') have been produced to study improvement possibilities. In addition to the normal green seedlings, a few albinos also emerged from both inbred and hybrid seeds. The frequency of albinos in the inbred population appears to be more than double that in the hybrids, 9.8 and 4.6, respectively (Sreekumari and Abraham, 2005). However, little is known of the extent of variation existing within the species and there is a need for further morpho-agronomic characterization of the accessions (Poddar and Mukherjee, 2015).

## SELECTION METHODS AND PROGRAMMES

It is now accepted that different taro gene pools have to be combined to broaden the base of national programmes. In the Pacific, local cultivars are the result of intense selection focusing on corm quality and yield. These cultivars produce well-shaped corms of good quality but susceptible to various pests and diseases. In Asia, co-evolution with numerous and diverse strains of *P. colocasiae* have produced resistant genotypes; but, because taro is not as important as it is in the Pacific, the Asian cultivars are not as much improved and present numerous suckers and stolons. Breeders should start with cultivars from diverse and distant geographic origins. Crosses between materials originating from the same country, or from neighbouring countries, will not produce a very diverse offspring, slowing down the selection process. If taro breeding is to have a constructive future, there needs to be international exchange of germplasm

(Lebot, 2005). This is particularly true for the Pacific, where recent segregation studies have confirmed narrow genetic bases (Ivancic *et al.*, 2003, 2004a, b).

Early steps in the establishment of base populations are the identification of a core sample of cultivars and the adoption of reliable quarantine procedures that can handle large numbers of cultivars. The TANSAO (Taro Network for South-east Asia and Oceania) core sample was distributed to all participating countries and is now being recombined with local material (Kreike *et al.*, 2004; Lebot *et al.*, 2004).

Genetically variable taro populations are created mainly by hybridization, whether controlled or natural. The majority of taro genotypes are considered to be at least partly heterozygous, and progenies are highly variable. Open pollination, within an artificial polycross population with a well-managed flowering induction system, is a simple and cheap way of producing high genetic variation for recurrent selection. Recurrent selection has been used successfully in the Solomon Islands and PNG. The process is, however, fairly slow. In repeated field trials of the selected clones from the cycle-1 population, only eight clones appeared to be superior (with high yield, good eating quality of corms and resistance to Phytophthora leaf blight). This represented less than 0.008% (8 individuals out of more than 100,000 tested individuals). At the end, only one was found to be suitable for farmers. In the cycle-2 population, the number increased a little, but not by much (Ivancic and Lebot, 2000).

One of the most efficient ways to improve breeding efficiency is to start selection at an early stage of development without waiting for the plants to be uprooted and corms characterized, which usually takes place at least 15 months after seed germination. This approach has been used for determining taro corm flesh and corm fibre colours, as these traits are important for marketing (Ivancic *et al.*, 2003) (Fig. 24.6).

**Fig. 24.6.** Hybrids of *Colocasia esculenta* being clonally propagated for evaluation and selection (photo: V. Lebot).

Mass selection results in the rapid accumulation of suitable genes but needs to be complemented with efficient screening techniques. Correlation coefficients between major constituents indicate that breeding for increased dry matter (DM) and starch contents will reduce sugars, proteins and minerals (Champagne *et al.*, 2009). Near infra-red spectroscopy (NIRS) calibrations have been developed to screen large populations to improve selection. NIRS could assist taro breeders in their choice and selection of the best genotypes, based on the chemical composition requested by consumers by predicting simultaneously starch, sugars, proteins and minerals from a single sample. As starch is significantly negatively correlated with the other three major constituents, the simultaneous prediction of all four constituents allows for rapid estimation of the variety chemotype and therefore its quality (Lebot *et al.*, 2011b, 2013). Secondary metabolite content in taro corms can also be improved through phenotypic recurrent selection. A study conducted using high performance liquid chromatography (HPLC) analysis has shown that it is fairly easy to improve total carotenoid content through this approach. Orange-fleshed taros have the highest carotenoid content and deep-purple-fleshed taros present the highest anthocyanin content. However, a simple visual assessment or use of a chromameter may not be the best option, because the measurements may be biased by the existence of orange and red pigment gradients within the corms. Red taro corms also contain significant quantities of both anthocyanins and carotenoids (Champagne *et al.*, 2013).

Some taro varieties are very rich in flavonoids. Ten flavones: luteolin-6-C-hexoside-8-C-pentoside, schaftoside, luteolin-30,7-di-O-glucoside, homoorientin, isovitexin, orientin, luteolin-40-O-glucoside, luteolin-7-O-glucoside, vitexin and apigenin-7-O-glucoside have been detected in the corm and are responsible for the attractive yellow colour of the flesh and fibres. Luteolin-6-C-hexoside-8-C-pentoside and schaftoside are the most important. However, only 18% of the varieties analysed presented these two compounds and 80% presented poor flavonoid composition. The most flavone-rich varieties originated from Vanuatu, Thailand, the Philippines, Malaysia and Indonesia. These compounds were significantly and positively correlated, suggesting that there is potential for fast improvement through breeding (Lebot *et al.*, 2015b).

Not much is known, however, of the Mendelian segregations for such traits. The flavonoid fingerprints of more than 1800 hybrids belonging to 24 full-sib families were compared. Flavonoids differ among individuals both quantitatively and qualitatively. After the complete population screening, 377 high flavonoid content (HFC) hybrids were selected from 14 different families, but no clear segregation patterns were observed. The mean corm weight of HFC hybrids always appeared higher than the mean corm weight of the family they belong to, indicating that these flavonoids could contribute to taro genetic improvement for nutritional value and to strengthen corm tolerance to pests and diseases (Lebot and Legendre, 2014). More studies will be needed, however, to fully understand the genetic control of these secondary metabolites.

Genotypes with a large number of suckers are not desired because generally they have a lower yield. Profuse stolon production can cause important competition effects between neighbouring plants and a deformed corm shape. Corm branching is another complex, undesired and rare trait which is expressed because of the proliferation of lateral buds. Genetic control involves the interaction of at least two loci and appears to be associated with inbreeding depression (Ivancic *et al.*, 2004a).

The corm yield is correlated to the weight of the propagule planted and genotype performance is, therefore, difficult to assess accurately if calibration is not conducted properly before planting. The potential yield is also closely dependent on plant architecture. A vegetative growth index (VGI) has been developed which takes into consideration only four vegetative traits and allows assessment at 6 months of genotypes with good yield potential. Because it takes generally 3 years from true seed before sufficient homogenized clonal material is produced for accurate evaluation, this index is useful for screening large populations. The VGI takes into consideration the LA of the plant. This can be estimated from the longest leaf length, there being no significant variation in the number of leaves per main stem (the one from which the corm yield is measured) between dasheen varieties. Most varieties are assumed to have at least five functional leaves per main stem, with a lamina length on average equal to 1.4 of the lamina width. The following formula is used to compute the index:

$$VGI = [((\text{leaf length} / 1.4) \times 5) \times h / 100] - (\text{suckers} + \text{stolons})^2$$

When this index is correlated with the mean corm yield, a highly significant and positive correlation coefficient is obtained. Genotypes with a high VGI at 20 weeks after planting (WAP) (at the beginning of phase four of growth) have the potential to produce a high corm yield when mature at 36–40 WAP. In fact, a high VGI translates to a good aptitude of the plant to stock energy in its corm. Tall cultivars bear large leaves forming a wide canopy for maximum light interception and storage of energy. A low number of stolons and suckers avoid this energy being translocated into useless, secondary vegetative growth. This VGI index does not take into consideration the computation of an accurate leaf area index (LAI) for taro (Miyasaka *et al.*, 2003), but is easier to compute for screening numerous genotypes with different architectures.

Maximum yield is, however, difficult to measure accurately because optimum maturity is difficult to determine precisely in all aroids. Depending on how the measurements are made, maturity of the corm and cormels is reached when the average or the maximum fresh yield is achieved, an acceptable quality (DM content) is obtained and the corm diameter starts to decline near the petiole base.

Overall, tall plants tend to produce more and bigger leaves, more suckers and fewer stolons. They also tend to produce bigger corms with a lower DMC (dry matter content). In contrast, small plants generally produce more stolons

and smaller corms. VGI is an early predictor of corm yield which can be used by breeders to remove undesirable genotypes quickly (Soulard *et al.*, 2016). Phenotypic correlations between major morphological traits for dasheen type taro hybrids are presented in Table 24.1.

Successive clonal generations allow the propagation of sufficiently homogenized planting material to improve the evaluation accuracy of the hybrids. However, aroids are very sensitive to plant density variation: the closer the spacing, the smaller is the yield. It is, therefore, important to evaluate new hybrids at the right density. For taro, several experiments conducted in Hawaii have attempted to determine the optimum plot size. It is recommended that 16 (4 × 4) to 24 (6 × 4) inner-measured taro plants could be considered the smallest optimum plot size. However, when the means are limited it is possible that fewer inner-measured taro plants could suffice to test for differences (3 × 3) with inner-measured plants surrounded by border rows (Miyasaka *et al.*, 2013).

Successful taro breeding programmes have been implemented in Hawaii, Samoa, Fiji, Vanuatu, PNG, the Philippines and India. Through several cycles of phenotypic recurrent selection they have generated several thousand hybrids, which have been evaluated on-station, and some have been distributed internationally *in vitro* and virus free.

In PNG, the National Agricultural Research Institute (NARI) in Lae developed improved varieties with high yield, yield stability across broad agroecological sites, resistance to TLB and good eating quality. The first cycle of selection was conducted at one location (Bubia research station) on a population generated by mating TLB-resistant wild and partly domesticated accessions with local cultivars. For the following cycles the programme then focused on incorporating horizontal resistance to TLB originating from different geographical sources. Under trials, these varieties perform well in farmers' fields, giving over 50% higher yields than standard popular check varieties like 'Numkowec' (Singh *et al.*, 2006; Yalu *et al.* 2009).

Overall, farmers' response has been enthusiastic. Improved varieties are first planted in plots adjacent to landraces and evaluated separately. If appreciated, often on taste basis, they are propagated for further agronomic evaluation. The process is quite slow and it will take several years to see if an introduced variety is widely adopted and shared among farmers (Camus and Lebot, 2010; Lebot *et al.*, 2018c). Most taro breeding programmes have been project driven, and often with very limited support from the international community.

Unfortunately, there is no breeding programme presently working on taro leaf quality. Eating quality depends on several other components such as proteins, vitamins, aromatic substances, water, fibres and of course low acridity. Commercial growers cultivate taro for its petioles in Thailand (around Phichit), where they are dehydrated and exported to Japan to be used in soups. These varieties present very long and tender petioles. Taro inflorescences are used as a source of food in several Pacific countries, Vietnam, India, Japan and Yunnan province, China. Their eating quality depends on genotype and stage of development.

**Table 24.1.** Phenotypic correlations between traits and between seminal ($F_1$) and first clonal ($C_1$) generations, at the individual level, measured on 1765 hybrids (Source: Soulard *et al.*, 2016).

| Traits | Stolons $F_1$ | Suckers $F_1$ | Pt height $F_1$ | Lf length $F_1$ | Inflo $F_1$ | *VGI* $F_1$ | FW $F_1$ |
|---|---|---|---|---|---|---|---|
| Stolons $C_1$ | −0.665**** | −0.564**** | −0.118**** | −0.112**** | −0.008$^{NS}$ | −0.132**** | −0.193**** |
| Suckers $C_1$ | −0.389**** | −0.531**** | −0.078** | −0.044$^{NS}$ | −0.108**** | −0.053* | −0.103**** |
| Leaves $C_1$ | −0.002$^{NS}$ | −0.015$^{NS}$ | −0.074** | −0.079** | −0.066** | −0.081*** | −0.120**** |
| Pt height $C_1$ | −0.074** | −0.064** | −0.320**** | −0.257**** | −0.007$^{NS}$ | −0.299**** | −0.230**** |
| Lf length $C_1$ | −0.066** | −0.007$^{NS}$ | −0.202**** | −0.265**** | −0.060* | −0.262**** | −0.199**** |
| Lf width $C_1$ | −0.078** | −0.025$^{NS}$ | −0.208**** | −0.254**** | −0.033$^{NS}$ | −0.255**** | −0.192**** |
| Inflo $C_1$ | −0.007$^{NS}$ | −0.013$^{NS}$ | −0.082*** | −0.009$^{NS}$ | −0.425**** | −0.038$^{NS}$ | −0.111**** |
| VGI $C_1$ | −0.076** | −0.019$^{NS}$ | −0.259**** | −0.280**** | −0.045$^{NS}$ | −0.293**** | −0.224**** |
| FW $C_1$ | −0.093*** | −0.040$^{NS}$ | −0.260**** | −0.289**** | −0.033$^{NS}$ | −0.300**** | −0.341**** |
| DMC $C_1$ | 0.094*** | −0.033$^{NS}$ | −0.138**** | −0.120**** | −0.073** | −0.138**** | −0.098*** |

$^{NS}$: not significant at the 0.05 probability level; *Significant at the 0.05 probability level; **Significant at the 0.01 probability level; ***Significant at the 0.001 probability level; ****Significant at the 0.0001 probability level. $F_1$: traits measured in the seminal generation; $C_1$: traits measured in the first clonal generation. VGI: Vegetative growth index.

The Hawaiian breeding programme has released a few ornamental varieties which are being used by commercial nurseries in Florida, USA. In Vicosa, Minas Gerais, Brazil, several local accessions of taro have been evaluated for ornamental traits and it is suggested that some Brazilian taro accessions have characteristics which qualify them as ornamental plants, pot plants or garden plants (Pereira *et al.*, 2005).

## HERITABILITY OF MAJOR TRAITS

Some investigations have been looking at the heritability of major traits in Indian taro by comparing the performance of local and introduced varieties and hybrids, followed by analysis of variance (Dwivedi and Sen, 1997). In Vanuatu, experiments have been conducted in two clonal generations with different statistical designs. It appears that both family and narrow-sense heritabilities are higher for the number of suckers and DM content than for corm weight. The family heritability values, compared to the narrow-sense heritabilities, suggest the possibility of using family selection in the first cycles (Table 24.2).

Heritability trial results indicate that it is appropriate to create a few large full-sib families when working with a narrow genetic base, and numerous small full-sib families when dealing with a broad genetic base. When working with large collections, only the parents showing the most valuable agronomic characteristics should be recombined, so that a high frequency of good offspring genotypes can then be expected. When working with a narrow genetic base, significant heterosis effects are not likely to be apparent if large numbers of different crosses are conducted, so only the best parents should be selected to produce large progenies (Quero-García *et al.*, 2006b).

The correlation between parental genetic distance (estimated with amplified fragment length polymorphism (AFLP) and simple sequence repeat (SSR) markers) and hybrid vigour is weak (Quero-García *et al.*, 2006b), although hybrids show a significant superiority compared to parents for all traits, with the exception of the DM content (Quero-García *et al.*, 2009). However, for a

**Table 24.2.** Family heritabilities (H) and estimations of variance for the family (F) in first clonal generation.

| | Number of suckers | | Corm weight | | Dry matter content | |
|---|---|---|---|---|---|---|
| Trial | H | F | H | F | H | F |
| RCB1 | 0.80 | 0.18 | 0.50 | 0.03 | 0.52 | 4.7 |
| RCB2 | 0.81 | 0.30 | 0.59 | 0.04 | 0.49 | 4.24 |
| RCB3 | 0.95 | 0.46 | 0.62 | 0.01 | 0.71 | 7.15 |
| RCB4 | 0.45 | 0.03 | 0.78 | 0.03 | 0.96 | 11.74 |

RCB = randomized complete blocks. Source: Quero-García *et al.* (2006a).

vegetatively propagated crop like taro, hybrids may have an advantage only in their first clonal generations which result from true seeds, and the rapid accumulation of viruses and of negative mutations may induce a progressive loss of this superiority. Consequently, it will take time for hybrid superiority to be truly demonstrated in farmers' fields.

Heritabilities have been estimated in full-sib families and compared in $F_1$ (seminal generation) and $C_1$ (first clonal generation). Fresh corm weight, DM content, the number of stolons and the number of suckers are the most heritable traits. Qualitative traits such as the presence or absence of suckers, stolons and inflorescences are stable across generations (from $F_1$ to $C_1$), thus suggesting strong genotypic control. At the family level, the most heritable traits are the number of stolons (0.96 in $F_1$, 0.87 in $C_1$), the number of suckers (0.97 in $F_1$ and 0.81 in $C_1$), corm weight (0.79 in $F_1$ and 0.83 in $C_1$) and DM content (0.80 in $C_1$). The VGI (0.65 in $F_1$ and 0.75 in $C_1$) and the number of leaves (0.75 in $C_1$) are also strongly heritable traits. Plant height (0.71 in $F_1$ and 0.68 in $C_1$), leaf length (0.61 in $F_1$ and 0.74 in $C_1$) and leaf width (0.64 in $C_1$) are heritable but to a lesser extent. Moderate to high genetic gain is found for the most heritable traits (number of stolons, number of suckers, fresh weight, DM content and the VGI), indicating that genetic improvement is possible as early as the first generations. Smaller values would be expected in later selection cycles. In the first clonal generation, the genetic gain is greater for mass selection than for family selection but this could be explained by the difference in selection intensity between these two strategies (Soulard *et al.*, 2016).

## GENOTYPE × ENVIRONMENT (G × E) INTERACTIONS

Some cultivars are adapted to paddy conditions and others to upland conditions, while some tolerate relatively long periods of drought. There are cultivars that grow well only in coastal areas, while others do so at higher altitudes. There are also obvious differences in adaptability to different soil pH. It is impossible to create a genotype that will perform equally well in all environments and all cropping systems. Genotypes from segregating populations have to be tested in different environments.

In PNG, to identify genotypes characterized by general or wider adaptability, seven taro elite lines resistant to TLB and a susceptible, but highly preferred, control cultivar, 'Numkowec', have been tested in seven diverse agroecological environments.

The analysis of variance indicates that there are significant differences in yield among genotypes at all sites, except one. Further pooled analysis of the sites with homogeneous variances detected significant G × E interactions with a low degree of genetic determination for corm yield (heritability in broad sense = 0.19) and a high heritability for leaf blight resistance (0.72) (Okpul, 2005) (Tables 24.3 and 24.4).

**Table 24.3.** Adaptability of eight taro genotypes evaluated across sites.

| Genotype | Corm yield | Stability | TLB resistance* | Relative culinary quality | Mean sucker number | Remarks |
|---|---|---|---|---|---|---|
| E1 | High | Unstable | MR | Low | 5 | Unstable, less acceptable quality |
| E3 | High | Stable | MR | High | 3 | Widely adaptable |
| E4 | Medium | Stable | MR | High | 5 | Widely adaptable |
| E7 | Medium | Unstable | MR | Low | 5 | Unstable, less acceptable quality |
| E8 | Medium | Unstable | MR | High | 5 | Unstable |
| E10 | Medium | Unstable | HR | Low | 1 | Unstable, low yield, poor quality |
| E11 | Low | Stable | HR | High | 3 | Unstable, low yield |
| Numkowec | Low | Stable | Susceptible | High | 3 | Stable, low yield, susceptible to TLB |

TLB, taro leaf blight. *TLB resistance categories: MR = moderate resistance, HR = high resistance. Source: Okpul (2005).

**Table 24.4.** Summary of analysis for corm yield (t/ha) obtained from eight genotypes tested over six sites with homogeneous variance.

| Genotype | Mean corm yield (t/ha) | Mean separation† | | Stability parameter | |
|---|---|---|---|---|---|
| | | LSD‡ | SNK§ | *b* | $S^{2d}$ |
| E1 | 8.90 | * | ab | 0.81 | 2.41** |
| E3 | 10.49 | ** | a | 1.62 | –0.04 |
| E4 | 7.68 | *ns* | ab | 0.83 | –0.53 |
| E7 | 8.14 | *ns* | ab | 1.39 | 1.05* |
| E8 | 7.65 | *ns* | ab | 0.88 | 4.45** |
| E10 | 7.95 | *ns* | ab | 0.65 | 2.51** |
| E11 | 5.92 | *ns* | b | 0.70 | –0.31 |
| Numkowec | 5.89 | | b | 1.14 | 0.58 |

†Based on data from sites' means; ‡least significant difference from Numkowec at 5% (2.3 t/ha) and 1% (3.1 t/ha) level of probability; §Student–Newman–Keul's test. Different letters indicate significant difference between genotypes: *, **= significance at $P < 0.05$ and $P < 0.01$, respectively; *ns* = not significant. Source: Okpul (2005).

Experiments for salinity tolerance conducted in PNG in 1995 included local genotypes of *A. paeoniifolius*, *A. macrorrhizzos*, *C. bicolor*, *C. esculenta* (about 200 hybrids), *X. sagittifolium*, *I. aquatica*, *I. batatas*, *M. esculenta*, *Oryza sativa* and *Zea mays*. These studies showed that *C. esculenta* was the most sensitive to salinity. In India, promising lines of taro evaluated for photosynthetic efficiency and yield under different levels of salinity have shown that a few responded well under salinity stress, with less variation in photosynthetic efficiency and low yield reduction compared to the accession control. The effect of high salinity, however, is remarkable and the yield per plant decreased by 17% to 52% in comparison to the control. Three accessions have been identified as tolerant to salinity, showing less than 25% yield reduction (Sahoo *et al.*, 2007a).

In Nicaragua, cocoyam (*Xanthosoma* spp.) is the third most important starch food crop and is cultivated countrywide. The agronomic performance of three purple genotypes established in four locations with different climatic conditions was evaluated over 2 years. G × E interaction exists for both phenotypic and yield traits. A differential response of the genotypes to the varying climatic conditions at the locations is suggested as one of the causes of the interaction. The genotypic differences regarding the time when the area of the largest leaf reached its maximum size and the variation in sprouts and roots on the cormels at harvest indicate differences in optimal harvest time between varieties. It is also observed that the percentage of plants infected with dasheen mosaic virus (DsMV) differ between locations but not between varieties (Reyes *et al.*, 2005).

The environment also has an effect on the corm's chemical composition. Starch was extracted from two cocoyam (*X. sagittifolium*) cultivars planted in

summer, winter and spring. The physico-chemical properties of the starch were determined to investigate the seasonal effect and it was observed that cocoyams planted in the summer showed higher contents of total starch than those planted in other seasons (Lu *et al.*, 2005).

## USE OF RELATED SPECIES

There is speculation that *A. macrorrhizos* has hybridized with *A. portei* in the Philippines to give a form with slightly wavy leaf margins. Interestingly, a hybrid has been produced between *C. esculenta* var. *aquatilis* from Nepal and *A. brisbanensis*, but only one plant was produced (Yoshino *et al.*, 2000). In Vanuatu, all attempts to cross *A. macrorrhizos* and *C. esculenta* have failed. The most interesting species is *C. gigantea*, a vigorous plant resistant to *P. colocasiae*. It seems that when it is used as the mother plant, the pollen tubes of *C. esculenta* have difficulty in reaching the ovaries; however, when used as the pollen donor, *C. gigantea* can generate seeds in crosses, although very few.

Wild taro genotypes cannot always be clearly distinguished from cultivated types. Extensive cross-fertilization between cultivated and wild genotypes produces hybrids in all areas where the majority of taros flower naturally. Wild genotypes produce more pollen and also attract more insects. Wild genotypes have been used as the source for resistance to Phytophthora leaf blight and nematode diseases. The offspring generation results in immediate segregation because of high heterozygosity of the parents, and individuals will generally express wild characteristics. These individuals usually germinate better, grow better and faster inside the greenhouse, are less affected by diseases and generally have a better appearance. Unfortunately, they are often non-edible or of poor quality.

## POLYPLOIDY BREEDING

In India, it was observed that naturally occurring triploids were significantly superior to diploids in yield. Various attempts were made to produce artificial tetraploids to be crossed with diploids for the production of improved triploids. The induction of tetraploids with colchicine, however, is not simple. The treatment is successful when 0.2% solution is applied to the emerging shoot tip for 6–8 h. The occurrence of tetraploids varies from 0% to 31%, depending on the genotypes treated (Sreekumari *et al.*, 2004).

Germinating seeds treated with relatively high concentrations of aqueous solutions (1%–5%) of colchicine failed to produce tetraploids. Because the number of abnormal plants was extremely low and there were almost no dead plants, it was assumed that colchicine had not penetrated embryos because of the thick mucilage surrounding them when germinating. The addition of

dimethyl sulfoxide (DMSO) did not improve the performance of the treatments (Ivancic and Lebot, 2000).

## USE OF MOLECULAR MARKERS

The size of the nuclear genome of taro 4*C* = 16.3 pg is 23 times larger than that of *Arabidopsis thaliana*, four times larger than potato or tomato, but somewhat smaller than barley (Bennett and Leitch, 2012).

Using isozymes, it is possible to appreciate the extent of genetic variation existing between and within countries, using a simple index that is nothing other than the number of distinct zymotypes divided by the number of distinct morphotypes. At the isozyme level, there is limited variation in PNG and the Philippines (0.05 and 0.11, respectively) and significant genetic variation in Indonesia and Malaysia (0.28 and 0.50, respectively). The isozyme data suggest that genotypes existing in Polynesia share zymotypes identical to those occurring in PNG and the Solomons, which are susceptible to TLB (Lebot and Aradhya, 1991). This means that if TLB is introduced into some Polynesian islands, the existing genotypes will be severely affected. The introduction of *P. colocasiae* in Western Samoa in 1993 was a sad example which confirmed the reliable prediction of isozymes (Lebot *et al.*, 2004, 2010).

Isozymes (and rDNA) have also been used to study the variation in taro from China, Taiwan, the Ryukyu Islands and the main islands of Japan. The geographical distribution suggested two different dispersal routes of triploid taro into Japan, one through Taiwan and the other directly from mainland China (Matsuda, 2002).

Random amplified polymorphic deoxyribonucleic acid (RAPD) has been used to characterize 44 taro accessions. Their results generally agree with cytological and isozyme groupings. They confirm high genetic diversity associated with accessions of Indonesian origin. However, just like isozymes, RAPDs are not able to distinguish among accessions of Hawaiian origin and between triploids and diploids (Irwin *et al.*, 1998). In India, genetic diversity assessed using RAPDs reveals wide genetic distances among varieties. Similarity measures and cluster analysis reflect the expected trends in relationships of diploid and triplod taro varieties (Das *et al.*, 2015).

AFLP markers have confirmed that diversity is greater in South-east Asia than in the Pacific, and that the genetic diversity of the cultivars within most countries is relatively low (Kreike *et al.*, 2004). Stratification of germplasm collections using AFLP analysis failed to correlate molecular markers to morphotypes but proved useful for detecting duplicates and fingerprinting accessions (Quero-García *et al.*, 2004). AFLPs were also used to study the diversity maintained in a remote village of an oceanic island, in Vanua Lava, Vanuatu. They confirmed traditional knowledge and the three sources of genetic diversity known to farmers: introductions, somatic mutations and sexual recombination

(Caillon *et al.*, 2006). SSR markers used to screen taro germplasm (Noyer *et al.*, 2004) have confirmed the image revealed by isozymes, RAPDs and AFLPs. AFLPs have also been used in Malawi (East Africa) to differentiate the two species *X. sagittifolium* and *C. esculenta*, and to analyse the diversity within each of them (Mwenye *et al.*, 2016).

Eleven microsatellite markers (SSRs) were used to study cultivated taro global diversity in 19 countries in Asia, the Pacific, Africa and The Americas. The highest genetic diversity was observed in Asia, especially in India. While taro has been diversified in Asia and the Pacific mostly via sexual reproduction, clonal reproduction with mutation appeared predominant in Africa and America. Two groups of diploids were identified, one from the Asia-Pacific region and a second from India, but admixed cultivars between the two genetic pools were also found. In West Africa, most cultivars were found to have been introduced from India. As expected, cultivars in Madagascar were found to originate from India and Indonesia but, surprisingly, the South African cultivars shared lineages with Japan. In the Caribbean Islands cultivars were found to have originated from the Pacific, while in Costa Rica they were found to be from India or Asia. (Chaïr *et al.*, 2016b).

SSRs have also been used to analyse diversity in northern Queensland, Australia, to demonstrate that natural breeding and population spread occurs in Australian wild taro (Hunt *et al.*, 2013). SSRs are also considered as useful markers to study the genetic diversity of taro in China (Lu *et al.*, 2011; You *et al.*, 2015).

There are no correlations between isozymes, AFLP, RAPD, SSR markers and the so-called botanical varieties (var. *esculenta* or var. *antiquorum*), which today appear as an obsolete taxonomic artefact. Molecular markers cannot differentiate clearly the type of cultivar (i.e. *dasheen* or *eddoe*) and/or particular or outstanding morphotypes.

The first genetic taro maps were developed with 169 markers, mainly AFLPs and eight SSRs, and are characterized by a high density of markers and a short map length. A quantitative trait loci (QTL) detection study conducted on two progenies revealed several putative QTLs for corm yield and corm dimensions, whereas no QTL were detected for DM content. This result is relatively unexpected since DM content is a more highly heritable trait than corm yield and dimensions. A major dominant gene, responsible for the yellow colour of the corm flesh, was also identified. No QTL have been detected for the presence of stolons. It will probably be necessary to map other progenies in order to detect QTL (or major genes) for this highly heritable deleterious trait (Quero-García *et al.*, 2006b). Genotyping-by-sequencing (GBS) has been used to identify single nucleotide polymorphism (SNP) loci in two mapping populations. Linkage maps were constructed with SNPs in association with 14 SSR markers, but the colinearity between homologous groups was low and map lengths were globally inflated (Soulard *et al.*, 2017).

In Hawaii, the taro diversity has been studied with a set of SNP markers. Phylogenetics suggests that Polynesian settlers introduced several genetically

and morphologically distinct taro varieties which were further diversified by a selection of mutants, genetic drift and occasional hybridization. It is thought that SNPs may assist taro breeders and facilitate investigations of the genetic basis of relevant phenotypes including quality, taste, disease resistance or abiotic stress resistance (Helmkampf *et al.*, 2018).

In China, the cultivar 'Xinmaoyu' is an eddoe-type characterized by its attractive flavour, glutinous texture and high nutritional value. The Trademark Office of the State Administration for Industry and Commerce awarded 'Xinmaoyu' a geographical indication certification. Consequently, an efficient molecular marker for the identification of this cultivar has been developed to facilitate its conservation and use. Through a two-step screening procedure using psbE-petL and SSR (simple sequence repeat) - SCAR (sequence characterized amplified region) markers, a pair of primers was developed to discriminate 'Xinmaoyu' from other common cultivars in Jiangsu and Fujian Provinces (Dai *et al.*, 2016).

To reveal the candidate genes of starch synthesis in taro, approximately 2.2 Gb sequence data of taro transcriptome were obtained. Sequence similarity analyses against public databases found 17,047 contigs that could be annotated with gene descriptions. Among the important metabolic pathways, 26 genes related to starch synthesis were validated by RT-PCR. It is thought that this transcriptome data set can serve in further genomic studies on *C. esculenta* (Liu *et al.*, 2015).

An attempt to identify genes that are differentially expressed in *P. colocasiae* during a compatible interaction with taro has been conducted, using a suppression subtractive hybridization (SSH) approach. A cDNA (complementary DNA) library enriched for upregulated *P. colocasiae* genes was generated and analysis of randomly selected clones revealed clear induction of these genes during infection. Reverse transcriptase quantitative PCR (RT-qPCR) assay of selected *P. colocasiae* genes showed an increased expression of these genes during infection of taro (Nath *et al.*, 2015). Less work has been done on cocoyam and other aroids. However, DNA analyses of *X. sagittifolium* in the cocoyam collection in Florida, USA, showed very little genetic variation (Schnell *et al.*, 1999). In Java, Indonesia, the intraspecific variation in 32 accessions of elephant foot yam was conducted using AFLP and the resulting dendrogram grouped the genotypes into six clusters, which did not correspond with clustering based on habitat and origin (Sugiyama *et al.*, 2006).

Retrotransposon-based molecular markers have been used within *X. saggitifolium* and *C. esculenta* to assess intraspecific variability. Retrotransposons were sequenced and long terminal repeat (LTR) primers were designed to obtain inter-retrotransposon amplified polymorphism (IRAP) fingerprints. Cluster analysis placed all accessions into two groups according to their species, and *X. sagittifolium* accessions were further divided into two subgroups corresponding to their ploidy level. It is believed that this type of marker may contribute to better germplasm management, systematic studies and breeding, as well as for exploration of the role of retrotransposons in cocoyam and taro polyploid formation

(Doungous *et al.*, 2015). Finally, using information on the location of oligonucleotide repeats in the chloroplast genome of taro, 30 primer pairs were identified to amplify and sequence polymorphic loci. The primers were tested in a range of intraspecific to intergeneric comparisons, including ten taro accessions from diverse geographical locations, four *Colocasia* spp. and three other related genera (*Remusatia*, *Alocasia* and *Amorphophallus*). These primer pairs appear suitable for phylogeographic and evolutionary studies of aroids (Ahmed *et al.*, 2013).

Microsatellite markers used to study the population structure of *Amorphophallus paeoniifolius* revealed that Indonesia and Thailand populations could be alternative centres of the gene pool, together with India. However, gene flow was apparent within the regions but was restricted among the regions (Santosa *et al.*, 2017).

## TRANSGENIC TECHNOLOGIES

Despite the various *in vitro* protocols for taro callus culture, no genetically modified cultivar has been released. Taro yields have been declining in Hawaii over the past 30 years, partly because of disease. The University of Hawaii has developed an efficient *A. tumefaciens*-mediated transformation method for taro. Compared to the particle bombardment transformation, the *Agrobacterium*-mediated transformation method obtained 43-fold higher transformation efficiency. In a laboratory bioassay, six transgenic lines exhibited increased tolerance to the fungus *S. rolfsii*, ranging from 42% to 63% reduction in lesion expansion (He *et al.*, 2008). Native Hawaiian activists organized several public demonstrations in Honolulu to protest against potential plans to produce genetically modified taros. This apparent controversy was rather futile, considering that the breeding programme in Hawaii did not use transgenic techniques (Cho, 2004).

However, the *A. tumefaciens*-mediated transformation method for taro has been improved. Embryogenic calluses were infected with a super-virulent *A. tumefaciens* strain harbouring the plant transformation plasmid that contains the rice chitinase gene. Analysis of six independent lines indicated that three had integrated a single copy of the transgene, and the other three lines had two or three copies of the transgene. Compared to the particle bombardment transformation method, which was used in the previous studies, this new transformation method obtained much higher efficiency. In a laboratory test, all six transgenic lines exhibited increased tolerance to the fungal pathogen *Sclerotium rolfsii* (He *et al.*, 2008).

## GERMPLASM CONSERVATION

Genetic resources are now distributed worldwide. Taro germplasm collections exist in many countries (Jackson, 1994) and these collections often include

other aroids as well. To date, close to 6000 taro accessions have been collected and described by various institutions. The existing collections are far from being complete and it is thought that there are probably more than 15,000 varieties of *C. esculenta*.

Most allelic diversity is found within the wild gene pool, but most morphological variation is found within the cultivars which present a narrow genetic base (Lebot, 1992). National cultivar collections are, therefore, assembling limited allelic diversity (Kreike *et al.*, 2004). If taro breeding is to have a constructive future, it is important to preserve, characterize, evaluate and exchange germplasm on an international scale.

However, exchanging taro germplasm can be dangerous since it can spread viruses, which decreases yield severely. Propagation via *in vitro* culture may produce pathogen-free taro cultivars but a certification programme and strict quarantine are required to distribute this genetic material internationally. Thanks to INEA (the International Network for Edible Aroids) a core sample of 170 elite cultivars has been selected, distributed to participating countries and a few others, including Hawaii, and is maintained *in vitro* in germplasm centres in Fiji (Secretariat of the Pacific Community, SPC) (Lebot *et al.*, 2018c).

Rationalization of the *ex situ* field collections is essential once there are more than 100 or so accessions. To rationalize a collection, a curator has to have the exact data about the existing variation, and stratification using a dichotomous key is a practical way of doing this (Fig. 24.7).

*In vitro* conservation is considered to be safer than field conservation and may be cheaper, although there are no data to confirm this. Field collections are subjected to constant genetic erosion. A problem associated with *in vitro* conservation may be the genetic stability of the conserved material. *In vitro* corm formation of taro can be achieved on Murashige and Skoog (MS) medium and the corm-forming cultures can be preserved up to 15 months at 25°C (± 2°C), whereas the shoot-forming cultures last for only 6 months. Plantlets with *in vitro*-formed corms show 100% survival in the field and develop normal uniform

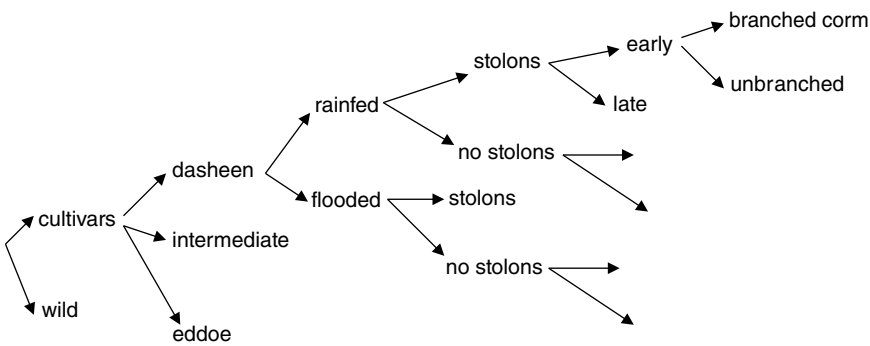


**Fig. 24.7.** Dichotomous morphological key used for stratification of germplasm collection.

corm-producing plants. The genetic stability of these plants has been tested with molecular markers and the results confirm that the *in vitro* formation of corms is a cost-effective mean for germplasm conservation (Hussain and Tyagi, 2006).

The droplet vitrification cryopreservation technique is another attractive solution. The optimum protocol involves excision of ~0.8-mm shoot tips from *in vitro* plants, then 20–40 min PVS2 (plant vitrification solution 2) exposure at 0°C, followed by rapid plunge into liquid N. Thawing is then performed at room temperature (25°C) and shoot tips are inoculated on MS medium with 0.1 M sucrose to regenerate them into plantlets 4–6 weeks later (Sant *et al.*, 2006, 2008).

A simple procedure for cryopreservation of *in vitro*-grown shoot tips of red bud taro (var. 'Hongyayu') by encapsulation–vitrification has been developed successfully. Shoot tips are excised from 8-week-old stock shoots and encapsulated into alginate-gel beads. Encapsulated shoot tips are then precultured in liquid MS medium. After dehydration at 25°C for 20 min, the encapsulated and dehydrated shoot tips are plunged directly into liquid N. After rapidly rewarming in a 40°C water bath for 3 min, they are post-cultured on solidified MS medium supplement in the dark for 3 days and then transferred to light conditions. The average survival rate is about 80% and the plantlets regenerated from cryopreserved shoot tips appear morphologically uniform. It is thought that this encapsulation–vitrification procedure may become a routine method for the cryopreservation of shoot tips (Wang *et al.*, 2015). Another cheap way of preserving genetic variation is with true botanical seeds which, when obtained in openly pollinated and highly variable populations, can preserve genes (but not genotypes) efficiently. It has been shown that taro seeds can be conserved for at least 2 years at constant 5°C or at −20°C when seed moisture content is reduced to 10%–12% and in regional trials (RTs) (21.5–34.4°C, mean 27.2°C) when seed moisture content is reduced to 7.3% (Price *et al.*, 2007). A study conducted in Vanuatu indicates that a dynamic *in situ* conservation strategy favouring broadening of the genetic base might be appropriate for taro (Caillon *et al.*, 2006). This approach has been tested with the distribution of allelic diversity in the form of introduced exotic cultivars, and is efficient to broaden smallholders' genetic bases (Sardos *et al.*, 2012).

Some work has been done on the characterization of *Xanthosoma* spp., such as that in Cuba where *X. violaceum*, *X. atrovirens*, *X. caracu* and *X. sagittifolium* have been described morphologically (Milián *et al.*, 2001). Major collections of *X. sagittifolium* from Cameroon, Equatorial Guinea, Gabon, Ghana and Togo were also made during the 1980s. Over 300 accessions were assembled and evaluated for yield and incidence of *Pythium* infection (Onokpise *et al.*, 1993, 1999; Tambong *et al.*, 1997). The collection maintained at the University of Ghana is composed of 70 *X. sagittifolium* accessions with sufficient diversity to interest plant breeders (Offei *et al.*, 2004). Root disease is also a problem in Brazil and a few species of the *X. maximilianii* × *X. hyleae* complex have resistance to *Pythium* spp. *In vitro* cultivation enables healthy propagation material to be exchanged and distributed (Giacometti and León, 1994).

# 25

# Developmental Physiology

Taro and other aroids have a similar growth cycle, although for *Alocasia* and *Cyrtosperma* it is much longer than for *Colocasia* and *Xanthosoma*, which need to be replanted every year to produce good-quality corms and cormels. The life cycle of *A. paeoniifolius* is almost identical to that of taro, except for the greater duration (at least 16 months) of the period from seed germination to flowering.

## GROWTH CYCLE

There are six major growth phases in aroids: root formation; shoot development; increase in corm size; rapid dry matter (DM) accumulation in the aerial parts; predominant corm and cormel growth to maturity stage; and, finally, corm and cormel dormancy.

### Phase one: establishment of the plant with root formation and leaf production

When a sucker, stolon or headset is planted, the propagule starts to produce new roots very rapidly, between 2 and 6 days after planting (DAP), depending on the soil moisture. During this phase, the plant develops roots using the water and nutrient reserves within the propagule. The greater the weight of the propagule, the faster it will produce roots to anchor the young plant and begin uptake of water and nutrients. This phase usually lasts from 1 to 3 weeks after planting (WAP) until a functional root system can feed the plant.

### Phase two: rapid root and shoot development with corm initiation

From 3 to 10 WAP, the propagule will produce new leaves rapidly, which will allow the young plant to produce a functional canopy composed of four to five well-developed leaves.

### Phase three: maximum root and shoot growth with rapid increase in corm size

From 10 to 20 WAP, the plant is producing a vigorous but shallow root system, radiating for 1–2 m around it. It is also producing new leaves regularly to replace the senescing ones. There is little variation in the number of leaves per main stem between taro genotypes. For dasheen-type varieties, this is five to six, depending on whether the oldest leaf is senescing and if the youngest leaf is fully open.

### Phase four: rapid DM accumulation in the aerial parts

Between 20 and 30 WAP, the plant reaches its greatest height and there is a significant accumulation of DM in the petioles and laminas, which become more stiff and leathery.

### Phase five: senescence period of decreasing root and shoot growth with continued increase in corm and cormel size

From 25 WAP onwards, the height of the plant will decline and the main corm and side cormels will bulk and accumulate DM until the plant reaches maturity, which varies from 30 to 40 WAP according to taro genotypes.

### Phase six: dormancy and decreasing corm weight due to new vegetative growth

After 40 WAP, taro plants usually enter into dormancy for 1–2 months, depending on the climate. Vegetative growth will then start again (Fig. 25.1). In annual cultivars (*C. esculenta* and *X. sagittifolium*), the quality of the corm and cormels deteriorates when the plant uses its own reserves to initiate new vegetative growth. It is, therefore, necessary to replant cultivars annually. In temperate countries, dormancy is induced by low temperatures. Dormancy is also a significant phenomenon in some subtropical countries, such as New Caledonia, and begins in autumn (from April to May onwards) and aerial parts can disappear completely before they sprout again in November–December (Ivancic and Lebot, 1999).

In cocoyam, the first 10 WAP are characterized by low rates of DM accumulation with only the petioles and the leaves producing significant vegetative growth. From 10 to 30 WAP, roots, petioles and leaves accumulate DM rapidly. From 30 WAP onwards, there is a significant increase in DM in the corm and cormels only; the DM content reaches a maximum of 46% at 36 WAP for early-maturing cultivars and at 45 WAP for late-maturing cultivars. Cormel DM

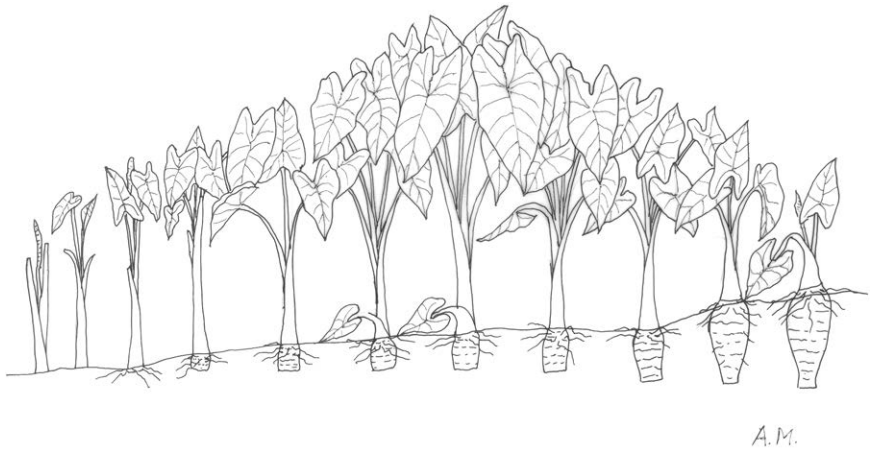


**Fig. 25.1.** Growth cycle of taro (*C. esculenta*).

accumulation continues after the leaf area index (LAI) has reached a maximum at 28 WAP. Cormel bulking during the period of declining LAI occurs because older senescing leaves contribute assimilates to the corm and cormels, and because the products of current photosynthesis are being translocated to new leaves as well as to corm and cormels. Cocoyam corm is not edible and competes for assimilates with cormels. Also, a reduction in leaf area (LA) reduces corm growth and benefits cormel growth. Ultimately, cormel sprouting – and consequently sucker development – render the cormels non-marketable (Goenaga and Singh, 1991). In eddoe-type cultivars of taro, corms and cormels are competing sinks for photosynthates. The plant can be considered harvestable when DM accumulation in the cormels is greater than in the central corm (Goenaga, 1995).

When taro plants grow from true seeds, it takes about 5–9 months from germination to flowering. The growth cycle of a taro plant can be analysed from its corm surface. This surface shows several types of residuals, such as those from leaves, stolons or suckers, floral clusters and roots (Fig. 25.2). The age of the plant can be estimated from the number of leaf residuals and the time needed for the development of each new leaf. Analysis of floral cluster residuals (the number of clusters and the number of peduncle residuals per cluster) gives an idea of the flowering ability of the plant. The changes in the corm diameter indicate changes in environmental conditions. Narrow portions usually indicate dry periods or periods of flooding when the corm was submerged.

The pattern of partitioning of taro during its growth and development is somewhat different from other root crops which present two types of partitioning.

**1**. Phasic partitioning occurs when early vegetative growth is characterized by shoot and fibrous development and when the storage organ growth begins later in the growth cycle.
**2**. Continuous partitioning occurs when storage organ growth begins early in the seedling stage and continues throughout the vegetative period of plant

**Fig. 25.2.** Taro (*C. esculenta*) corm with surface showing residuals of leaves and roots. The bottom end corresponds to the original headset planted, on which the corm has gradually developed (photo: V. Lebot).

growth. A balance between vegetative (shoot and leaf) growth and storage organ growth is maintained throughout the growing season.

Taro and other aroids exhibit continuous partitioning with an almost linear increase in fresh and dry weights, like cassava. Sweet potato and yam develop through phasic partitioning. The continuous partitioning of aroids is similar to that of sugarbeet.

## PHOTOPERIODISM

Day length variation has a limited effect on DM corm yield (see Table 25.1). To study photoperiodism incidence, two popular Hawaiian varieties were planted at two different altitudes (280 m and 640 m) with two different mean temperatures and with different photoperiod treatments (natural day length, plus 0.5 h, 14 h, 17 h and 20 h). The extension of photoperiod had a noticeable effect on leaf appearance rate. Changes in photoperiod at the 640 m site (lower mean temperatures) had a significant effect on corm dry weight, which was lowest for the long photoperiod of 20 h. Leaf appearance, leaf opening and DM production were not affected by increasing the photoperiod (Prasad and Singh, 1991).

The rate of photosynthesis increases with growth and reaches a maximum 2 weeks after complete leaf expansion. It remains at this level for approximately 10 days and then declines with senescence. The maximum rate of photosynthesis of a single leaf under full light saturation is about 30–35 mg

**Table 25.1.** Main effect of photoperiod on taro.

| Photoperiod | Cormel number | Dry weight (in g/plant) | | |
|---|---|---|---|---|
| | | Corm | Cormels | Total biomass |
| Natural | 16.9 | 397.3 | 500.4 | 989.8 |
| Natural + 0.5 h | 18.7 | 367.9 | 541.9 | 1023.6 |
| 14 h | 21.0 | 406.4 | 568.0 | 1073.3 |
| 17 h | 20.4 | 428.3 | 583.7 | 1098.7 |
| 20 h | 22.3 | 361.8 | 572.5 | 1002.2 |

Source: adapted from Prasad and Singh (1991).

**Table 25.2.** Effect of shade on taro.

| | Fresh corm Yield kg/ha | Dry corm Yield kg/ha | Corm dry matter % | Shoot dry weight kg/ha | Sucker dry weight kg/ha | Total plant dry weight kg/ha | Suckers no. |
|---|---|---|---|---|---|---|---|
| Shade | 5182 | 1614 | 31.0 | 404 | 1619 | 3637 | 93 |
| No shade | 4977 | 1424 | 28.5 | 271 | 987 | 2862 | 69 |

Source: adapted from Rogers and Iosefa (1993).

$CO_2$ for lower leaves but only 20 mg for upper and middle leaves (Sunell and Arditti, 1983).

The potential photosynthesis per plant is determined by plant density, which controls the sunlight area available. Aroid plants have a dominant meristem and their leaves expand to cover the area fully so that the photosynthesis rate per plant reaches a maximum value and declines. In Egypt, the growth characteristics, different physiological parameters, photosynthetic activity ($14CO_2$ fixation) and the translocation rate of photoassimilates have been studied in local genotypes to determine the possible use of these parameters as selection criteria for different cultivars. There is a positive correlation between photosynthetic activity, translocation efficiency and total yield, and these are found to be useful for reliable selection (Moussa and Salem, 2006).

Aroids are shade-tolerant crops. Taro plants grown at 30% of full sunlight have increased stomatal and chlorophyll density, probably increasing photosynthetic efficiency at low levels of light (Onwueme and Johnston, 2000). Results of experiments conducted under artificial shade provided by a canopy of 50% shade cloth indicate that plant height and LA are higher under shaded conditions compared to full sunlight. Total plant biomass is also increased by shade (Rogers and Iosefa, 1993) (Table 25.2). The corm yields are not affected by shade, but the number and weight of plant suckers are increased. Corm percentage DM, which reflects quality, is higher under

shade. The fact that total plant biomass is increased by shade indicates greater photosynthetic efficiency.

## TEMPERATURE

The preferred temperature range for maximum photosynthesis is between 25 and 35°C, with 30°C being the optimum. Leaf appearance rate for taro is correlated positively with temperature; the duration of leaf appearance and leaf opening are both longer when the temperature is lower than the optimum conditions. Days to maturity increase with lower temperature. The lower the temperature, the smaller the corm and cormel yield (Prasad and Singh, 1991). Low temperatures (below 15°C) generally lead to dormancy of the corm and cormels. Taro does not tolerate freezing temperatures.

## NUTRITION

Aroids can exhibit spectacular chlorosis when nutrient deficiencies occur. Taro is considered to be a heavy feeder and is often planted first in a crop rotation, just after the fallow. It is quite sensitive to mineral deficiencies and responds well to fertilizers. Tentative critical nutrient concentrations have been measured, the plant tissue selected as an index tissue being the youngest, fully expanded leaf blade (O'Sullivan *et al.*, 1996) (Table 25.3).

**Table 25.3.** Tentative critical concentrations and adequate concentration ranges for a number of nutrition disorders.

| Disorder | Critical concentration | Adequate range |
|---|---|---|
| Deficiency of: | | |
| N (%) | 3.7 | 3.9–5.0 |
| P (%) | 0.33 | 0.5–0.9 |
| K (%) | 4.60 | 5.0–6.0 |
| Ca (%) | 2.0 | 2.6–4.0 |
| Mg (%) | 0.15 | 0.17–0.25 |
| S (%) | 0.26 | 0.27–0.33 |
| Fe (mg/kg) | 56 | 68–130 |
| B (mg/kg) | 23 | 26–200 |
| Mn (mg/kg) | 21 | 26–500 |
| Zn (mg/kg) | 22 | 22–50 |
| Cu (mg/kg) | 3.8 | 5.8–35 |
| Toxicity of: | | |
| Mn (mg/kg) | 1133 | 26–500 |
| Zn (mg/kg) | 400 | 22–250 |

Source: adapted from O'Sullivan *et al.* (1996).

Experiments conducted in Papua New Guinea (PNG) to assess the nutrient requirements of taro have shown that, when plants are fertilized with 100 kg N/ha (sulfate of ammonia), 50 kg P/ha (triple superphosphate) and 100 kg K/ha (muriate of potash), they produce twice the root biomass of unfertilized taros. Root biomass develops within 120 DAP but does not increase thereafter (Table 25.4). Taro is, therefore, highly responsive to nutrient uptake during phase three of its growth cycle (around 18 WAP), when the plant needs to produce a vigorous root system. Subsequent plant yield depends on its ability to develop its whole root system during this critical period.

In Sri Lanka, the response of *X. sagittifolium* to various K rates and times of application shows that K deficiency delays cormel initiation. Conversely, high levels of available K enhance the translocation of photosynthates during the early stage of growth, thereby increasing the availability of carbohydrates for cormel initiation. The number of cormels per plant then increases with increasing levels of K (Sangakkara, 1990) (Table 25.5).

**Table 25.4.** Biomass production and dry matter content of unfertilized and fertilized taro.

| | | Midseason (126 DAP) | | At harvest (231 DAP) | |
|---|---|---|---|---|---|
| | Plant part | Unfertilized | Fertilized | Unfertilized | Fertilized |
| Dry weight mg/ha | Roots | 0.26 | 0.52** | 0.51 | 0.50 |
| | Corms | 0.82 | 1.21 | 2.53 | 6.99* |
| | Leaves | 0.68 | 2.13* | 2.00 | 3.64* |
| | Total | 1.75 | 3.86* | 5.04 | 11.13* |
| Dry matter content (%) | Roots | 4 | 5** | 12 | 11 |
| | Corms | 21 | 19 | 30 | 30 |
| | Leaves | 8 | 7 | 16 | 16 |

Leaf biomass includes petioles. * and ** indicate significant differences at $P < 0.05$ and $P < 0.001$, respectively. DAP, days after planting. Source: adapted from Hartemink and Johnston (1998).

**Table 25.5.** Effect of K on the number of cormels per plant of cocoyam 9 months after planting.

| | 0 | 175 | 200 | 225 | 250 | 275 | LSD |
|---|---|---|---|---|---|---|---|
| Application | kg $K_2O$/ha | | | | | | $p = 0.05$ |
| Basal | 0.0 | 5.2 | 5.7 | 7.1 | 10.6 | 9.8 | 0.84 |
| Split | 0.0 | 3.1 | 4.3 | 5.4 | 5.8 | 6.1 | 0.59 |

Basal = all K at planting. Split = 100 kg $K_2O$/ha at 90 days after planting, the remainder at planting. LSD: least significant difference Source: adapted from Sangakkara (1990).

## WATER DEFICIT AND STRESS

Aroids are known for their relatively high water requirements. They produce large leaves and transpiration is related directly to LA. High rainfall is needed during the first 20 WAP, corresponding to the period of maximum leaf development. Drier conditions can be tolerated from then until harvest. Mean yields for irrigated taro exceed non-irrigated crops, in some cases by as much as 50% for the same genotype. This is, however, genotype-dependent as some genotypes are typical upland types and do not tolerate flooded conditions. *X. sagittifolium* is much more tolerant to drought and sensitive to waterlogging. However, it is observed that yields always increase with higher irrigation, even though total rainfall during the growth cycle exceeded standard pan evaporation (SPE). A severe reduction in yield is observed in cocoyam if the depth of the water table is reduced from 0 to 15 cm.

Taro leaf information can be used to determine how evapotranspiration (ET) varies with growth stage, and is also useful to predict foliage biomass production. Taro ET is estimated from the SPE and the ratio of ET to SPE. This ratio is related closely to the LAI. A ratio between 0.9 and 1.0 is appropriate when LAI is less than 1.0, before canopy closure. It is between 0.73 and 0.75 when LAI is greater than 1.0, after canopy closure. It is possible to estimate the ET requirements for irrigation scheduling or for water resource planning and management in accordance with available SPE data and the ET/SPE ratio (Shih *et al.*, 1988).

Most water loss occurs during summer, when temperatures are high. Genotypes differ in osmotic values, solute content and wilting point. Taro leaves can secrete water at the tip of their laminas through guttation, and the amount of water exuded in field conditions varies from 10 ml to 23 ml per night (Sunell and Arditti, 1983).

Drought tolerance of taro is a major objective in breeding programmes. In India, a taro hybrid, along with its parents, was evaluated for water stress tolerance under polyethylene glycol- (PEG-) mediated osmotic stress conditions. The plantlets were hardened and transferred to pots for evaluation of various parameters under stress conditions. Significant variations were observed in plant height, number of leaves, LA, percentage relative water content, chlorophyll stability index and percentage injury by desiccation and yield. The hybrid showed more tolerance to osmotic stress with minimum yield reduction. It is thought that the development of drought-tolerant lines is, therefore, feasible (Sahoo *et al.*, 2006).

In South Africa, it is observed that taro landraces are susceptible to drought stress under rainfed conditions. Drought avoidance is achieved through stomatal regulation, energy dissipation and reduced canopy size. Drought escape is observed through phenological plasticity and, under water-limited conditions, taro matures earlier. Some landraces show greater adaptability to limited water availability under rainfed conditions (Mabhaudhi and Modi, 2015).

In Madeira, Portugal, significant variation exists between taro cultivars for drought stress tolerance and yield stability. Drought-tolerant and susceptible cultivars have been identified and it is observed that different cultivars have different drought avoidance and tolerance strategies to cope with water scarcity. Better yield performers minimized biomass and canopy loss. Drought tolerance was observed in cultivars that presented low potential yield, but efficiently transferred resources to enhance corm formation. Among the 33 accessions evaluated, two local Madeiran cultivars showed high yield stability and may be considered as suitable parents for breeding programmes (Ganança *et al.*, 2017).

C and N isotopic compositions ($\delta 13C$ and $\delta 15N$) are used to provide useful information on the chemical processes involved in C and N as physiological indicators. They can be used to assess taro's response to drought stress and to clarify its water use efficiency (WUE) and carbon isotope discrimination ($\Delta 13C$). A study conducted in Madeira attempted to determine how taro $\delta 13C$ and $\delta 15N$ are related to the whole-plant biomass, WUE and $\Delta 13C$ under drought conditions. Three accessions appeared to be drought-tolerant genotypes and showed the highest levels of WUE and nutrient acquisition. All $\delta 13C$ values indicated relatively open stomata for C3 plants. It appears that WUE is improved under drought conditions by minimizing water loss through evapotranspiration. A negative correlation between taro shoot $\Delta 13C$ and plant WUE is observed and is consistent with previous reports for C3 plants. It is suggested that $\Delta 13C$ values could be used for screening germplasm for WUE, while $\delta 15N$ may serve as a physiological indicator of stress (Gouveia *et al.*, 2019).

## CLIMATE CHANGE ADAPTATION

The most important factor limiting yield is the availability of water. With proper irrigation or abundant rainfall and good soil fertility it is not unusual to obtain fresh corms weighing between 6 and 10 kg. In traditional cropping systems, taro yields of 60–110 t/ha have been recorded. Cocoyams can produce between 3 and 5 kg cormels with proper solar radiation and soil fertility. Giant taro corms can reach the impressive weight of 10–15 kg but, for all these species, a reduction in plant spacings also reduces yields.

The use of validated crop models may prove useful to generate information regarding taro adaptation to climate change. However, crop models have not been fully tested for taro landraces. A study conducted in South Africa aimed to evaluate the Food and Agriculture Organization's (FAO's) AquaCrop model for a taro landrace. Model simulations for biomass and yield were very satisfactory. However, the model showed limitations with regard to canopy cover of taro under rainfed conditions. This suggests that this model has limitations for effectively capturing taro growth under water deficit conditions. It is assumed that these limitations may be due to the particular nature of taro growth,

which is not adequately taken into consideration in the FAO's model for root and tuber crops. Nevertheless, the model provided a baseline for further work aiming at adapting this model for taro. It is suggested that the model should include the vegetative growth index (VGI) which captures taro's canopy traits. The model revealed that the taro 'Umbumbulu' landrace was drought tolerant (Mabhaudhi *et al.*, 2014).

Taro cultivars are known to present a relatively narrow genetic base in most countries where they have been introduced clonally, and this is the case in Africa. As genetic variation is the most important source of adaptive variation, it appears interesting to increase taro diversity in these countries to strengthen smallholders' capacity to adapt to climate change. Farmers will assess the suitability of introduced cultivars to satisfy their agronomic needs and will use this genetic variation to adapt to climatic change. A global experiment was conducted to compare the performances of cultivars and improved hybrids distributed to farmers in 14 different countries in Asia, Africa, the Americas and the Pacific. The approach was participatory and aimed to distribute genotypes to farmers in the shortest time possible. In most participating countries it worked well, but it was observed that in South Africa the landraces performed better than the introduced and improved hybrids, while in other countries different hybrids performed well and in all cases they outperformed farmers' landraces (Lebot *et al.*, 2018c).

# 26

# Agronomy

Aroids can be grown throughout the year in the wet tropics. They are best adapted to high temperatures, a moist environment and high humidity. Evenly distributed rainfall, between 200 and 300 mm/month, is ideal for optimum growth and production. Irrigation is, however, necessary for taro and swamp taro in low rainfall areas, while cocoyam, giant taro and elephant foot yam (*Amorphophallus paeoniifolius*) are more drought tolerant. For all species, and for a given genotype, the time needed to reach maturity varies according to temperature, sunlight and water availability.

## SEED SYSTEMS AND PROPAGULE SELECTION

Different parts of the taro plant (corm, cormels, suckers, stolons) can be used for rapid multiplication when a clone is selected. Experiments using single-node cuttings from stolons obtained from plants raised with drip irrigation give an average multiplication ratio of 1–24 (Pardales and Dalion, 1986).

A promising new technique has been developed in Western Samoa in which selected clones are propagated rapidly. The corms are dipped in solutions of gibberellic acid ($GA_3$) at concentrations of 500 ppm for 10 min. This treatment induces the corms to produce stolons (rather than suckers, when untreated with $GA_3$). Single-node cuttings from the stolon are then sprouted. By this means, a large number of plantlets can be produced from a single corm. In 11 weeks, the propagation ratio is 1–120. The higher concentration of $GA_3$ gives the best results (Faatonu *et al.*, 2004).

A rapid *in vitro* propagation system developed in Fiji and evaluated against other multiplication protocols has proved to be superior (Taylor *et al.*, 2004a) (Fig. 26.1). It is based on Murashige and Skoog (MS) medium supplemented with sucrose and 8 g/l agar, and consists of three stages. This protocol has been compared with MS medium supplemented with 150 ml deproteinized coconut water. Both methods use a temperature of 25°C and a photoperiod of 16 h but give different results after 9 weeks (Table 26.1).

**Table 26.1.** Sucker numbers obtained from two different multiplication systems.

| Cultivar | Method | Explant no. at start of Stage 1 | Sucker no. at end of Stage 1 | Sucker no. at end of Stage 2 | Sucker no. at end of Stage 3 |
|---|---|---|---|---|---|
| CPUK | Taylor | 7 | 19 | 21 | 212 |
| | Chand | 7 | 13 | 9 | 48 |
| TNS | Taylor | 7 | 13 | 20 | 77 |
| | Chand | 7 | 8 | 12 | 25 |
| Hybrid | Taylor | 7 | 11 | 11 | 38 |
| | Chand | 7 | 6 | 9 | 12 |

Source: adapted from Taylor *et al*. (2004a).


**Fig. 26.1.** Taro (*Colocasia esculenta*) *in vitro* plantlets in pouches for international distribution (photo: V. Lebot).

In Taiwan, taro meristems cultured on MS medium supplemented with 6-Benzyladenine (BA) and indole-3-acetic acid (IAA) gave the best explant establishment and development. It is believed that this *in vitro* propagation protocol provides a uniform production system, is easy to manage and yields high-quality cormels for commercial production (Ko *et al.*, 2008).

Once *in vitro* cultured plantlets have been produced they can be acclimatized in a hydroponic system. In Vietnam, *in vitro* taro plantlets 5 cm in height were derived from mass propagation by shoot tip culture on MS medium. Two acclimatization systems were compared: normal acclimatization in soil and acclimatization in a hydroponic system carried out in a Styrofoam™ box, after 15 or 30 days. It is observed that microcorms are formed early after culturing in hydroponics for 15 or 30 days and that plantlet growth is also enhanced

compared to soil culture. The survival rate, plant height, number of leaves and number of microtubers of plantlets in the hydroponic system were also higher than those in soil culture. Finally, once transferred to the field, the taro plantlets cultured in hydroponics also had a superior performance compared to those from the soil system (Nhut *et al.*, 2004).

The efficiency and impact of using taro tissue-cultured plants has been demonstrated. In Fiji, varieties grown *in vitro* from shoot tips, and pathogen-tested (PT) plants were compared with field-collected (FC) plants over 3 years. For three varieties, there were no significant differences between heights and corm yields of PT and FC plants. However, for a fourth variety, PT plants outgrew FC plants and yielded more than double. A major change appeared to be in response to Dasheen mosaic virus (DsMV) infection. By the 3rd-year trial, FC plants per plot showed virus symptoms compared to PT plots; but, whereas FC plants were stunted and low yielding, PT plants were similar in height and yield to the other varieties (Jackson *et al.*, 2001).

In Kenya, a study conducted to evaluate a low-cost protocol for the micropropagation of three varieties of taro (dasheen, eddoe and wild) compared three media types: Omex foliar feed (LCM1), Stanes' micronutrients (LCM2) and micro food (LCM3) as substitutes for MS media. The results showed significant differences in the shoot generation for eddoe and wild varieties in 'Omex' and 'Stanes' media, respectively, compared to 'micro food' and MS. Plants grown in MS media and 'micro food' had their longest heights compared. All the regenerated plants were similar in morphology and vigour. Media cost was reduced by 95% for 'Omex', and by 96% for both 'Stanes' and 'micro food', indicating that it is possible to drastically reduce the cost of conventional micropropagation (Ngetich *et al.*, 2015).

In India, elephant foot yam is becoming an important cash crop but DsMV is the major constraint (Srinivas and Ramanathan, 2005). DsMV and other unreported putative viruses are involved in a mixed viral mosaic infection. *In vitro* propagation of corm bud tips for virus-free plantlet production has been carried out. A 100% survival rate was recorded on hardening in a sand: soil:coir pith (1:1:1) mixture, and 84% of regenerated plantlets were found to be virus-free when indexing 21 *in vitro* lines with species-specific/genus-specific serological and molecular diagnostic techniques. Transcriptome sequencing was carried out and none of the known potyviruses were traced in the transcriptome profiles of supposed virus-free plants, confirming complete potyviruses elimination. Also, when the virus-free lines were hardened in pots maintained in a net house, disease symptoms were not observed (Kamala and Makeshkumar, 2015).

When selecting propagules from the previous crops, plants with pest and disease symptoms should be carefully avoided when sourcing planting material, as they are the main cause of crop infections.

For cocoyam, corm-setts weighing 150–200 g, or suckers weighing between 200 and 400 g, are ideal for direct field planting. Taro planting materials

are prepared from the suckers or the top (head) of the main corm. The headset consists of the upper 1–2 cm section of the corm and the first 30 cm of the petiole. Headsets also can be prepared from the suckers but, in most cases, cormels are not cut and are planted whole. The heterogeneity of the propagules (suckers, stolons or headsets) results in highly variable performance of the resulting individual taro plants, so planting material should be sorted before intensive cultivation. Heavy headsets (300–700 g) are more tolerant to drought and, in case of water shortage, propagules that have not survived should be replaced to maintain an even plant density during crop development. In good growing conditions, heavy headsets will result in higher yields.

Variation between plants within the same genotype is considerable, however, even if the propagules have been sorted properly. This clonal variation has been computed, using calibrated headsets of 500 g, for five major traits in Vanuatu with 96 varieties originating from different countries. Intraclonal variation is quite high for the number of stolons per plant. Asian cultivars exhibit a remarkably high intraclonal variation of the number of stolons per plant within the same variety, which indicates that this trait is not stable when present. The intraclonal variation of the number of suckers per plant is also high and not stable. The mean intraclonal variation for corm yield from different plants of the same genotype also varies significantly (Lebot *et al.*, 2004) (Table 26.1).

In the Phichit plain, Thailand, taro growers develop and calibrate their own healthy propagating materials which are first raised in home-made nurseries in their backyards, where they have access to permanent water for generous irrigation. In Futuna, Polynesia, growers apply pig manure in their taro nurseries, maintained next to their houses, in order to produce heavy propagules rapidly for transplanting in irrigated plots, to maximize crop earliness and productivity.

Taro and cocoyam can be grown from suckers split longitudinally in halves or quarters with their attached pieces of corms but, once established, these materials result in a reduced leaf area (LA) per plant. This technique should preferably be used for raising plants in nurseries but not for direct field planting.

In Japan and other temperate countries (northern China, Egypt, New Zealand), planting can be done when propagules start to sprout. Some studies conducted to elucidate the effect of harvesting time and low-temperature treatment on taro

**Table 26.2.** Mean intraclonal variation measured on five traits for 96 cultivars of taro.

| | Trait measured | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Height (cm) | *cv (%)* | Leaf (cm) | *cv (%)* | Number of stolons | *cv (%)* | Number of suckers | *cv (%)* | Corm (g) | *cv (%)* |
| Intraclonal mean | 77.6 | *(17.8)* | 35.0 | *(16.8)* | 4.9 | *(118.2)* | 5.6 | *(69.1)* | 1094 | *(20.8)* |

Source: adapted from Lebot *et al.* (2004).

corm sprouting indicate that the sprouting rate is low in corms planted just after harvesting or after storage at 25°C for 60 days. Low-temperature treatment at 3°C for 15 days or at 10°C for more than 30 days promotes sprouting. In Japan, taro corms remain dormant from late September to early October, but the extent of dormancy varies with cultivar (Murakami *et al.*, 2007).

## SOIL PREPARATION

Aroids prefer well-drained soil but taro and swamp taro also thrive in soil with a tendency to waterlogging or which is saturated for long periods. Upland taro and other aroids can also be cultivated on slopes in marginal soils when rainfall is sufficient. In most countries, soil preparation is never mechanized and the field is not levelled.

Flooded taro is cultivated in low-lying areas, in valleys with alluvial soils and where the pond system is very similar to that used for irrigated rice in South-east Asia. The constant movement of water is important to keep its temperature low and so avoid root rots. Taro fields are prepared by breaking the soil after the plots have been flooded completely and soaked for a few days. To control weeds during land preparation, the plot is rotavated two to three times at 1-week intervals. The water depth is maintained at 5 cm to prevent weed growth. Farmers use water buffalo and oxen to pull instruments when tractors are not available. The plots are then left for a few days to allow the soil to settle before the propagules are planted. In northern Vietnam, on the Red River plain near Hanoi, taro is planted in winter after rice, on raised beds approximately 1 m wide and 20 cm high and the plots are flooded. In the high plateaus of Madagascar, taro is also planted after rice but in holes, the plots being drained.

For upland taro, existing weeds are first slashed by hand, burnt or kept for use as mulch. The soil is prepared in the planting spot by hand with a sharp spade or a planting stick. A hole of approximately 30 × 30 × 30 cm is dug and the propagule placed at the bottom. The holes will be filled slowly with compost or organic matter as the plant matures. The holes provide humidity and the roots grow into moist soil. The corm then develops in the upper part of the hole. Cocoyams are not planted as deep as taro and, in intensive cropping systems in Nicaragua and Costa Rica, field preparation is increasingly mechanized. The field is first ploughed and rotavated, and the soil is ridged or furrowed.

## PLANT DENSITIES AND CROP ESTABLISHMENT

Overall yield of taro may be improved by increasing the number of plants per unit area. However, genotypes differ significantly in their tolerance to high density, and the majority of traditional cultivars are adapted to intermediate densities (i.e. 0.8 m × 0.8 m, 0.7 m × 0.8 m, 0.5 m × 1.0 m). When the density

is too high (i.e. 0.3 m × 0.3 m), the leaves die earlier, the plants have fewer leaves and are frequently affected by leaf diseases. In fact the closer the spacing, the smaller the corm, and export markets usually require an average 2 kg corm, which can be obtained with intermediate spacing. In traditional cropping systems, spacing is usually wider and plants are intercropped. The average corm yield is also higher (4–6 kg/plant). In Hawaii, taro spacing ranges from a close 45 × 45 cm to a wide 1 × 1 m (10,000 plants/ha) but, with wide spacing, weed control is a serious and expensive problem. In Fiji, 60 × 60 cm triangular spacing is recommended.

In Ethiopia, the minimum planting density (15,000 plant/ha) was shown to outscore higher densities in vegetative growth, dry matter (DM) production, marketable and total yield per plant. However, the right choice of planting date is also an important management practice, and late March planting was identified as the most suitable; however, the availability of soil moisture is more important than the time of planting (Dessa *et al.*, 2016).

In the Dominican Republic, closer spacing significantly reduces the number of suckers per plant during the dry season, when moisture is a limiting factor (Robin, 2004) (Table 26.2).

In PNG, experiments have shown that the popular taro cultivar 'Numkowec', planted at a spacing of 1.0 × 0.25 m (40,000 plants/ha), produces a 66% yield increase from standard check (1.0 × 1.0 m) (Sar *et al.*, 1998; Gendua *et al.*, 2001) (Table 26.3).

The yield of taro increases significantly at 40,000, 80,000 and 160,000 plants/ha. The mean corm weight is reduced at all planting densities above 10,000 plants/ha. Plant densities between 20,000 and 60,000 plants/ha can give optimum yields in terms of marketable individual corm sizes (Gendua *et al.*, 2001). The proper plant spacing for a particular farm does not depend on the final yield only but also on other factors, such as the uniformity of individual corm size to meet various market demands; the weed maintenance programme; the number of propagules the farmer can afford to prepare; and,

**Table 26.3.** Mean number of suckers per taro plant for different spacing during wet and dry seasons in two locations in the Dominican Republic.

| | Number of suckers/plant | | | |
|---|---|---|---|---|
| | Grand Bay area | | Wet area | |
| Spacing (cm) | Wet season | Dry season | Wet season | Dry season |
| 55 × 55 | 3.4 | 3.5 | 4.0 | 4.3 |
| 65 × 65 | 3.6 | 4.2 | 4.1 | 4.5 |
| 75 × 75 | 3.9 | 5.1 | 4.4 | 5.7 |
| Standard error | 0.51 | 0.58 | 0.4 | 0.42 |

Source: adapted from Robin (2004).

finally, the time of year the plot is planted. Farmers may consider planting with a wider spacing during cooler months and with a narrower spacing during hotter months to optimize corm size and production.

Optimal density depends also on the phenotypic characteristics of genotypes. Density-tolerant plants have erect leaves with smaller laminas set vertically and supported by long and erect petioles. There is also another, less important type of density-tolerant plant which is characterized by extremely short petioles and small laminas. Breeders prefer tall, erect plants, however, some of which have been found to be resistant to leaf blight (Ivancic *et al.*, 1996).

In Indonesia, experiments showed that there was no significant interaction between NK fertilizer application and plant density on growth and yield of taro. The NK fertilizer application significantly influenced LA, net assimilatory rate (NAR), fresh corm yield and starch content. Plant density, on the other hand, only significantly influenced the number of corms per plant and starch content. The optimum application rate of NK fertilizers was 127.04 kg N/ha (282.3 kg of urea/ha) and 164.6 kg $K_2O$/ha (274 kg KCl/ha) with fresh corm yield of 16.7 t/ha, while the highest starch content (29.5%) was obtained at plant density of 18,000 plants/ha (Suminarti *et al.*, 2016).

## INTERCROPPING

In traditional agroforestry rainfed systems, intercropping of aroids is the rule. In Hawaii, taro yields measured at harvest show that intercropping does not adversely affect the corm yields of the 'Bunlong' variety. These yields range from a low 37 t/ha for the control to more than 50 t/ha with groundnut. There were no significant statistical differences between treatments but there are various other benefits from intercropping with beans and legumes (Peña, de la and Melchor, 1993) (Table 26.4).

**Table 26.4.** Effect of planting density on taro yield in Papua New Guinea.

| Spacing (m) | Plant population | Mean corm weight (g) | Yield (t/ha) | Marketable yield (t/ha) | Non-marketable yield (%) |
|---|---|---|---|---|---|
| 1 × 1 | 10,000 | 839* | 14.85 | 9.33 | 10.2 |
| 1 × 0.5 | 20,000 | 576* | 16.27 ns | 9.17 | 13.0 ns |
| 0.5 × 0.5 | 40,000 | 445* | 23.29* | 15.88 | 8.7 ns |
| 1 × 0.25 | 40,000 | 479* | 24.64* | 16.41 | 13.0 ns |
| 0.5 × 0.25 | 80,000 | 340* | 26.84* | 15.21 | 15.3 ns |
| 0.25 × 0.25 | 160,000 | 295* | 33.55* | 13.75 | 43.3* |

*Significantly different from standard check ($P < 0.05$), ns = no significant difference. Source: adapted from Sar *et al*. (1998) and Gendua *et al*. (2001).

In Nigeria, taro, cocoyam and rice thrive well in similar ecologies and an efficient utilization of the land is achieved when these are intercropped. It has been shown that growing rice with taro as an intercrop is more profitable than rice or taro alone. The recommended planting is of two rows of taro at a spacing of 60 × 60 cm, alternating with four rows of rice. Cultivation practices such as weeding, fertilizer application and water management remain the same as for single crop management.

## WEEDING

Proper weed control during the first 4 months of growth reduces competition for moisture, light and nutrients. In traditional systems, weeding is done by hand every 2–3 months and represents the only input during the whole growth cycle (8–10 months). In commercial cultivation, taro is planted in lines and the early establishment of leaf canopy cover is favoured by frequent applications of manure or fertilizers and adequate irrigation. In this case, the methods of minimizing weeds include proper field preparation and periodic tilling of newly emerged weed seedlings with hand-drawn tillers. Weeding taro at 30, 60, 90 and 120 days after planting (DAP) produces higher yields than weeding or rototilling at 60 and 120 DAP.

In flooded systems, the water surface contributes efficiently to the maintenance of weed-free ponds. However, some filamentous algae species can present serious problems and necessitate weekly removal. In Futuna, Polynesia, these algae (known as *limu*) are pulled out by hand and piled in a heap in the middle of the pond. If they are not removed on a regular basis, the flow of the water slows down, its temperature increases and *Pythium* rots develop.

Contact herbicides such as Gramoxone™ can be sprayed between the lines when side protectors are used. Systemic herbicides (glyphosate) are also very efficient but are rarely used. Taro is, in fact, very sensitive to glyphosate, which can cause interveinal chlorosis and distortion of the emerging leaves. A high dosage causes 'shoestringing' in the emerging leaves and finally kills the plant. Drift control by spraying with thickening agents during windless early mornings is a necessary measure to avoid damage.

Planting taro or cocoyam directly into a dried mulch is a convenient weed control technique. A legume (*Glycine*, *Pueraria* or *Mucuna* spp.) is used as a cover crop during the fallow and then sprayed with herbicide to produce a thick cover of dried biomass through which holes are dug to plant the propagules. In traditional cropping systems, taro is also planted through an existing sweet potato crop which acts as a ground cover to control the weeds. However, the sweet potato needs to be harvested before the taro overshades the crop. If not, the yield will be diminished considerably.

Mulching with organic or artificial materials contributes greatly to weed control in upland taro, although it does not increase yields significantly.

**Table 26.5.** Taro corm yield and growth measurements as affected by intercropping.

| Intercrops | Corm yield (t/ha) | Growth height (cm) | Suckers per plant |
|---|---|---|---|
| Control (no intercrop) | 37.04 | 100 | 7.5 |
| Bush beans | 45.57 | 98 | 8.5 |
| Lucerne | 49.80 | 105 | 9.0 |
| Sweetcorn | 39.95 | 102 | 8.7 |
| Sweet potato | 40.19 | 88 | 3.2 |
| Groundnut | 50.58 | 103 | 7.7 |
| LSD (0.05) | ns | 13 | 3.2 |

LSD: least significant difference. Source: adapted from Peña, de la and Melchor (1993).

Throughout Polynesia, taro is often mulched with dried coconut leaves. In Hawaii, yields of unmulched taro are lower than of mulched taro because of the combined effect of moisture conservation and weed control (Peña, de la and Melchor, 1993) (Table 26.5).

The potential of mulching has been tested on the Big Island of Hawaii. Plots that had mulch produced significantly higher yields and higher percentage of corm DM content. However, they also showed a higher incidence of corm rots compared to non-mulched plots. Unfortunately, the increase in crop value was not sufficient to cover the increase in production costs (Miyasaka *et al.*, 2001).

## FERTILIZATION AND NUTRIENT DISORDERS

The large LA of aroids causes partial shading of the basal leaves, which ultimately results in reduced net assimilation and corm growth rates. Profuse LA development may result from high N uptake but, under optimum N supply, relatively low amounts of N are apparently used for canopy development. In upland rainfed taro, the DM allocated to the corms is generally high under optimum N supply but in lowland, irrigated taro, the DM of the corms is relatively low and stable across different N regimes (Manrique, 1994). N-deficient plants are often stunted, with pale green leaves that are smaller than normal. The older leaves develop a pale, dry necrosis around the margins and towards the lamina tip.

P-deficient plants show considerable reduction in growth before other symptoms are visible. Acute symptoms consist of necrotic lesions on the oldest leaves and usually follow a generalized or localized yellowing of the leaves. When this necrosis is preceded by yellowing, it is often confused with N deficiency but, in the case of P deficiency, plants are distinguished by the dark green colour of the youngest leaf, which allows its identification.

K requirement is high and deficient plants exhibit necrotic lesions around the margins of the oldest leaves. These lesions are usually paired on each side

of the major vein. The necrosis is usually surrounded by yellow tissue. K deficiency may exacerbate water stress and, if expanding leaves are affected, upward cupping occurs.

Taro has high Ca requirements. Ca deficiency symptoms include: failure of the leaf blades to unfurl; interveinal chlorosis and necrosis; petiole collapse; root dieback; and death of the shoot tip (Miyasaka and Bartholomew, 1979).

Estimation of required fertilizer rates can be based on the nutrient removal by the crop. In the case of taro, there is wide variation in nutrient concentrations in corms (Blamey, 1996) (Table 26.6).

Taro is rarely fertilized, except in Hawaii and Egypt. Cocoyam is sometimes fertilized in Central America when grown as an export cash crop. Taro responds well to K and P fertilization (Sunell and Arditti, 1983). In traditional cropping systems of the South Pacific, N and P deficiencies are invariably found to be increased following continuous cultivation. In field trials conducted in Tonga, it was observed that taro responded strongly to P fertilizer and that its poor response to N fertilizer was probably due to its slow establishment. In Tonga, the greatest gross margin per ha is obtained with N (75 kg/ha), P (100 kg/ha) and K (400 kg/ha) (Halavatu *et al.*, 1998).

In west Bengal, India, the performance of three upland cultivars of taro on a moderately fertile sandy loam soil was studied under varying N and K levels. The petiole length showed an increasing trend up to 120 DAP, with the highest values obtained with 150 kg N + 150 kg K/ha. The dry weights of leaves and cormels were highest with 150 kg N + 150 kg K/ha, but this treatment was almost on a par with 100 kg N + 150 kg K/ha, indicating a weak response to an increase in N. The values of the other growth attributes, such as the leaf area index (LAI), were highest with 100 kg N + 150 kg K and 150 kg N + 150 kg K/ha. (Preeti *et al.*, 2002). In Nigeria, cocoyam has been found to be responsive to split applications of 100 kg/ha of 60–50–90 (NPK) at 3 and 4 months after planting.

In the lowlands of PNG, the application of N failed to increase the yield of taro on coarse-textured soils with low native N levels. The low N recovery is thought to be due to leaching losses of applied N. It is thought that the addition of N is uneconomical and likely to have adverse environmental implications.

**Table 26.6.** Growth and yield performance of upland taro under different mulches.

| Mulches | Taro height (cm) | Suckers per plant | Corm yield (t/ha) |
|---|---|---|---|
| Control, unmulched | 107.6 a | 6.9 a | 38.2 a |
| Plastic | 109.1 a | 6.9 a | 40.0 a |
| Rice straw | 114.9 ab | 7.8 a | 39.7 a |
| Banana leaves | 121.6 b | 9.1 b | 50.7 a |
| Maize stalks | 116.9 ab | 9.2 b | 48.9 a |

Figures followed by the same letter are not significantly different at 5% level. Source: adapted from Peña, de la and Melchor (1993).

**Table 26.7.** Nutrient removal by taro crops of 8 and 65 t/ha.

| Nutrient | Concentration (dry matter basis) in the corm | Nutrient removal in kg/ha with fresh corm yield of: | |
|---|---|---|---|
| | | 8 t/ha | 65 t/ha |
| N (%) | 0.6–1.43 | 14–34 | 117–280 |
| P (%) | 0.17–0.47 | 4.0–11.2 | 39–91 |
| K (%) | 1.08–1.77 | 25–42 | 210–345 |
| Ca (%) | 0.04–0.13 | 1.0–3.0 | 8.5–24.7 |
| Mg (%) | 0.07–0.38 | 1.6–9.2 | 13–75 |
| S (%) | 0.03 | 0.68 | 5.5 |
| Fe (mg/kg) | 16–57 | 0.038–0.14 | 0.31–1.11 |
| Mn (mg/kg) | 11–16 | 0.027–0.038 | 0.22–0.31 |
| Cu (mg/kg) | 7–9 | 0.016–0.019 | 0.13–0.16 |
| Zn (mg/kg) | 40–120 | 0.096–0.29 | 0.78–2.34 |
| B (mg/kg) | 3.0 | 0.007 | 0.06 |

Source: adapted from Blamey (1996).

Inputs other than inorganic N fertilizer, are therefore, required for substantial yield increases of taro (Hartemink *et al.*, 2000).

In Nigeria, taro leaves are also consumed in soups and some cultivars (such as 'Coco India') produce higher number of leaves and suckers. The application of NPK 15:15:15 fertilizer at 200 kg/ha was found to be the optimum rate for leaf production (Orji and Ogbonna, 2015).

The levels of nitrate in taro corms are variable depending on cultivar and corm part, but they are fairly low and taro can be considered as a low nitrate content crop. The upper part (the headset) has the highest content and is used for replanting the next crop. It is, therefore, useful to plant headsets with higher nitrate content to enhance growth and plant development at the early stage, when the young plant relies on the nutrients present in the propagule. This can be done in nurseries where the propagules are enriched with manure. As the headset has no roots, the initial growth of the new taro plant depends entirely on the nutrients accumulated in the upper part of the corm. However, this part of the corm is rarely used as food because it is watery and tasteless. It is recommended, therefore, to cut a thicker portion of this part to produce heavier headsets with higher nitrate content (Kristl *et al.* 2016).

In India, growing concerns regarding food safety and human health have developed interest in organic farming. Research into elephant foot yam show that organic farming favours canopy growth and corm biomass. DM and starch contents of organic corms are higher than those of conventional corms; they also present higher crude protein and lower oxalate contents. K, Ca and Mg contents in corms are higher. After 5 years of farming, the organic plots showed higher pH and higher organic C. Overall, organic farming

proved superior and produced 20% higher yield (57.1 t/ha) over conventional practice (47.6 t/ha) (Suja *et al.*, 2012).

Field experiments were then conducted to compare the growth, yield and quality performance of five elephant foot yam varieties under organic compared with conventional systems. It was observed that the varieties × production system interactions were not significant. The varieties responded equally well to both systems, with average corm yields of 27.7 t/ha under organic and 28.5 t/ha under conventional practice. However, the corms of the varieties had slightly higher DM, sugar, P, K and Fe contents under the organic system (Suja *et al.*, 2016).

For taro (*C. esculenta*) the same type of experiments were conducted to compare growth, biomass, yield, proximate composition and mineral contents of different varieties. The organic system (10.6 t/ha) performed similar to that of the conventional system (11.1 t/ha), and both elite and local varieties responded equally well to organic management. However, the cormel quality was found to be better under organic management, with higher DM, starch, sugars, P, K, Ca and Mg contents. A technological package involving farmyard manure, green manure, neem cake, biofertilizers and ash was evaluated on-farm and was validated at seven locations in southern India. The yield under organic management was higher by 29% and organic farming proved to be an eco-friendly alternative for stable yield and quality cormels as well as for maintaining soil health (Suja *et al.*, 2017).

## HARVESTING

Taro is mature when the leaf petioles become shorter and leaf blades smaller, older leaves start dying, young leaves regenerate slowly and corms are well formed (Fig. 23.3). Farmers consider taro to be mature when the corms are observed to be reduced in diameter near the petiole and form a 'bottleneck' shape. The growth period from planting to harvesting varies from 5 to more than 12 months, depending on the genotype and the environment. Very early varieties, which can be harvested 5 months after planting, are rarely grown. Their yield generally is very low, but they have several advantages. They occupy the field for a shorter period of time and they may escape drought, viral diseases and taro beetle attack. Very late varieties are also rarely grown, especially in areas close to the equator. They may have high yield and good eating quality, but they occupy the field almost all year, sometimes even longer.

Taro plants are harvested by pulling strongly on the petiole or uplifting the corm gently with a flat-bladed fork. The roots are then cut around the plant with a bushknife and trimmed off the corm gently to obtain a smooth surface. The petiole is cut approximately 30 cm above the corm to ease handling and prevent desiccation.

Cocoyam is ready for harvesting after 6–12 months, depending on variety, but can stay in the soil for up to 20 months and can be harvested when needed. Harvesting can be piecemeal, removing cormels of a satisfactory size while leaving others to develop further. The cormels are usually stored in traditional coconut leaf baskets in well-shaded and ventilated conditions. The influence of harvesting time on the yield, protein and ash components of cocoyam and taro has been studied in Nigeria. The percentage protein content in the leaves, cormels and corms is highest at 12 weeks after planting (WAP), whereas ash content increases with delayed harvesting. Cormel and corm yields obtained at 24 WAP are not significantly different from those obtained at 36 WAP, when bulking is supposed to be at the optimum (Ndon *et al.*, 2003).

When labour costs are high it is possible to mechanize the harvest of upland taro. When plants are established on loose and light soil, in lines suitably spaced, a tractor-drawn harvester of the type used for carrots is used. It consists of an adjustable flat blade, 1.2–1.5 m wide, which cuts the roots at a depth of about 20 cm. Labourers walking behind the tractor can then pull the plants up gently and without effort. The plants are pruned by hand, leaving about 30 cm of the plant top, and the leaves are left in the field. This type of mechanized harvest has been tested successfully in New Caledonia and is quite efficient if the plants have not been planted too deep. Damage of the corms is minimal and the cost is offset by the reduction in labour costs.

# 27

# Pests and Diseases

Aroids are fairly robust plants with leathery leaves, which are difficult for most insects to chew. As a group, they are often left to grow without pesticides and still manage to produce significant yields. There are, however, several pests and diseases which deserve attention, especially in intensive, commercial production (Table 27.1).

## PESTS

The most important taro pests are the taro beetles, the taro leafhopper, aphids, the taro hawkmoth and the apple snails.

The taro beetles (*Papuana* spp. and *Eucopidocaulus* spp., order: Coleoptera, family: Scarabaeidae) are one of the most serious production constraints to taro yield and quality throughout Melanesia. These beetles are shiny black scarab beetles with a size ranging from 1.5 to 2.5 cm. There are about 19 different species, but seven have been reported as major pests of taro. Their centre of origin is the large island of New Guinea. The most important species are *P. woodlarkiana*, *P. biroi*, *P. ininermis*, *P. huebneri*, *P. szentivanyi*, *P. trinodosa* and *P. uninodis*. The males of most of these species have horns on their heads. The beetles breed in the soil and their life cycle lasts from 19 (*P. uninodis*) to 28 weeks (*P. huebneri* and *P. woodlarkiana*). The adults burrow into corms, making smooth-sided tunnels the diameter of their body width (Fig. 27.1). These species can also damage the other aroids, giant taro, cocoyam, elephant foot yam and swamp taro, as well as yam tubers and banana corms (Aloalii *et al.*, 1993).

Control methods include the application of wood ash, flooding, trap cropping, mulching, intercropping, repellent plants, time of planting and biological control. In the Solomon Islands, farmers apply wood ash at the bottom of the planting holes and observe that this simple technique reduces damage. Trapping plants such as *Saccharum spontaneum* and bananas planted around taro plots are effective in reducing the population. Direct planting into dried mulch from a ground cover in the preceding fallow of 1 or 2 years is a very

**Fig. 27.1.** Taro beetle (*Papuana* spp.) damage on dasheen-type corms (photo: V. Lebot).

efficient means of keeping the population at very low levels. Papuana beetles cannot live in plots shaded by thick vines (e.g. *Glycine*, *Mucuna* or *Pueraria* spp.). In Vanuatu, Melanesia, farmers notice that new plots after fallows covered by the weedy vine *Merremia peltata* are usually immune to taro beetles, for the same reason. Chemical control has been reported feasible in Papua New Guinea (PNG). Application of lindane granules (6% of active ingredient, a.i.) is recommended, applied in the planting hole at 1 kg/ha, just before planting and again 3 months later. For the export of fresh corms, fumigation with methyl bromide is recommended (Macfarlane, 1987) (Table 27.2).

In Fiji and PNG two insecticides, imidacloprid and bifenthrin – on their own or in combination – were found to provide good control and to give marketable yields up to 95%. Both are common insecticides used for managing other pests. Imidacloprid is recommended at a dose of 1.5 ml/l water; and bifenthrin at a dose of 2.5 m/s applied at 125 ml formulation per plant at planting and 3 months after planting is recommended (Lal *et al.*, 2008).

The fungus *Metarhizium anisopliae* var. *anisopliae* has been shown to be an effective pathogen on larvae and adults, but not on the eggs. When the fungus is applied on its own, it can reduce beetle damage significantly and can remain effective for 3 years after release into the soil (Masamdu and Simbiken, 2004). However, maintaining the level of the pathogen may require constant breeding and re-inoculation of the soil. The practicalities of such a method are not yet directly transferable to growers.

Resistance to taro beetle is one of the most difficult objectives for taro breeders. So far, no resistant genotypes have been identified. Because taro beetle damage is underground, breeders in PNG are trying to solve this problem indirectly by breeding for corms that develop aboveground. Taros with corms

**Table 27.1.** Major pests and diseases of aroids.

| Pest or pathogen | Aroid | Africa | America | Asia–Pacific |
|---|---|---|---|---|
| Insects: | | | | |
| *Papuana* spp. | Taro, cocoyam | | | × |
| *Tarophagus proserpina* | Taro | | | × |
| *Aphis gossypii* | Taro, cocoyam | × | × | × |
| *Patchiella reaumuri* | Taro | | | × |
| *Hippotion celerio* | Taro | | | × |
| Snails: | | | | |
| *Achatina fulica* | Taro, cocoyam | × | × | × |
| *Pomacea canaliculata* | Taro | | | × |
| Nematodes: | | | | |
| *Aphelenchoides* spp. | Taro | | | × |
| *Helicotylenchus* spp. | Taro | | | × |
| *Hirschmanniella miticausa* | Taro | | | × |
| *Longidorus sylphus* | Taro | | | × |
| *Pratylenchus* spp. | All | × | × | × |
| *Rotylenchulus reniformis* | All | × | × | × |
| *Meloidogyne* spp. | All | × | × | × |
| *Longydarus sylphus* | Taro | | | × |
| *Tylenchorhynchus* spp. | Taro | | | × |
| Bacteria: | | | | |
| *Erwinia carotovora* | Taro, cocoyam | × | × | × |
| Fungi: | | | | |
| *Phytophthora colocasiae* | Taro | × | × | × |
| *Pythium myriotylum* | Taro, cocoyam | × | × | × |
| *Cladosporium colocasiae* | Taro | | | × |
| *Sclerotium rolfsii* | Taro | | | × |
| *Phyllosticta colocasiophila* | Taro | | | × |
| Viruses: | | | | |
| Dasheen mosaic virus (DsMV) | All | × | × | × |
| *Colocasia bobone* disease virus (CBDV) | Taro | | | PNG + Sol. |
| Taro bacilliform virus (TaBV) | Taro | | | Pacific only |
| Taro vein chlorosis virus (TaVCV) | Taro | | | Pacific only |
| Taro reovirus (TaRV) | Taro | | | Pacific only |

PNG = Papua New Guinea; Sol. = the Solomons. Blank cells mean that the pest or pathogen is not present in that continent. Source: adapted from Ooka (1997).

permanently aboveground can frequently be found among wild taro populations. This character can be transferred easily into cultivars, but it is too soon to predict the outcome because there are several problems associated with this trait. Plants are physically unstable, the wild genes can affect eating quality

seriously and beetle response to an aboveground corm is unknown. The beetles may have no choice but to feed on these corms.

Taro leafhopper (*Tarophagus proserpina*, order: Homoptera, family: Delphacidae) is one of the main vectors of the Alomae–Bobone virus complex. The adults and nymphs can also cause severe damage by sucking sap from leaf blades and petioles.

Aphids (*Aphis* spp., *Pemphigus* sp., order: Homoptera, family: Aphididae) are the vectors of the various viral diseases which affect taro. There are, however, significant differences in sensitivity between genotypes, and breeders are planning to breed for resistance. In Hawaii, 50 cultivars of taro and one of cocoyam were screened for their tolerance to *A. gossypii*. The life history data for *A. gossypii* were collected by assessing survivorship and fecundity of aphids caged on taro leaves in the field. Significant differences in aphid reproductive rate and longevity were observed among the taro cultivars. A choice test where *A. gossypii* aphids were offered four leaf discs excised from different taro cultivars has also been conducted in the laboratory, and field observations of aphid abundance on taro cultivars were carried out to corroborate laboratory experiments. It appears that cultivars such as 'Iliuaua', 'Rumung Mary', 'Maria', 'Ketan 36' and 'Agaga' are the most resistant in terms of reducing aphid fecundity, whereas the 'Purple', 'TC-83001' and 'Putih 24' cultivars are least preferred in aphid choice tests. The cocoyam genotype consistently exhibited strong aphid resistance. Resistant taro cultivars may form the basis of breeding programmes seeking to combine aphid resistance with other desirable traits (Coleson and Miller, 2005).

The taro root aphid (*Patchiella reaumuri*) is a serious pest of upland taro. It sucks the sap from taro roots and greatly reduces plant vigour, yield and corm quality. This species is yellow (unlike the typical bright light-green colour of *Aphis* spp.). The first signs of infestation appear as white mould on the fibrous roots. This aphid is not a problem under wetland conditions. The aphid population is often associated with ants, which probably move them around. In Hawaii, up to 75% damage to plants has been reported and usually coincides with drought conditions. No insecticide is truly efficient and spread occurs mainly by planting infested headsets or suckers. When infestation occurs, destruction of the crop is recommended (Sato *et al.*, 1990).

**Table 27.2.** Methyl bromide fumigation rates for destroying papuana beetles in taro corms.

| Fumigation ($g/m^3$) | Duration (h) | Temperature (°C) |
|---|---|---|
| 40 | 3 | 16–20 |
| 32 | 3 | 21–26 |
| 24 | 3 | 27–32 |

Source: adapted from Macfarlane (1987).

The hawkmoth (*Hippotion celerio* L., order: Lepidoptera, family: Sphingidae) is an occasional pest of taro which can cause severe defoliation. In Hawaii, the impact of apple snails on taro yields can be a very serious problem on wetland crops. There are numerous species in the family Ampullariidae and all are freshwater snails which are found throughout the tropics. Four species have been recorded in Hawaii: *Pomacea canaliculata*, *P. bridgesii*, *P. paludosa* and *P. conica*. The first species is the most devastating apple snail. The snails cause considerable damage by feeding on all parts of the plant. Wounds from feeding provide infection points for a variety of pathogens. These snails can measure up to 7.5 cm in diameter and are vigorous feeders. Hand picking the snail from taro patches and destroying their eggs is possible but Cayuga ducks are very effective predators and can be introduced if the snail is a problem.

## NEMATODES

There are several species of nematodes that may cause significant yield losses (i.e. *Aphelenchoides* spp., *Helicotylenchus* spp., *Hirschmanniella miticausa*, *Longidorus sylphus*, *M. javanica*, *M. incognita*, *Pratylenchus* spp., *R. reniformis and Tylenchorhynchus* spp.) (Ooka, 1997). The most serious is probably *H. miticausa*, which causes mitimiti disease. It is spread in the western part of the Solomon Islands and the north-eastern part of PNG. Local cultivars are highly susceptible to the disease. Resistant wild genotypes were used in the Solomon Islands taro breeding programme in the 1980s and a number of resistant hybrids were produced (Patel *et al.*, 1984), but their level of calcium oxalate was too high for consumption. They needed to be improved further for yield and eating quality, and to be tested in areas affected by the disease. If the resistance to corm-infecting nematodes is caused by extremely high concentrations of calcium oxalate or other undesirable chemical substances, the resistant genotypes will not be edible. Before a breeding strategy is initiated, it will be necessary to know why some of the wild genotypes are resistant, how this resistance is inherited and whether the resistance is related to low yield and poor eating quality.

Root-knot nematodes (*Meloidogyne* spp.) can damage upland taro when the crop is planted in infested soils. Their attacks are characterized by galls on the root and swelling and malformations on the corm. Severe attacks result in chlorotic and stunted taro plants.

## BACTERIA

Bacterial soft rot is a disease caused by *E. carotovora* and *E. chrysanthemi*. This rot produces a strong-smelling, watery soft rot, ranging in colour from white to dark blue. Wounds and bruises caused by various pests, insects or snails are the most frequent infection sites for this disease. Control measures include

the careful handling of corms to minimize injuries, air-drying and storage of healthy corms at low temperatures.

## FUNGI

Taro leaf blight (TLB) (Phytophthora leaf blight) is caused by the fungus *Phytophthora colocasiae*. The disease is present in Africa, South-east Asia and the Pacific (Misra and Chowdhury, 1997; Fullerton and Tyson, 2004; Singh *et al.*, 2012). Phytophthora blight is considered to be the most destructive disease of taro leaves. It reduces leaf area available for photosynthesis, as well as the number of functioning leaves (Cox and Kasimani, 1990a, b). The first symptoms of infection are small, circular water-soaked spots. When conditions are favourable for the pathogen and when the plants are highly susceptible, the spots enlarge quickly and their shapes become irregular lesions with a yellow margin. The first spots can initiate secondary infections which lead to a rapid colonization and destruction of the entire leaf. The disease can also affect leaf petioles, peduncles of inflorescences, spathe and spadix (Fig. 27.2)

Epidemics usually occur during rainy, overcast weather with very high relative humidity, when night temperatures are relatively low (20–24°C) and day temperatures are not high (25–28°C). Under such optimal conditions, the pathogen spreads very rapidly and within 1 week nearly all susceptible plants in a field may be heavily affected. The pathogen spreads more easily and quickly in densely planted plots.

Leaves are infected either through direct or indirect germination of the sporangia or zoospores. Spores are spread by wind-driven rain and dew to other parts of the same leaf, from leaf to leaf, from plant to plant and from plot to plot. Over longer distances, the pathogen is spread mainly through infected plant material (infected leaves, corms, planting material and plant debris). The disease survives as a mycelium in the soil and in affected corms and plant debris.

**Fig. 27.2.** Taro leaf blight (TLB) caused by *Phytophthora colocasiae* (photo: V. Lebot).

Leaf blight can be controlled with chemicals, by various cultural practices (e.g. use of clean planting material, crop rotation, wide spacing, interplanting with other crops, removal of affected leaves and isolation of unaffected plots) and breeding resistant genotypes, as well as preventing the spread of the disease to countries at present free of it. Sanitization is effective during the endemic phase and regular removal of the infected leaves has a marked effect on the severity of the incidence of the disease (Fullerton and Tyson, 2004). In India, the severity of infection has been shown to be reduced significantly when planting was done later in the season (in July rather than in May), but yields were higher in May, despite the severity of the disease. This was thought to be due to seasonal factors. May planting with early-maturing types can escape much yield loss. When irrigation is available, planting in February or March can escape the disease, as the crop would be harvested before the climax of the epidemy (Misra and Chowdhury, 1997) (Table 27.3).

By adjusting the planting dates accordingly and by using tolerant cultivars, it appears possible to manage TLB. Among the various fungicides tested, metalaxyl (Ridomil at 0.05% a.i.) is the most effective, followed by Mancozeb (e.g. Dithane, 0.05% a.i.), both sprayed every 2 weeks. The efficacy of fungicides is, of course, dependent on the severity of the disease at the time and the prevailing weather conditions.

*P. colocasiae* is a diploid and heterothallic species. Its sexual reproduction allows genetic recombinations between complementary sexual strains, A1 and A2, and can induce high genetic variability within the species. Intraspecific variability of this fungus has been studied in several South-east Asian and Pacific countries. Polymorphism of the species was assessed by using isozymes from 94 isolates collected on susceptible and resistant accessions in five countries. None of the studied isolates was present in more than one country and all had unique fingerprints, indicating tremendous genetic variation. Although differences in pathogenicity are not yet established, different *P. colocasiae* genotypes are likely to recombine and evolve rapidly, since this species is heterothallic (Lebot *et al.*, 2003). Limiting its spread within

**Table 27.3.** Effect of the date of planting on the incidence of leaf blight on yield.

| Plantating dates | % plants infected | % leaf area damaged | % disease severity | Corm yield (t/ha) |
|---|---|---|---|---|
| 1 May | 88.8 | 42.3 | 54.8 | 9.0 |
| 15 May | 79.7 | 35.3 | 48.2 | 8.6 |
| 1 June | 68.4 | 31.0 | 32.2 | 5.7 |
| 15 June | 67.8 | 29.5 | 31.9 | 4.6 |
| 1 July | 50.8 | 20.7 | 19.1 | 2.7 |
| 15 July | 39.1 | 13.2 | 15.7 | 1.6 |

Source: adapted from Misra and Chowdhury (1997).

countries may be important for preventing an increase in its virulence through broadening of its genetic base.

In India, the genetic variation found in *P. colocasiae* indicates that it is due to both asexual and possibly infrequent sexual mechanisms and that genetic differentiation has taken place as a result of geographic isolation. The larger than expected random amplified polymorphic deoxyribonucleic acid (RAPD) variation in isolates of *P. colocasiae* and the presence of distinct zymotypes among these isolates suggests that genetic recombination is possible in this fungus. Isolates collected from the same habitat have different RAPD patterns, indicating that populations are composed of more than one genet (Kumar *et al.*, 2010).

A survey attempting to assess the diversity present in the vast Asia–Pacific geographical zone has been conducted. Mating types were determined in 54 *P. colocasiae* isolates from the Pacific region, India and South-east Asia. Forty isolates were found to be A2 mating type and 14 did not form oospores with either mating type. No A1 or self-fertile isolates were found in this set of isolates (Tyson and Fullerton, 2007).

Single nucleotide polymorphism (SNP) markers have been developed for *P. colocasiae* and used to characterize 379 isolates collected in Hawaii, Vietnam and Hainan Island, China. Genotyping of these isolates revealed that three clonal lineages were shared among countries. For Hawaii and Vietnam, more than 95% of isolates were the A2 mating type. On Hainan Island, isolates within single clonal lineages had A1, A2 and A0 mating types, indicating that this large island in the China Sea may be the area of origin of *P. colocasiae* (Shrestha *et al.*, 2014).

Resistant cultivars are probably the most sustainable control measure. The resistance system to TLB cannot be considered as simple and uniform. Genetic studies conducted in PNG indicate that resistance reactions can be highly variable. In addition to strong and distinct resistance reactions, there are weaker, not clearly distinct ones which probably involve minor genes (Ivancic *et al.*, 1996). Breeders in PNG regularly prepare spore suspensions which are used for spraying plants. For breeding purposes, spore suspensions can be prepared in many different ways but the simplest is to collect 20–100 leaves affected by the pathogen, place them in a transparent plastic bag with moistened absorbent tissue paper to maintain high humidity, and leave the bag in a dark room at 20–22°C. After 24–36 h, the leaves are transferred to a container of clean water (3 l water for 1 kg leaves), squeezed and filtered. This filtered suspension is then used as inoculum for spraying taro and screening large progenies (Ivancic *et al.*, 1996).

Resistant traditional cultivars exist in the germplasm collections of several countries where leaf blight has been present for a long time: the Philippines, Vietnam, Thailand, Malaysia, Indonesia and PNG, but most cultivars from Vanuatu, as for other Pacific Islands, are known to be susceptible (Lebot *et al.*, 2003) (Table 27.4).

**Table 27.4.** Geographical distribution of resistance to leaf blight caused by *Phytophthora colocasiae* (percentages of accessions).

| Country | PH | VN | TH | MY | ID | PNG | VU* | Total |
|---|---|---|---|---|---|---|---|---|
| No. of accessions | 172 | 350 | 300 | 135 | 685 | 278 | 378 | 2298 |
| Very susceptible | 4.1 | 0 | 0 | 0 | 0.15 | 0 | – | 0.35 |
| Susceptible | 21.5 | 1.7 | 95.7 | 0 | 65.4 | 100 | – | 45.8 |
| Tolerant | 73.8 | 34.9 | 0.3 | 4.4 | 32.3 | 0 | – | 20.8 |
| Resistant | 0.6 | 41.1 | 5 | 43.7 | 1.5 | 0 | – | 10 |
| Immune | 0 | 22.3 | 0 | 51.9 | 0 | 0 | – | 6.4 |
| Not determined | – | – | – | – | 0.7 | – | 100 | 16.7 |

The taro germplasm collection of Vanuatu could not be evaluated as leaf blight was absent. Source: adapted from Lebot *et al*. (2003). PH, Philippines; VN, Vietnam; TH, Thailand; MY, Malaysia; ID, Indonesia; PNG, Papua New Guinea; VU, Vanuatu.

Several of these resistant cultivars have been tissue cultured, indexed for viruses and distributed by the Taro Network for South-east Asia and Oceania (TANSAO) to various countries. They are presently being used in breeding programmes to improve resistance (Lebot *et al*., 2004). Some of the breeding lines from TANSAO have been tested in American Samoa for resistance to TLB using a detached-leaf bioassay and field trials. Mean lesion diameters from bioassays appear highly correlated with field estimates of the number of healthy leaves per plant and corm weight. Taro resistance increased with plant age and the second-oldest leaf was found to be more resistant than the third-oldest leaf. This bioassay appears to be a quick, space-saving and effective method of screening taro lines for post-penetration resistance to *P. colocasiae*. It also provides a standardized method of evaluating host–pathogen interactions under controlled conditions and this should be helpful to breeders when evaluating genotypes (Brooks, 2008).

In India, another test was evaluated. Some 172 taro accessions were screened for TLB using a cell wall glucan elicitor and spore suspension cultures on leaf discs. Results indicated that 14 lines showed resistance to leaf blight. These 14 lines, and two susceptible lines, were then selected for further evaluation under *in vitro* conditions, when only three lines showed resistance. Three accessions, 'Duradim', 'DP-25' and 'Jhankri', have been isolated for breeding programmes (Sahoo *et al*., 2005). Subsequently, an assessment of expression of antioxidative enzymes and their isozymes was done in 30-day-old *ex vitro* raised plants of these three resistant and one susceptible ('N-118') genotypes. Increase in antioxidative enzymes was higher (67%–92%) in the resistant genotypes than in the susceptible one (21%–29%). Induction and increased activity of particular isozymes against infection of *P. colocasiae* in the resistant

genotypes indicates a potential linkage and these may also be useful criteria to use when breeding for resistance (Sahoo *et al.*, 2007a, b).

To accelerate the breeding and selection process a test was developed using a modified floating leaf disc assay. There are significant differences between genotypes in their response to *P. colocasiae* infection in the detached-leaf assay. It is observed that, with this test, the accessions can be efficiently classified into various resistance groups based on a simple 0–4 score. Furthermore, the results were consistent with the field evaluation scores of the varieties. Thus, it is thought that this test represents a rapid, simple and repeatable assay that can be used to screen large numbers of taro genotypes (Nath *et al.*, 2016). However, a comparison with simple, straightforward, field evaluation of new hybrids established in the field under natural pressure needs to be done to confirm the efficiency of this technique.

Pythium corm and root rot is another serious fungal disease of taro which occurs mostly in irrigated crops, but also under upland conditions. It also attacks cocoyam and giant taro. The following species have been recovered from diseased plants: *Pythium aphanidermatum*, *P. carolinianum*, *P. graminicolum*, *P. irregulare*, *P. middletonii*, *P. myriotylum*, *P. splendens* and *P. vexans*, but *P. myriotylum* is found most often. The first symptom is a slowing of leaf production rate due to the restriction of supply to the leaves when the roots are attacked. Infected plants are pulled out of the soil more easily than healthy ones because of the rotted roots. Root decay then leads to corm rot, especially when taro is grown in wetland conditions. If the disease develops, the main plant is killed but the suckers remain alive. Outbreaks depend on the presence of the fungus, the susceptibility of cultivars, the soil moisture and the high soil or water temperature. Yield loss can range from 10% to 100% but is always less in upland conditions.

Once the soil has been contaminated, control becomes difficult as the fungus can survive in plant debris. Solarization of the ponds (complete drainage and exposure to full sun) for several weeks helps to reduce the inoculum. It is recommended that taro is not replanted in the same plot once *Pythium* has been found. Cover crops established during the fallow also contribute to its reduction. So far, no cultivars seem to be resistant to root rot. When the soil is heavily infested, the severity of attack can be reduced by incorporating Captan (50% wet product at a rate of 112 kg/ha) in the planting hole, before planting. Metalaxyl (Ridomil) may also be useful. The headsets should be treated before planting and dipped into a solution of Captan (4 g/l) or in Ridomil (1 g/l). This precaution provides protection for a few days after planting.

*P. splendens* also causes postharvest corm decay. Control has been achieved when the corms were dipped in a mixture of benomyl and Ridomil (1 g/l) (Jackson, 1985).

In Cameroon, cocoyam root rot disease (CRRD) caused by *P. myriotylum* is the most serious constraint to production. High temperatures (30–40°C) favour its development, with a maximum growth of the mycelia at around

33°C. A comparative analysis of suppressive and conducive soil properties was performed around Mount Cameroon to identify soil variables that may contribute to soil suppressiveness of *P. myriotylum*. Soil chemical analysis results showed that organic matter content and Ca, K, Mg and N contents are higher in andosols than in ferralsols. These variables are correlated negatively with disease severity. By contrast, sand and clay, which are higher in ferralsols than in andosols, are related positively to disease severity. High organic matter probably mediates *P. myriotylum* suppression in andosols by improving soil structure, increasing soil nutrient content and sustaining microbial activity (Adiobo *et al.*, 2007).

The intraspecific variability of *P. myriotylum* from cocoyam and other host species has been analysed using amplified fragment length polymorphisms (AFLPs) and rDNA–ITS (ribosomal DNA-internal transcribed spacer) sequencing. Isolates virulent to cocoyam could easily be differentiated from others by their optimum growth temperature. Isozyme profiles based on esterase analysis showed that cocoyam isolates formed a related group while *P. myriotylum* isolates from other host plants also grouped together and could clearly be distinguished from the cocoyam group. AFLPs grouped all isolates originating from cocoyam together, confirming isozyme results. In a limited pathogenicity test, all isolates from cocoyam were able to infect tissue culture-derived cocoyam. It is thought that isolates of *P. myriotylum* that infect cocoyam are distinct from isolates from other crops (Perneel *et al.*, 2006).

Breeding for resistance to *P. myriotylum* is the approach used in Cameroon and a test has been developed to assess genotypes. After inoculation, there is an increase in peroxidase activity in the roots of tolerant genotypes. It is supposed that electrolyte leakage in infected roots can be used to assess tolerance and susceptibility in different genotypes and that tolerance to the root rot disease may be associated with an increased peroxidase activity in the roots. This may help breeders to screen large progenies and capture useful genes (Nyochembeng *et al.*, 2007).

Phyllosticta leaf spot (*P. colocasiophila*) occurs after a period of cloudy and rainy weather for 2–3 weeks accompanied by cool temperatures. The spots on the leaves measure between 8 and 25 mm and are oval or irregular in shape. This fungus is not considered to be economically important, and the spots usually disappear with warm temperature and dry weather.

Cladosporium leaf spot (*C. colocasiae*) frequently appears during the cool months of the year and can be particularly spectacular in New Caledonia during winter (May to September). The fungus attacks wetland and upland taro and occurs mostly on older leaves. The spots are yellow and round, and tend to dry on the lamina edges. This disease has limited economic importance but its incidence on yields has not yet been assessed accurately.

Sclerotium or southern blight (*S. rolfsii*) is sometimes a problem in dryland taro, especially in over-mature corms. The fungus persists in the soil, causing outbreaks of the disease in warm and wet weather. Affected plants

are stunted and the corms rot at their base. Sanitization by pruning or removal of old leaves is recommended.

## VIRUSES

The most common viral disease of taro is dasheen mosaic virus (DsMV), which is distributed worldwide. It affects taro and several other aroid species (i.e. *Caladium bicolor*, *Alocasia*, *Xanthosoma* and *Dieffenbachia* spp.). In the Pacific and South-east Asia, DsMV is not considered a dangerous disease but it can reduce the corm yield per plant by up to 60% by reducing its photosynthetic rate (Fig. 27.3). The main vectors of dispersal are various aphids but the disease can also be spread by planting materials. The leaves of affected plants are characterized by a feathery mosaic pattern along the veins. A commercially available (enzyme-linked immunosorbent assay) kit exists but its cost is a constraint to growers. Rogueing is the appropriate measure.

Although cocoyam is an important export crop in Nicaragua, the total planted area and yield have decreased significantly during the past few years owing to diseases disseminated with planting materials. A study conducted to evaluate the re-infection of DsMV and its effect on yield has been conducted with virus-free and virus-infected *in vitro* plants from three genotypes, which were then established in a non-traditional production area. Regardless of

**Fig. 27.3.** Dasheen mosaic virus (DsMV) symptoms on taro (*Colocasia esculenta*) leaf (photo: V. Lebot).

genotype, the virus-free plants produced a larger number of cormels that were heavier and longer than those of infected plants. This resulted in a higher yield from virus-free plants (18.2 t/ha) compared with infected plants (13.6 t/ha). Between 60% and 90% of the virus-free plants, depending on genotype, were infected with DsMV 7 months after planting. *Aphis gossypii* was the only aphid observed in the field trial and was therefore probably the vector responsible for the transmission of the virus (Reyes *et al.*, 2006).

Reverse transcription polymerase chain reaction (PCR) used to analyse ten Nicaraguan DsMV isolates revealed high nucleotide identity to DsMV isolates from the USA, eastern Asia and Australasia. However, phylogenetic analyses showed that the Nicaraguan isolates formed two distinct subgroups corresponding to distinct geographic regions. It is suggested that this structure of the diversity may be explained by the different geographical origins of the cocoyam genotypes grown in these regions (Reyes *et al.*, 2009).

The most dangerous viral taro disease is *Colocasia bobone* disease virus (CBDV), which is widespread in the Solomon Islands (Malaita, San Cristobal, Choiseul Islands) and in PNG (mainland and almost all bigger islands). When the taro bacilliform virus (TaBV) combines with CBDV, it causes Alomae disease. The symptoms are crinkling of the young leaves, which fail to develop; shortening of the petioles; and thickening of veins and laminas. Plants are often stunted and then die. On *Alocasia*, the symptoms are very similar. CBDV particles are spread through planting material and transmitted from plant to plant by insect vectors. The main vectors are taro leafhopper (*T. proserpina*), aphids and mealy bugs. Fortunately, there are varied levels of tolerance to this disease. Wild taros from areas heavily affected by the virus complex appear to have higher tolerance to the disease (Ivancic *et al.*, 1993). The breeding for resistance and tolerance to CBDV conducted in the Solomon Islands and in PNG has been based on the population approach, aimed at accumulating resistance genes. The genotypes with higher tolerance (mostly wild or primitive materials) were intercrossed and their offspring generation was tested in both screenhouse and field conditions. The vectors for the virus transmission were various aphids and taro leaf hoppers. The first generations of young plants were heavily affected by the virus complex but the differences appeared in their recovery. Fully recovered plants were considered to have at least some tolerance (Ivancic *et al.*, 1993).

A putative rhabdovirus, taro vein chlorosis virus (TaVCV), causes a distinctive vein chlorosis and is found in Fiji, Vanuatu, New Guinea and the Philippines, but has no economic importance. Sensitive and reliable diagnostics for DsMV, TaBV, TaVCV and a recently identified virus of unknown etiology, the taro reovirus (TaRV), have been developed (Harding *et al.*, 2004).

A new taro bacilliform CH virus Taro bacilliform CH virus (TaBCHV), a novel badnavirus infecting taro plants, has been identified but its pathogenicity remains unclear (Kazmi *et al.*, 2015).

## INTEGRATED PEST AND DISEASE MANAGEMENT

In traditional agroforestry systems, a number of taro varieties can be found growing in the same plot and, in such situations, outbreaks of pests and diseases rarely occur. When virus symptoms appear, the only remedy is to uproot the infected plants and to destroy them. Continuous cropping is avoided by farmers as they know that it tends to develop *P. colocasiae* and *P. myriotylum* inoculums. The same is true for *Papuana* spp. population build-up (Masamdu and Simbiken, 2004).

Crop rotations, fallow management with appropriate cover crops and proper planting material management are the essential compounds of integrated pest management (IPM) (Lebot, 1992). Special emphasis is given to the natural predators and parasites in traditional agrosystems, rather than the use of pesticides. As several pests and diseases are fairly limited in geographical range, strict quarantine is the rule for international exchanges and the movement of germplasm has to follow Food and Agriculture Organization (FAO) guidelines and go through a laboratory, a transit centre (where selected genotypes are put *in vitro* and exchanged internationally) *in vitro*.

Proper fallow management is seen as a practical solution to manage pest populations, especially of *Papuana* spp., but also of nematodes. In Hawaii, studies have been conducted to determine the best green manure crops to rotate with rainfed taro. Ten different cultivars and seven green manure species were evaluated in a greenhouse study to determine their ability to suppress root-knot nematode *Meloidogyne javanica*. These green manure species were: black hollyhock (*Alcea rosea*); canola (*Brassica napus*); cabbage (*B. oleracea*); French marigold (*Tagetes patula*), sorghum-sudangrass (*Sorghum bicolor* subsp. *drummondii*); sunn hemp (*Crotalaria juncea*) and yellow mustard (*Sinapis alba*). All plants were inoculated with eggs of *M. javanica* and, after 6 weeks, nematode eggs and reproduction factor (Rf) of *M. javanica* were determined. As expected, French marigold did not host *M. javanica*. Other species that were poor hosts were canola, sorghum and sunn hemp. Based on these results, eight green manure species were grown for 3 months in a field trial. Marigold, sorghum and sunn hemp appeared to be the best species to control nematodes in rainfed taro cropping systems (Miyasaka *et al.*, 2016).

# 28

# Postharvest Quality and Marketing

Cocoyam, taro and other aroids have much potential in terms of fresh and processed products and are, in fact, industries with considerable expansion potential, especially as biofunctional foods (Chandrasekara and Kumar, 2016). Taro is already processed and prepared into many consumable and diverse forms. Corms may be roasted, baked, boiled, steamed or fried. They may be processed into fresh or fermented paste, canned corm portions, flour, beverage, chips and flakes. The leaves, petioles, stolons and inflorescences are also consumed and are steamed or boiled.

## CHEMICAL COMPOSITION

The edible taro leaves are very nutritional and are a good source of proteins and vitamins (Bradbury and Holloway, 1988) (Table 28.1). They are also very rich in antioxidants, especially flavonoids (Isabelle *et al.*, 2010). In the 'Okinawa' taro, the following flavonoids have been identified: schaftoside, isoschaftoside, orientin, isovitexin, isoorientin, vitexin and luteolin 7-O-sophoroside in fresh leaves (Leong *et al.*, 2010). In the Azores Islands, no fewer than 41 different phenolic metabolites (11 hydroxycinnamic acid derivatives and 30 glycosylated flavonoids) have been identified in the leaves of two *C. esculenta* varieties (Ferreres *et al.*, 2012) (Fig. 28.1).

Antioxidants are also present in the corms of taro in Vanuatu. Ten flavones: luteolin-6-C-hexoside-8-C-pentoside, schaftoside, luteolin-30,7-di-O-glucoside, homoorientin, isovitexin, orientin, luteolin-40-O-glucoside, luteolin-7-O-glucoside, vitexin and apigenin-7-O-glucoside were successfully detected in the corm and are responsible for the attractive yellow colour of the flesh and fibres, but there is significant variation between varieties (Lebot *et al.*, 2015b).

Aroid cultivars have similar corm compositions. Depending on genotype, aroids may contain oxalic acid deposited in plant tissues as crystals of calcium oxalate (Englberger *et al.*, 2003). When in sufficient quantity, calcium oxalate crystals cause mechanical abrasion of the mucous membranes.

**Table 28.1.** Composition of edible corms and leaves of major aroids.

| | Taro leaves | Taro corm | Cocoyam cormels | Giant taro corm | Swamp taro corm | Elephant yam corm |
|---|---|---|---|---|---|---|
| Moisture % | 85.4 | 69.1 | 67.1 | 70.3 | 75.4 | 77.8 |
| Energy (kJ/100) | 114 | 480 | 521 | 449 | 348 | 324 |
| Protein % | 4.2 | 1.12 | 1.55 | 2.15 | 0.51 | 2.24 |
| Starch % | 0.07 | 24.5 | 27.6 | 21.5 | 16.8 | 16.6 |
| Sugar % | 0.92 | 1.01 | 0.42 | 0.96 | 1.03 | 0.14 |
| Dietary fibre % | 5.03 | 1.46 | 0.99 | 1.85 | 2.78 | 1.45 |
| Fat % | 0.61 | 0.10 | 0.11 | 0.10 | 0.16 | 0.06 |
| Ash % | 1.58 | 0.87 | 1.04 | 0.92 | 0.67 | 1.36 |
| Total oxalate (mg/100 g) | 426 | 65 | – | 38 | 299 | 288 |
| Calcium oxalate (mg/100 g) | 400 | 43 | – | – | 399 | 382 |
| *Minerals (mg/100 g):* | | | | | | |
| Ca | 182 | 32 | 8.5 | 38 | 182 | 127 |
| P | 61 | 70 | 53 | 44 | 16 | 67 |
| Mg | 90 | 115 | 27 | 52 | 21 | 47 |
| Na | 7.9 | 1.8 | 6.6 | 30 | 72 | 4.1 |
| K | 487 | 448 | 530 | 267 | 67 | 622 |
| S | 24 | 8.5 | 7.9 | 11.9 | 3.3 | 11.8 |
| Fe | 0.62 | 0.48 | 0.4 | 0.83 | 0.61 | 0.51 |
| Cu | 0.15 | 0.20 | 0.19 | 0.07 | 0.11 | 0.18 |
| Zn | 0.66 | 3.6 | 0.52 | 1.51 | 2.3 | 1.05 |
| Mn | 4.5 | 0.34 | 0.17 | 0.62 | 0.69 | 0.31 |
| Al | 1.81 | 0.39 | 0.53 | 0.36 | 1.36 | 0.41 |
| B | 0.36 | 0.09 | 0.09 | 0.10 | 0.09 | 0.17 |

*Continued*

**Table 28.1.** Continued.

| | Taro leaves | Taro corm | Cocoyam cormels | Giant taro corm | Swamp taro corm | Elephant yam corm |
|---|---|---|---|---|---|---|
| *Vitamins (mg/100 g):* | | | | | | |
| Vitamin A | – | 0.007 | 0.005 | 0 | 0.005 | 0.15 |
| Thiamin | – | 0.032 | 0.024 | 0.021 | 0.025 | 0.05 |
| Riboflavin | – | 0.025 | 0.032 | 0.018 | 0.019 | 0.07 |
| Nicotinic acid | – | 0.760 | 0.80 | 0.48 | 0.46 | 0.7 |
| Pot. nic. acid = Trp 60 | 1.0 | 0.19 | 0.33 | 0.46 | 0.07 | – |
| Vitamin C | – | 15 | 13.6 | 17.0 | 15.7 | – |
| *Limiting amino acids:* | | | | | | |
| First | Leu 57 | Lys 66 | Lys 57 | Mys 64 | Lyd 70 | – |
| Second | Lys 62 | Thr 94 | Leu 81 | His 91 | Trp 70 | – |
| Trypsin inhibitor (TIU/g) | 0 | 13.6 | 0.3 | 269 | 2.5 | – |

Source: adapted from Bradbury and Holloway (1988).

**Fig. 28.1.** Taro (*Colocasia esculenta*) leaves are rich in proteins, vitamins and antioxidants (photo: V. Lebot).

When a genotype rich in these is ingested, the mouth, tongue and throat are covered with needles and a very unpleasant burning sensation occurs. In aroids, these crystals occur as needle-shaped sharp raphides and are a virulent defence strategy against herbivores. Because the calcium oxalate content of non-acrid and acrid genotypes is often similar, it has been suggested that there is another, unknown compound causing the acridity. Some cultivars are not acrid and can be eaten almost raw. This is the case of *lampung hitam* cultivated in Bogor, Indonesia. Others are not acrid when baked but are acrid when boiled.

It has been observed that the oxalate content variation depends on drought stress and is consistent with the photosynthetic rate, carbohydrate metabolism and protein synthesis. Drought-tolerant accessions have good osmotic response, oxalate precipitation and mobilization from the shoots to the corms. Drought-sensitive accessions, however, present less mobilization of calcium oxalates. Drought stress can, therefore, impact negatively the nutritional quality of the plant (Gouveia *et al.*, 2018). Surprisingly, when crossing two non-acrid parents, which most varieties are, one will discover acrid hybrids in the progeny. This can be a constraint when breeding, especially if programme staff fails to volunteer for palatability tests.

Chemically, there is also significant variation in the major nutritional compounds between taro cultivars. These differences are controlled genetically and are well known to consumers and traders. Some experiments have been conducted to understand the relationships between the chemical composition and consumer preference. The results of the physico-chemical analyses of 31 taro cultivars selected for their taste quality, planted and harvested the same day in the same plot, indicate that, except for the temperatures of gelatinization, all characteristics (minerals, lipids, proteins, amylose, dry matter (DM) and different sugars) are very variable (Lebot *et al.*, 2004) (Table 28.2).

Most cultivars rated as 'very good' in palatability tests have high DM, amylose and starch contents and low minerals and sugars. It is likely that selection for these traits will be effective for improving chemotypes. Starch content

**Table 28.2.** Physico-chemical characteristics of the corms of 31 selected taro cultivars.

| | DM (%) | Starch (% DM) | Amylose (% starch) | Proteins (% DM) | Minerals (% DM) | Lipids (% DM) | Glucose (% DM) | Fructose (% DM) | Sacchar. (% DM) | Maltose (% DM) |
|---|---|---|---|---|---|---|---|---|---|---|
| Minimum | 12.5 | 36.6 | 03.4 | 3.70 | 01.6 | 00.5 | 00.1 | 00.1 | 00.8 | 00.0 |
| Maximum | 55.9 | 77.9 | 12.0 | 15.8 | 06.6 | 01.5 | 02.7 | 02.6 | 08.7 | 00.2 |
| Mean | 27.9 | 65.5 | 08.2 | 6.50 | 03.4 | 00.7 | 00.6 | 00.6 | 03.4 | 00.1 |
| Coeff. var. % | 38.8 | 14.2 | 25.0 | 34.9 | 31.2 | 37.1 | 90.9 | 97.6 | 56.7 | 40.5 |

Source: adapted from Lebot *et al*. (2004). DM, dry matter.

**Fig. 28.2.** Taro (*Colocasia esculenta*) corms are rich in antioxidants; yellow corms (left) are rich in flavonols and pink corms (right) are rich in anthocyanins (photo: V. Lebot).

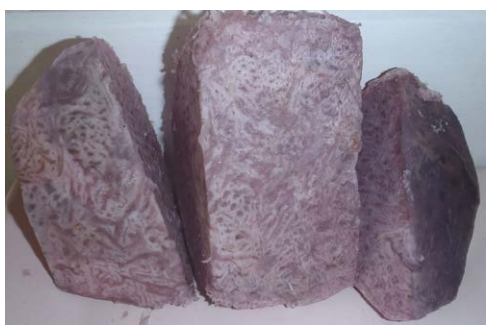

**Fig. 28.3.** Anthocyanins are present in the cooked flesh and fibres of the corm of taro (*Colocasia esculenta*) (photo: V. Lebot).

varies less than do the other compounds but, like other important compounds, starch content is determined as a percentage of the DM and is correlated to it.

Taro starch has very interesting properties. The lower glycaemic index value of taro resistant starch makes it suitable for formulation of foods for diabetic people and those who are interested in weight loss. Its *in vitro* bile acid binding capacity has a health-promoting potential owing to its potential cholesterol-lowering

effect (Simsek and El Nehir, 2012). Taro starch is also highly digestible and more than the 50% of the starch is composed of rapidly digestible starch. The impact of boiling and microwave cooking on starch fractions is not significant. The estimated glycaemic index (GI) of taro corm is 63.1, indicating that taro is a medium GI food and a good dietary carbohydrate alternative (Simsek and El Nehir, 2015).

Taro is a good source of K and Fe. Exposure to toxic metals (Cd and Pb) through taro consumption is, however, low (Luis-Gonsález *et al.*, 2015). The concentrations of most minerals (P, Mg, Fe, Cu and Zn) are higher in the upper and the central parts of the main corm but K is mostly accumulated in the central part. The upper part of the taro corm, which plays a critical role in vegetative propagation based on headsets, is an important storage location for most minerals. The central part of the corm, which is the most important for human nutrition, is characterized by higher concentrations of K, P, Mg, Zn, Fe, Cu and Cd. Taro is a valuable source of Mg, Zn and Cu in the diets of children, and of Zn and Cu in the diets of adults. On the other hand, taro cannot satisfy the daily needs for Ca, Fe and P, and therefore it is recommended to combine taro with other foods. The great variation between cultivars reveals that there is scope for biofortification through breeding (Mergedus *et al.*, 2015). However, in South Africa, it has been shown that cooked samples presented a general decrease in the mean values, especially of P, Ca, K and Zn, and that these minerals were significantly eliminated in boiling water (Lewu *et al.*, 2010).

In Japan an increasing volume of taro is imported from China to satisfy local consumption. A method has been developed to analyse the mineral composition to distinguish taro produced in Japan and China. The concentrations of 15 elements (Al, Ca, Cl, Mg, Mn, Br, Co, Cr, Cs, Fe, K, Na, Rb, Sc, Zn) were analysed. It was found that the mean concentrations of $H_2PO_4$, Co, Cr and Na differed significantly between the two countries. It was concluded that $H_2PO_4$ and Co concentrations alone could allow for differentiation between the two geographical origins (Kobayashi *et al.*, 2011).

There is also remarkable variation between eddo cultivars in India. Characterization of the nutrient and antinutrient (trypsin inhibitor, total oxalate, soluble oxalate and calcium oxalate) composition of cormels of 20 cultivars has been determined. The fat, sugar, starch and crude protein content in fresh cormels varied from 0.08% to 0.98%, 0.2% to 1.5%, 7.5% to 24.8% and 1.0% to 2.8%, respectively. Cormels provide 166–519 kJ energy/100 g fresh weight. These cormels are a good source of minerals, including K, Ca, P and Fe and a moderate source of Zn and Cu. Trypsin inhibitor, total oxalate, soluble oxalate and calcium oxalate contents vary from 52 to 1020 trypsin inhibitory units/g, 8 to 130, 4 to 89 and 4 to 93 mg/100 g, respectively (Sen *et al.*, 2005).

Taro corms are also rich in anthocyanins and carotenoids (Champagne *et al.*, 2010, 2011, 2013; Muñoz-Cuervo *et al.*, 2016) (Figs 28.2 and 28.3). Finally, taro represents an interesting source of immunostimulatory proteins which are new candidates as additives for food and pharmaceutical industries (Pereira *et al.*, 2015).

## PHYSIOLOGICAL DISORDERS IN FRESHLY STORED CORMS

Dormancy in aroids has not been well studied and varieties from higher, temperate latitudes are known to have a longer dormancy than equatorial and tropical ones. Taro corm and cocoyam cormels have respiratory rates of approximately 22 and 41 ml $CO_2$, respectively, when they are stored between 27 and 32°C. These respiratory rates increase with temperature and are lower at temperatures between 10 and 15°C, which are adequate for storing fresh corms and cormels (Ravi and Aked, 1996). Internal browning may occur when fresh corms of taro are preserved over 10 days at 4°C, although this phenomenon varies greatly with varieties. Fresh corms and cormels, peeled, frozen and packed in plastic film as 100–200 g portions, in slices or as French fries, show no chill injury when they are defrosted.

In Cameroon, polyphenol oxidase enzyme was characterized along with the combined effect of heat and salt on the texture of taro corms. Polyphenol oxidase activity is influenced by the pH and temperature, with optimal conditions at pH 6.0. An efficient and effective heat treatment reduces polyphenol and enzymatic browning. Seven inhibitors were tested and the most effective inhibitors were found to be NaCl, $CaCl_2$ and KCl (Aboubakar *et al.*, 2012).

## MARKETING AND QUALITY STANDARDS

The markets are linked strongly to cultural preferences and each country has its preferred varieties. However, there is a considerable market potential if product diversification is to match the changing lifestyles of consumers. The present markets for fresh corms and cormels are mostly the ethnic markets in New Zealand, Australia, the USA and the EU. The Dominican Republic, Costa Rica, Nicaragua and others supply the US market and cocoyam production in Florida, USA, cannot satisfy demand because of the high cost of labour. The Californian market has good potential for Pacific Island countries willing to diversify their production. Taro tends to sell at a higher price than other root crops. Therefore, the quality requirements have to be enforced throughout the production chain to ensure that high quality reaches the consumer (Brown, 1995; Vernier, 2011). The common grading standards for fresh corms are:

- No excess soil, softness and decay.
- No bruises and deep cuts.
- Spherical to round shape.
- No major abnormal deformities.
- No roots.
- Approximately 5 cm of petiole left attached to the corm.
- No double tops.

The sizes found in most markets are 1–2 kg and 2–3 kg. The best size for packaging and for consumers is 1–2 kg. The internal flesh colour ranges from creamy to pink and colour preference is influenced strongly by ethnic background. For example, the Samoan community in New Zealand prefers pink-fleshed taros. New Zealand imports yearly about 10,000 t dasheen-type taro and the Polynesian population there is expected to double over the next 20 years. Australia imports about 3,000 t. China supplies about 90% of estimated total Japanese imports, equivalent to 40,000 t fresh eddoe-type taro annually.

Because of the high moisture content of the corms, mould and disease can develop easily in improperly prepared containers and, on arrival, such containers will create quarantine problems. Some countries require fumigation treatments with methyl bromide to be conducted at the exporter's expense.

Although taro corms can take relatively rough handling, improper postharvest handling reduces shelf life by causing numerous wounds. Just after harvest, the corms are cleaned by hand or with high-pressure water sprays, or both.

## STORAGE METHODS

For taro, excess surface water is dried before the corms are packed, to minimize rots during storage. An immediate transfer to cool temperatures between 10 and 15°C, at 80%–90% relative humidity, extends shelf life. The corms are packed either in polypropylene bags or wooden crates with good aeration to reduce corm sweating. Exporters usually pack with approximately 5% extra weight to compensate for corm shrinkage during shipment.

For cocoyam, the basic requirements are the same as taro except that the cormels have to be very uniform in size and shape. Cocoyam is more robust than taro and the cormels may be kept for up to 2 months in well-ventilated warehouses at 10–15°C.

Aroids are not season-bound and are grown and harvested throughout the year. Cocoyam cormels have a good shelf life at room temperature and can be stored for up to 6 weeks. Taro corms can be stored after harvest in a cool, shaded place at room temperature for up to 1 month if undamaged and depending on the DM content of the corms. Different storage methods are used for different parts of the plant (Matthews, 2014) (Table 28.3).

After 2 weeks of storage under tropical ambient conditions of 24–29°C with 86%–98% relative humidity, there is no significant change in the protein content of taro and cocoyam corms. There is, however, a significant reduction in starch content and an increase in total sugar content. In the Solomon Islands, experiments have shown that without any chemical treatment, taro corms survive for up to 1 month if kept in polyethylene bags, retaining acceptable taste and texture, although roots and leaves were observed to grow. Dipping corms in 1% sodium hypochlorite before their storage in polyethylene

**Table 28.3.** Storage methods for taro.

| Storage method | Corms or cormels | Petioles | Leaves | Observations |
|---|---|---|---|---|
| Ambient temperature | × | × | – | In locations with moderate ambient temperatures (10–20°C), the fresh corms and leaves can be stored for a few weeks |
| Lower than ambient | × | × | × | In tropical locations, pits, shade or refrigeration temperature are used to preserve fresh corms and leaves |
| Above ambient | × | – | – | In temperate countries, fresh corms are stored temperature in pits or insulated mounds |
| Freezing | × | – | × | Applied to raw or partially processed corms and leaf parts |
| Dehydration | × | × | × | Solar desiccation of peeled corms and cormel parts |
| Humidification | × | – | – | To prolong fresh storage by applying moisture to reduce dehydration of living corms |
| Aeration | × | × | × | Corms stored in pits or mounds are aerated to permit respiration |
| Airtight containers | × | – | – | Canned sweet dessert from corms, full corms or *poi* in bags |
| Clean surface | × | × | × | With hand, brush or knife, with or without water |
| Sterilization of surface | × | – | – | With chemicals or heat (raw corms before or after peeling) |
| Pickle | – | × | – | Petiole pieces, dipped in a solution with vinegar, salt and sugar |
| Fermentation after | × | – | – | Involves yeast and lactobacilli aerobic cooking fermentation (e.g. *poi*) |
| Fermentation before | × | – | – | Initial semi-aerobic compression and wrapping cooking inside pit |

Source: Matthews (2014).

bags neutralizes the effect of fungi. Such treatment provides protection that might be practical and useful when the corms are transported to distant markets (Jackson *et al*., 1979). For commercial handling, when cleaned, the corms and cormels can be dipped in a fungicide solution to improve postharvest shelf life. Treatment with Captan at 10 and 20 g/l shows a reduction in decay of 30% and 40%, respectively. Benomy at 0.5 and 1 g/l shows a reduction of 20% and 35%, respectively.

Refrigeration is used for the commercial transport and export of taro. Corms with 5–10 cm of petioles are shipped to New Zealand from Fiji packed in wooden boxes and placed in containers cooled to approximately 5°C. Such storage reduces the incidence of corm rots to very low levels. When taro corms are sea-freighted in refrigerated containers they are held in market stores at the same temperature. Such corms can remain in good condition for up to 6 weeks but, once removed from cold storage, they have a relatively short life and start deteriorating after only 2 days at room temperature.

## TRADITIONAL PROCESSING TECHNIQUES

*Poi* is a purplish paste made mainly from taro corms of the cultivar 'Lehua maoli' in Hawaii and sold in plastic bags in supermarkets. It is digested easily, non-allergenic and an excellent food. Its preparation involves washing, pressure cooking, peeling, trimming, straining out the fibres and mixing with 30% water. Fermentation of the *poi* is rapid, usually within the first 24 h and, during this time, acidity goes from pH 6.3 in the fresh corms to pH 4.5 in the *poi*. This is a naturally fermented product caused by lactic acid-producing bacteria (*Lactococcus lactis*, *Lactobacillus plantarum* and *Leuconostic lactis*). The shelf life of unrefrigerated *poi* is only 3–4 days.

In Vanuatu, taro and other aroids are processed into *laplap*. The fresh corms are washed, peeled and grated finely to produce a fresh mass, which may be mixed thoroughly by hand with some coconut milk or left plain. The mass is spread on and wrapped in *Heliconia indica* leaves and then steam cooked in a ground oven of hot stones. The result is a pudding, elastic in the mouth, which is highly appreciated by local consumers. Several experiments have been conducted to speed up the process and to allow the preparation of *laplap* with flours. For all aroid species, the results obtained from blind panel tasting tests show no difference between fresh and flour-based *laplap* (Bourrieau, 2000).

In Nigeria, *achicha* is made from fresh taro corms and cocoyam cormels. These are first boiled for about 3 h until they soften and change in colour, releasing a pleasant aroma. The skin is then peeled off and the flesh cut into slices about 1 cm thick and then sun-dried until they break easily between the fingers. They can be stored in a dry place and used when required (Nwana and Onochie, 1979).

The physico-chemical properties and texture of taro vary with cooking time and methods. The softening of corms or slices is a result of a decrease in soluble proteins and resistant starch, and an increase in the degree of starch gelatinization, cell separation and soluble sugars. On the basis of the contribution of each variable in this relationship, cell separation followed by susceptibility of starch to enzymatic hydrolysis, starch gelatinization and starch hydrolysis are the most probable changes inducing softening during cooking (Aboubakar *et al.*, 2009).

In Ghana, *achu* is a paste traditionally made from taro corms by boiling, peeling and pounding in a mortar to a smooth and homogeneous consistency. Some work has been done to define alternative and rapid methods to evaluate the textural hardness of *achu* reconstituted from taro flour. The functional properties of the taro flours, the sensory analysis of hardness and the acceptability of reconstituted *achu* have been evaluated. The results show significant variation in the functional properties of the flours. The rheological properties of the *achu*, the sensory hardness and overall acceptability are influenced significantly by the variety used (Njintang *et al.*, 2007, 2008).

In Cameroon, swamp taro (*Cyrtosperma merkusii*) is added to *achu* because it contributes to the smooth textural feel of this traditional dish. The smooth textural feel of *achu* is a function of the starch and mucilage contents of taro used in the preparation. It has been shown that swamp taro contains appreciable amounts of mucilage. This mucilage consists of a sugar moiety representing about 70%, and a protein moiety representing 30%, irrespective of the section part of the taro corm. Analyses revealed that glucose is the most important sugar in the mucilage, followed by galactose and mannose. Furthermore, the mucilage was found to act as a potent antioxidant (Nguimbou *et al.*, 2014).

Experiments have been conducted to assess the storability of dehydrated taro. Dehydrated slices and flour are preserved in polyethylene bags at 21°C and 38°C. These products undergo changes in acridity, degradation in anthocyanin pigments, increase in moisture content and decrease in catalase activity. After 1 year, the taste quality of dried samples was unpleasant. The energy value of such products, however, was comparable to that of rice and wheat. It is, therefore, supposed that these intermediate products, which can be processed at the farm level, could then be used as raw materials for further processing (Moy *et al.*, 1979; Moy and Nip, 1983).

Taro flour is made from corms that are trimmed, peeled, sliced transversely to 5 mm thick and air-dried at approximately 50°C for 12 h. The dried chips are then ground into flour with a normal hammer mill and can be stored successfully for 1 year. This type of flour is a base for baby food and taro-based bread. There are various improvements depending on location and means available.

In Indonesia, taro flour is increasingly attractive for the agroprocessing industry but data regarding the impact of the drying process on quality needs more research. A study comparing microstructural changes in taro chips during drying at elevated temperatures of 50°C, 60°C and 70°C revealed interesting results when the chips were analysed with scanning electron microscopy (SEM). When they were subjected to a drying temperature of 50°C, the corm cells opened; but, by increasing the drying time, it was observed that the cell membranes disappeared while the starch grains had shrunk. However, the grain size was comparable regardless of the drying time; but, by increasing the temperature to 70°C, the change in starch grain size was significant (Wibisono *et al.*, 2019).

Good-quality paste can be obtained from taro flour processed from cooked, sliced and solar-dried taro. The paste is prepared by adding flour to boiling water

to attain a moisture level of 70%–75%. Taro flour is well accepted as starting material for the preparation of several local foods in Chad and Cameroon but its quality is very variable. Taro corms are harvested at different periods of time after planting and the physico-chemical properties and chemical composition depend on the degree of maturity of the corms. The oldest maturity is accompanied with higher ash, protein and carbohydrate contents. It is observed that taro powders with higher water absorption capacity and higher water solubility index produce gels with lower least gelation concentration. It is concluded that harvesting taro at full maturity (10 months after planting), and sun-drying, produces flours with excellent gelling properties. (Himeda *et al.*, 2014).

Taro is often made into fried chips and sold in towns. An important factor is the right choice of a variety that will lose any acridity during frying. Chips are now prepared industrially to satisfy the ever-growing market for such snacks in Honolulu and on the US mainland. Taro is also used to prepare tasty French fries, which are very popular in most countries and can easily substitute frozen Irish potato fries imported by fast food outlets in Asian or African mega-cities.

With the availability of microwave ovens, frozen, peeled, pre-cooked and ready-to-use portions of corm preserved in vacuum-sealed plastic films are increasingly attractive to urban dwellers.

In Korea, a study has shown that the quality of freshly cut taro is not altered by treatment with hot water. After harvesting, taro corms are washed, peeled and dipped in hot water (55°C) for 45 s. After air-drying at room temperature, the samples are packed in polyethylene films or vacuum sealed in Nylon films. They can be stored at 4°C for 12 days. In general, the weight loss rate increases slightly when taro is hot-water treated, but the hot-water treatment delays browning. It has, therefore, been recommended to treat at 55°C during processing of freshly cut taro, as it improves the quality by inhibiting browning and extending the shelf life (Chang and Kim, 2015). Starch gelatinization characteristics differ between cocoyam varieties. Two varieties (white and red) were studied and both varieties had similar DM content, as well as physical and mechanical properties. However, depending on the variety and degree of gelatinization during cooking, up to four fast-interacting water populations were observed in the cormels. There is weak gelatinization of starch at approximately 80°C in both varieties. The significant differences in the structural and gelatinization characteristics indicated that not all *X. sagittifolium* varieties may be equally suited for further processing into flours or starches (Boakye *et al.*, 2017).

Traditionally, *Amorphophallus konjac* is grown in Japan (and now in Indonesia for export to Japan) to produce *konnyaku*, a gelatinous ingredient present in many Japanese foods. The large corms are sliced, soaked, dried and then pounded with lime and water into gelatinous grey cakes that are formed into vermicelli (*ito konnyaku*) or noodles (*shirataki*) and added to soups and stews. This species is now increasingly cultivated in China for the food industries, but other *Amorphophallus* spp. also have great potential. For commercial

processing, *Amorphophallus* spp. and konjac corms are harvested when 3 years old and weighing about 2 kg, while the domestic markets for fresh corms usually prefer younger, smaller and sweeter corms of about 200–500 g. The corms store well around 10°C and, to prepare konjac flour, they are washed, peeled, sliced and rinsed several times before boiling. The starch settles and is then dried and sieved. To prepare calorie-free mannan (from mannose), the corms are dried quickly and the dried slices are ground and sieved, which leaves the mannan particles intact, and this yellow-grey powder is known as mannan flour (Bown, 2000).

Cocoyam or taro leaves are steamed or boiled and are delicacies in Samoa, where they are known as *palusami*, in Hawaii (*laulau*), in India (curry *bhaji*), in the West Indies (*calalou* stew) and in many other countries. Corms and cormels are roasted, boiled, baked, steamed or fried.

In China, taro tops, leaves and petioles are fermented satisfactorily and ensiled with characteristics similar to other silages used for animal feed. Ensiling preserves taro forage without investing in energy for drying, and acridity is destroyed naturally during the process. The silage contains moderate levels of protein and fibre but has high levels of K. Its palatability is good and it meets the feed needs of brood sows that show no reproductive problems and produce good litters.

## INDUSTRIAL PROCESSING

The taro starch particle size is extremely small, between 1 and 6.5 μm, compared to 50 μm for the Irish potato. Taro starch extraction is, therefore, laborious and expensive. The starch to alcohol ratio is around 1.8 l of starch to 1 l alcohol, and the estimated alcohol yield per 1 t of fresh taro corms is approximately 142 l in 10 months (Griffin and Wang, 1983). There are more efficient sources for the production of biofuels.

The production of certified allergen-free, taro-based products is constrained by the need to use white-fleshed varieties. The University of Hawaii has conducted an impressive amount of research into taro processing during the past 40 years (Table 28.4). Taro can be very versatile in food applications and is a good carbohydrate source in lactic acid bacteria fermentation. In Hawaii, the costs and sufficient supply of taro are the main constraints in developing commercial products (Huang *et al.*, 2004).

For processing, dryland taro is a cheaper source of raw material than wetland taro in Hawaii and elsewhere. Many new products manufactured in Hawaii use taro paste as an intermediate product. Downstream processing has generated some attractive products, such as a taro non-dairy 'yogurt'. However, to have a pure cultured paste, taro must be pasteurized and cleaned before inoculation. The industrial process involves:

**Table 28.4.** Taro product development in Hawaii.

| | 1970–1990 | 1990–present |
|---|---|---|
| Corm source | Wetland taro | Dryland taro |
| Intermediate form | Dehydrated powder, taro flour | Taro paste, *poi* |
| Process technology | Spray-drying, freeze-drying | Baking, freezing, cold processing |
| End products | Pancake mix, drink powder, baby food | Bakery filling, yogurt, frozen dessert |
| Marketing position | Exporting, distant shipping | Local and tourist market |
| Outcome | Too expensive to compete | Competitive in niche markets |

Source: adapted from Huang *et al*. (2004).

**1**. Pressurized washing taro corms with tap water.
**2**. Peeling with a steam peeler.
**3**. Soaking overnight in 3% lactic acid solution.
**4**. Cutting into 5 cm cubes.
**5**. Second washing with distilled water.
**6**. Pressure cooking cubes for 30 min.
**7**. Cooling in a clean chamber.
**8**. Grinding with distilled water to obtain a paste.
**9**. Pasteurizing to a total bacteria count under 100.
**10**. Cooling in a clean chamber.

The taro paste is then ready for inoculation. Taro paste is used to develop taro-based frozen desserts and in bakery fillings to replace fat. Unfortunately, the rather expensive farm-gate price for taro in Hawaii is limiting further processing (Huang *et al*., 2004).

In Taiwan, the physico-chemical properties and molecular structure of starches from three cultivars planted in summer, winter and spring were investigated. Starches from taro planted in summer had the largest granule size, a low uniformity of gelatinization and a high tendency to swell and collapse when heated in water. They also showed an elasticity during gelatinization that was higher than that of starches planted in the other seasons. It was observed that the rheological and pasting properties of the starches were influenced by the amylose content and also by amylopectin, whereas swelling power and solubility only depended on the amylose content of starch. It was, therefore, concluded that taro starch with high amylose content and a long-chain fraction of amylopectin displayed high elasticity and strong gel during heating (Lu *et al*., 2008).

An extraction procedure has been tested for taro at a pilot plant scale and produced a starch yield of 81% on a dry weight basis. The Mexican variety used for this test had a low amylose content (2.5%) and the solubility and water retention capacity had a constant value in the temperature range of

50–70°C, with an average gelatinization temperature of 80.6°C, similar to cereal starches. It was suggested that taro starch may be an interesting alternative for the food processing industry as it has adequate physico-chemical and functional characteristics (Agama-Acevedo *et al.*, 2011).

The physico-chemical properties of starch of the commercial taro variety 'Bun-long' have been studied and compared to two sweet potato and potato starches. 'Bun-long' starch granules are small (from 1.3 to 2.2 mm), irregularly shaped and polygonal with a lower amylose content. Several tests were conducted to test the potential of taro starch when processed at high temperature. The onset temperature, peak temperature and completion gelatinization temperatures were 73.6, 80.3 and 88.3°C, respectively. The viscosity of 'Bun-long' taro starch started increasing at 77°C and it was observed that taro starch paste was more resistant to shear thinning than potato and sweet potato starch pastes. These results indicate that taro paste has the ability to withstand severe processing conditions (Zeng *et al.*, 2014).

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