Australian Government
Australian Centre for
International Agricultural Research

Yam nutrition:

nutrient disorders and soil fertility management

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Cover: *A yam farmer with his crop in Solomon Islands.* (Photo: Grahame Jackson)

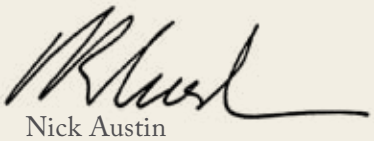
Foreword

Yams were among the first plants to be cultivated deliberately by humans, yet they remain among the least altered by the process of domestication. Despite being the tenth most important starchy staple in the world in terms of production volume (FAO 2009), yams remain little studied and poorly understood. Most yam cultivation today follows the traditional techniques developed in centuries past, and genetic improvement relies largely on recruitment of plants from the wild.

The lack of research and development devoted to yams is a result partly of its status as a subsistence crop, whose true economic value is not reflected in the small volumes traded. However, a greater part of its neglect is probably due to the poor returns on past research effort, as many idiosyncratic features of the crop pose formidable barriers to research for both genetic and agronomic improvement.

The Australian Centre for International Agricultural Research (ACIAR) began support of research into the mineral nutrition of yams in 1999, following successful projects on cassava, sweetpotato and taro. The research team, led by Dr Jane O'Sullivan at the University of Queensland, included researchers from the National Agricultural Research Institute in Papua New Guinea, the Vanuatu Agricultural Research and Training Centre, and the Tongan Ministry of Agriculture and Forestry. The project aimed to provide diagnostic information for three species, *Dioscorea alata*, *D. rotundata* and *D. esculenta*, as well as investigating ways of alleviating nutritional stress in yam crops in each participating country. At that time, neither ACIAR nor the research team fully appreciated the complexity and difficulty of this task. It is a credit to the team that these project goals were achieved so comprehensively.

This book draws together what is currently known about the mineral nutrition of yams. As very little research had been published on this subject before the ACIAR project, most of the information presented on diagnosis of nutrient deficiencies and toxicities is the original work of the author, and has not been published elsewhere. It is intended to be a useful reference for agronomists and extension personnel. However, because the material is not readily available elsewhere, it also contains additional information that may be useful to researchers.



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Acronyms and abbreviations

ACIAR	The Australian Centre for International Agricultural Research
Al	aluminium
B	boron
Ca	calcium
CEC	cation-exchange capacity
Cl	chlorine
Cu	copper
Fe	iron
IITA	International Institute for Tropical Agriculture (Nigeria)
K	potassium
Mg	magnesium
Mn	manganese
Mo	molybdenum
N	nitrogen
Na	sodium
P	phosphorus
S	sulfur
Zn	zinc

Units

cm	centimetre
cmol(+)	centimoles of positive charge
dS	decisiemens
g	gram
ha	hectare
kg	kilogram
L	litre
m	metre
M	molar concentration = mole/L
me	milliequivalent = millimoles of electrical charge
mg	milligram
ppm	parts per million
S	siemens (a unit of electrical conductivity)
t	metric tonne = 1,000 kg

Conversions

Units of measurement used in the literature have been converted to standard units for inclusion in this text. Following are the standard units and their synonyms or conversions to other commonly used units.

cmol(+)/kg	= me/100 g
dS/m	= mS/cm = millimho/cm
mg/kg	= ppm = µg/g
1 kg K/ha	= 1.20 kg K_2O/ha
1 kg P/ha	= 2.29 kg P_2O_5/ha

Introduction

Root crops are the primary staple foods of the wet tropics, with yams being the most prized crop. Although the New World crops of cassava and sweetpotato have overtaken yams in range and volume, yams remain the dominant crop in the regions where they are best adapted. Where they have become subdominant, their cultural significance exceeds their dietary contribution.

In the Pacific region, yams are grown throughout the lowlands, but are the dominant staple in relatively few areas (Bourke and Vlassak 2004). These areas are geographically and culturally distinct from each other, but share a seasonal rainfall pattern.

In each yam-growing society, the yam is central to social organisation. In the Maprik district of Papua New Guinea's East Sepik province, yams are the sacred icon of the secret Abelam yam cults described by anthropologist Richard Thurnwald. On the Trobriand Islands, yams are the focus of the garden magic and the hierarchical social structures described by anthropologist Bronislaw Malinowski. The island of Pohnpei in Micronesia practices similar magic and ritual (Raynor et al. 1992). The famous land jump (the original bungee jump) on the island of Pentecost in Vanuatu is held annually as part of the traditional yam harvest festival. In Tonga, the word for year is synonymous with a crop of yam. The names of months mark events in the crop cycle, and great pride is still taken in the production of large tubers. Yam tubers grown for competition or presentation to nobility can exceed 60 kg in weight and 2 m in length.

A typical yam storage house, filled with tubers of D. esculenta, *in a village on Kiriwina Island, an atoll in the Trobriand group in Papua New Guinea. (Photo: Philip Holzknecht)*

This rich cultural heritage has been in decline in recent years. The decline may be attributed in part to the loosening of social obligations and a shift from communal to family organisation of labour, accompanying the influence of western culture and the cash economy. However, the apparent decline in productivity of yams that has accompanied intensification of land use has also contributed to the crop's diminishing status. As fallows have been shortened or cropping cycles extended, yields have declined, and pest and disease problems have intensified. More recently, introduced crops, such as sweetpotato, maize and cassava, have proved to be better adapted to more intensive cropping. Globally, the production of yams has continued to expand, but not as fast as the population in yam-growing communities, so their dietary role has declined.

The dependence of yams on well-fallowed land, and the yield decline observed when fallow length is shortened, has led to a general belief that yams require high nutrient levels in the soil. Yet the reported responses of yams to fertilisers have been erratic and usually of low magnitude, compared with effects of other agronomic variables, such as staking or the size of planting setts.

The lack of information on the nutritional requirements of yams, and on effective means of maintaining yam yields, was the motivation for the work that led to this publication. Ironically, this research has

*A long yam (*D. alata*) carefully suspended for storage and destined for ceremonial presentation in East Sepik, Papua New Guinea. (Photo: James Ernest)*

Tubers of D. alata *for sale in a Vanuatu market, displaying the wide range of tuber shapes among cultivars. (Photo: Grahame Jackson)*

called into question the assumption of high nutrient requirements of yams. Other features of long-fallowed land, particularly the soil microbiology, are likely to play an important role in the vigour of yam crops. Future research may do well to focus on changes in populations of mycorrhizal fungi, on which yams are highly dependent, and the ability of soil micro-organisms to control populations of plant-parasitic nematodes. However, the challenges of such research are not to be underestimated.

Although yams may be quite efficient scavengers of soil nutrients, like all crops they must have adequate supplies to achieve their growth potential, and nutritional disorders are indeed common. Another outcome of our research has been to reveal the unusual expression of symptoms in yams, which has probably led to poor recognition of nutritional stress. It is hoped that this book will help yam farmers and their advisers to better evaluate and manage the nutritional status of their crops.

Botanical and agronomic characteristics of yams

The term 'yam' refers to all members of the genus *Dioscorea*, which contains over 600 species. About 10 species are commonly cultivated for food, while a number of others are harvested from the wild in times of food scarcity (e.g. Bhandari et al. 2003). Many wild yam species contain toxic or bioactive chemicals, and some of these are cultivated for pharmaceutical products (Coursey 1967).

Although highly variable in appearance both between and within species, all yams share a common growth habit of thin, twining vines and a shallow, widely radiating root system, both of which die and are renewed each year. All economically important species are tuberous, producing one or more underground tubers, which are starch storage organs derived from stem tissue. The tubers provide a means of vegetative propagation from one season to the next. In most cases the tubers are annual—they shrivel at the start of the new growing season and are replaced by new tubers. However, some genotypes of several species produce perennial tubers, which may continue to grow over several years. Many species produce aerial tubers, or bulbils, as a means of vegetative dispersal.

Vegetative propagation is much more common than propagation by true seed, even among most wild yam species. Cultivated yams are almost exclusively vegetatively propagated. As a result, cultivars are clones of an ancestral plant, but spontaneous somatic mutations may have contributed to the diversity and productivity of modern cultivars. Yams are dioecious, with male and female flowers borne on separate plants. Cultivars may be male, female or sterile. Female plants tend to produce fewer tubers and therefore are relatively rare among cultivated yams. Breeding is inhibited not

Dioscorea esculenta *genotypes produce multiple tubers at the end of short stolons. Individual tubers rarely exceed 3 kg, but single plants can yield in excess of 15 kg of tubers. (Photo: Marie Melteras)*

just because there are few suitable females and the fact that many of the plants with the most desirable features do not flower at all, but also due to the existence of multiple ploidy levels (chromosome numbers) in most species (Hahn 1995) and the flowering of different genotypes at different times. Fertile seeds are produced only when males and females of similar ploidy level flower simultaneously. Nevertheless, promising breeding programs are underway for the most important species, with the exception of *Dioscorea esculenta*, of which no female plants have been found.

Origin and current distribution of major food yam species

Dioscorea is a pantropical genus and different species have been independently domesticated on each continent (Coursey 1967).

Dioscorea alata (greater yam or water yam) is the most widespread species. It was thought to originate in southern Asia, but recent genetic studies have identified Melanesia as its centre of origin, and this region remains its centre of diversity (Lebot 1999). Evidence exists of its domestication in New Guinea at least 10,000 years ago, and its existence in northern Australia is believed to be due to human introduction before the continent was separated from New Guinea by sea level rise 10,000 years ago. It is believed to have been among several Asian crops introduced to Madagascar by Austronesians some 2,000 years ago, and from there spread into mainland East Africa (Lebot 2009). It is not clear whether *D. alata* was established in West Africa before European contact, but it has since come to rival African species both there and in the Caribbean.

In West Africa, *D. cayenensis* (yellow Guinea yam) and *D. rotundata* (white Guinea yam) are endemic, and the main species cultivated. The distinction between these species is unclear, and some researchers prefer to refer to them as the *D. cayenensis–rotundata* species complex (Hahn 1995), while others argue that they should be recognised as separate taxa (Mignouna et al. 2005). Among nongeneticists, the distinction is usually retained for practical morphological reasons. The species status of West African yams is poorly defined in any case, as cultivars of both yellow yam and white yam may have arisen through independent hybridisation of wild or feral parents, including *D. abyssinica* and *D. praehensilis*, with little genetic exchange occurring naturally among members of either group (Chair et al. 2005). Cultivation of these species in Africa is believed to have started at least 7,000 years ago (possibly much earlier), and domestication of wild types continues today (Lebot 2009).

In Central America, *D. trifida* was domesticated by Amerindians. It has since been widely dispersed in Asia and the Pacific region, but remains a minor crop in all areas in which it is grown.

The origin of *D. esculenta* (lesser yam, mami) has not been established, but may be either in South-East Asia or Melanesia. In Papua New Guinea, *D. esculenta* is the dominant staple food species grown by yam-dependent communities, although *D. alata* retains its status for cultural and ceremonial purposes. This suggests that the domestication or introduction of *D. esculenta* occurred later, but may only reflect the greater potential tuber size and taste preference for *D. alata*. Melanesia was also the centre of origin of *D. nummularia* (spiny yam, wild yam), from where it has been dispersed through the Pacific region and is locally important.

Dioscorea opposita (also known as *D. batatas* and *D. japonica*) is the only species grown in temperate regions, and is widely cultivated in China and Japan, and more recently in France.

Today, West African nations produce approximately 94% of all yams (Table 1). Across that region, yams are the second most important crop on the basis of production volume, only exceeded by cassava. The rest of Africa accounts for half the remainder. The remaining 3% is grown in the Americas (particularly the Caribbean, having been introduced there with West African slaves), the Pacific region and Asia. On a per capita basis, the Melanesian nations follow the West Africans in yam consumption. Production in Polynesia is patchy, as not all islands have appropriate soils, but on those that do (e.g. Niue and Tonga), yams are highly prized and consumed at higher rates than in most of Melanesia. Consumption in Caribbean nations is similar to that in Central and East Africa. Among Asian nations, Japan, China and southern India are significant producers, but per capita consumption is low.

Regional statistics belie the local importance of yams for particular communities and cultures. Yams are particularly important in areas that experience seasonal drought, as they are the only tropical root crop that can be stored satisfactorily for extended periods after harvest. This capacity for postharvest storage facilitated the dispersal of yams along human migration and trade routes. They were particularly important in the colonisation of the Pacific islands, hence their esteemed status in Polynesian culture.

The tuber characteristics of each species differ in terms of dry matter content, starch quality, texture and flavour, which affect their suitability for different preparation and cooking techniques. These characteristics influence the local selection of species and cultivars.

Table 1. Comparison of annual tropical root crop production in major yam-producing regions, on a total yield and per capita basis

	Cassava		Sweetpotato		Taro		Yam	
	×1,000 t	kg/person	×1,000 t	kg/person	×1,000 t	kg/person	×1,000 t	kg/person
West Africa	63,224	226.3	4,247	15.2	7,279	26.1	48,898	175.1
Caribbean	933	22.8	548	13.4	17	0.4	488	11.9
Melanesia	180	22.6	614	76.9	377	47.2	335	41.9
Polynesia	18	27.6	8	11.6	35	53.8	9	13.4
World	221,283	33.6	105,207	16.0	11,632	1.8	52,166	7.9

kg = kilogram; t = tonne
Source: FAOSTAT, 2006 data

Local environmental factors also affect the selection of species. Compared with *D. esculenta* or the African yams, *D. alata* has a shorter growing season and is more tolerant of wet soils and cold temperatures. It consequently has a larger range in terms of both altitude and latitude. However, its greater susceptibility to foliar diseases, particularly the yam anthracnose caused by the fungus *Colletotrichum gloeosporioides*, limits its use in some warm, humid areas. In general, greatest production is achieved with genotypes that can fully use the available growing season. Consequently, long-season crops such as *D. esculenta* or *D. nummularia* can outperform *D. alata* in areas with only a short or mild dry season.

Single stands of wild yams are often grown opportunistically, such as in this Solomon Islands village. Such plants may become the basis for new cultivars. (Photo: Grahame Jackson)

Nutritional value of yam

Yam is considered to be the most nutritious of the tropical root crops (Wanasundera and Ravindran 1994). It contains approximately four times as much protein as cassava, and is the only major root crop that exceeds rice in protein content in proportion to digestible energy (Bradbury and Holloway 1988). The amino acid composition of yam protein is suboptimal in sulfur-containing amino acids (cysteine and methionine), but the overall rating for essential amino acids is high and superior to sweetpotato (Splittstoesser et al. 1973; Bhandari et al. 2003).

Yam is also a good source of vitamins A and C, and of fibre and minerals. Its relatively low calcium content is related to low concentrations of calcium oxalate, an antinutritional factor (Bradbury and Holloway 1988). It is also low in the antinutrients phytate (Wanasundera and Ravindran 1994) and trypsin inhibitor (Bradbury and Holloway 1988).

A number of authors (Bradbury and Holloway 1988; Wanasundera and Ravindran 1994; Agbor Egbe and Treche 1995) have commented on the variability in protein content within yam species, indicating potential for selection for high protein content. However, some of this variability would be due to varying degrees of nitrogen deficiency in the tubers sampled (Bradbury and Holloway 1988). Improving nitrogen nutrition of yams will increase protein production. However, the relative contribution of nitrogen nutrition and genotype to the observed range of protein content has not been determined.

Soil fertility as a contributing factor in yam yield decline

Anecdotal evidence exists that yam yields have declined in response to shortened fallow periods in many places in the Pacific region and Africa, suggesting that mineral nutrient supply is limiting yields. Nutrient deficiency symptoms observed on yam crops throughout the Pacific region include a range of micronutrient disorders on coral soils and river sediments, and magnesium deficiency on some volcanic soils with a high potassium content. Pale foliage colour is almost universal in areas of intensive cultivation, where deficiencies of both nitrogen and potassium commonly limit production. It is likely that other disorders are commonly overlooked; as shown below, the symptoms displayed by yam species are often not typical of the same disorder in other plants.

However, a number of other changes to the agroecosystem occur as cropping intensity is increased. Weed severity tends to increase. Inoculum of plant diseases and parasites builds up in the soil, or is more easily transferred from nearby crops as the distance between gardens is reduced. Repeated soil disturbance and removal of vegetation reduces soil organic matter, and consequently reduces the activity of soil micro-organisms. These micro-organisms provide many benefits to the crop by cycling nutrients, directly assisting in nutrient uptake, or reducing plant parasites and diseases. All of these factors interact in the phenomenon of yield decline, and these interactions are poorly understood.

Sources of information for the diagnosis of nutrient disorders in yam species

The information presented in this book is derived primarily from research undertaken by the author, as part of a Pacific regional project of the Australian Centre for International Agricultural Research (ACIAR). The project, running from 2000 to 2005, involved researchers in Australia, Papua New Guinea, Tonga and Vanuatu. The project aimed to provide diagnostic information for three species, *D. alata*, *D. rotundata* and *D. esculenta*, as well as investigating ways of alleviating nutritional stress in yam crops in each country.

To provide a basis for diagnosis of nutrient disorders, it is necessary to study the response of yam genotypes to the supply of each nutrient at a range of levels, in terms of the plant growth rate, visible symptoms and nutrient concentrations in plant tissue. The ACIAR study has been the first to induce nutrient disorders at varying levels of severity, and the first to achieve visible symptoms for a number of disorders. See Appendix for a summary of the methodology and results.

Relevant information from other published work is also collated. Obigbesan (1981) provided a valuable review of earlier research on yam nutrition. Gaztambide and Cibes (1975) described leaf symptoms of several nutrient deficiencies in *D. rotundata* 'Habanero' grown in sand culture, but critical tissue concentrations were not established in their study. Shiwachi et al. (2004) published results of a sand culture omission experiment with both *D. rotundata* and *D. alata*, but few deficiencies were induced to sufficient severity to induce distinctive symptoms, and no new information was gained over that of Gaztambide and Cibes (1975) and O'Sullivan et al. (2001). Vander Zaag et al. (1980) provided a valuable account of the response of several varieties of the three species to varying soil solution phosphorus concentrations. Abruna-Rodriguez et al. (1982) found yam (*D. alata*) to be much less tolerant of aluminium toxicity than cassava, sweetpotato or taro, but noted that there is variation in tolerance among yam genotypes. Johnston (1996) identified severe chlorosis on *D. esculenta* grown on high-pH soils in Papua New Guinea to be due to manganese deficiency, not iron deficiency as earlier assumed.

Apart from these studies, almost all work on yam nutrition has been in the form of fertiliser response trials, which are often difficult to interpret as the nutrient status of the soil and the plants has been poorly characterised in these types of studies.

Crop nutrition and nutrient disorders

From a human perspective, nutrients are constituents of food that we need in adequate quantities to build our body tissues and to fuel our activities. Plants also need to capture substances from their environment, to build their tissues and to function normally. Humans and other animals must feed on complex organic substances, including proteins, fats, carbohydrates and vitamins. Plants make these substances for themselves. They need only the fundamental building blocks of organic material—the chemical elements.

The most abundant elements in plants—carbon, oxygen and hydrogen—are obtained from the air and water. The others, referred to as mineral nutrients, are supplied by the mineral and organic components of the soil. They are divided into two groups, according to their abundance in plants. The macronutrients comprise from 0.1% to 6% of dry plant material, and include nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), sulfur (S) and chlorine (Cl). The micronutrients have essential requirements in the order of 0.1–100 mg/kg of dry weight (0.00001% to 0.01%) but may be present in higher quantities. They include iron (Fe), boron (B), manganese (Mn), zinc (Zn), copper (Cu), molybdenum (Mo) and nickel (Ni). Cobalt (Co), silicon (Si) and sodium (Na) are required by some plants, but have not been shown to be essential for yams.

Good plant nutrition means that each of these elements is available to the plant at an adequate rate of supply. Too little of any essential element will impair the growth and function of the plant. Too much may cause toxicity, or may interfere with the supply of another nutrient. A nutrient disorder occurs whenever too little or too much of any element causes suboptimal or abnormal growth.

Soils are derived from a wide variety of parent materials, and differ widely in the availability of each nutrient. It is very common for crops to be deficient in one or more of the mineral nutrients.

Table 2 lists mineral elements of interest in plant nutrition. Not all of the elements are essential nutrients, and some (including nutrient elements) can cause toxicity.

Causes of nutrient disorders

Nutrient deficiencies may arise because:

- the minerals that formed the soil had low levels of that nutrient
- the soil characteristics cause the nutrient to be insoluble or bound very tightly, so plants cannot take it up (e.g. alkaline coral soils, acid soils, phosphate-binding or peaty soils)
- the soil has been depleted of the nutrient, because it was removed in crop products, leached out by rainwater or lost as gas through burning of vegetation
- the roots are restricted in their growth, so they can only reach a small volume of soil (e.g. by soil compaction, saline subsoil, waterlogging, aluminium (Al) toxicity in acid soils or root damage by nematodes).

The approach to correcting a deficiency depends on which of these causes is present. For instance, do we just need to add the nutrient in a fertiliser, mulch or manure, should we change the root environment so that nutrients are more easily available, or can we manage the cropping system better to reduce nutrient losses?

Deficiencies of macronutrients, particularly N, P and K, are often associated with fertility decline following sequential cropping. These elements are taken up in such large quantities by the crop that the soil's reserves become depleted after a number of crops have been produced. Increasing cropping intensity results in an increasing dependence on external supplies of these nutrients. In low-intensity agriculture, supplies may be replenished during a bush fallow by:

- allowing time for weathering of mineral particles
- redistributing nutrients into the crop's root zone from below, using deep-rooted plants
- allowing biological N fixation
- capturing wind-borne nutrients from sea spray.

Table 2. Mineral elements affecting nutrition of plants, and incidence of deficiency and oversupply in crops

Element	Symbol	Amount in 1 t of plant dry matter	Deficiency	Toxicity and oversupply problems
Aluminium	Al	10–300 g	Al not essential	The main cause of root damage on acid soils
Boron	B	10–200 g	Fairly common; some crops are more susceptible	Toxicity caused by natural B or overfertilisation
Calcium	Ca	5–15 kg	Fairly common; some crops are more susceptible	Not toxic, but associated with highly alkaline soils, which cause micronutrient deficiencies
Chlorine	Cl	2–20 kg	Extremely unlikely	Contributes to salinity damage
Cobalt	Co	0.2–0.5 g	Rare—required for nitrogen fixation in legumes	Rare
Copper	Cu	5–20 g	Less common, usually on alkaline soils	Can be caused by accumulation of fungicides containing Cu
Iron	Fe	50–200 g	Common on calcareous (alkaline) soils	Rare, only problematic in paddy rice
Magnesium	Mg	1–4 kg	Less common	Not toxic, but might suppress K uptake
Manganese	Mn	20–300 g	Fairly common on alkaline soils; yams are susceptible	Fairly common on some acid soils
Molybdenum	Mo	0.1–0.5 g	On some acid soils	Rare, but overfertilisation can interfere with Cu nutrition in both plants and animals
Nickel	Ni	Trace	Never recorded	Rare
Nitrogen	N	20–40 kg	Very common	Overfertilisation can cause leaf burn and fruit damage
Phosphorus	P	2–5 kg	Very common	Overfertilisation can be a problem for some sensitive species
Potassium	K	10–50 kg	Very common	Not toxic, but can suppress uptake of other nutrients (Mg, Ca)
Silicon	Si	2–20 kg	Si not essential for most plants	Not toxic
Sodium	Na	0.1–20 kg	Na not essential for most plants	Salinity and sodicity are increasing problems of coastal areas and dryland irrigation
Sulfur	S	1–4 kg	Quite common	Not toxic
Zinc	Zn	10–100 g	Fairly common	Rare

g = gram; kg = kilogram; t = tonne

Nutrients accumulated by plants during the fallow become available to the crop as the plant material decomposes, or when it is burned. Burning makes many nutrients immediately available to the following crop, but it also makes those nutrients easily lost by leaching. Burning also decreases the soil's ability to continue supplying nutrients, as there is less organic material to decompose. Some nutrients, particularly N and S, are lost into the atmosphere during burning.

Deficiencies of micronutrients are usually associated with low natural abundance in the soil, or unfavourable soil conditions causing insolubility of these nutrients. In the case of low abundance, correction usually requires the application of the deficient nutrient at a rate of only a few kilograms per hectare, sometimes less, which may be effective for a number of years. Such inputs are likely to be cost-effective, even when the application of N or P fertilisers is not. The management is more difficult when the deficiency is due to adverse soil conditions, such as at low pH in acidic soils or the very high pH in alkaline soils. Applying the nutrient as a foliar spray is one way to avoid it being fixed in such soils. Increasing the organic matter content of the soil is also beneficial.

A yam farmer with his crop in Solomon Islands. Yellowing of young leaves is a common feature on soils formed on coral, as their alkalinity makes micronutrients such as iron and manganese less available. (Photo: Grahame Jackson)

Mineral toxicities may have a range of causes. Some elements that are relatively abundant in soils may only be available to plants sparingly under normal conditions. Adverse soil conditions may greatly increase the bioavailability of the nutrient, to the extent that toxicity occurs. For example, acidity greatly increases Al availability, and waterlogging may increase Mn uptake to toxic levels. In other instances, unwanted concentrations of elements may accumulate from the application of crop inputs, such as salinity caused by salts in irrigation water, or Cu toxicity resulting from frequent use of copper-based fungicides. Accidental overfertilisation is a risk for some nutrients, such as B. Specific circumstances are discussed in the section on mineral toxicities.

Diagnosing nutrient disorders

The first response of a plant to a deficiency of any nutrient is to decrease its growth rate. Specific symptoms, which may allow the deficient nutrient to be identified, usually occur only at relatively severe levels of deficiency. Nevertheless, such symptoms are often the first thing to alert the grower that there is a problem, and these symptoms are very useful for diagnosis. Since plant species differ in sensitivity to particular nutrient stresses, observation of symptoms in other crops in the same area should indicate to producers and advisers that the problem may also be affecting yam growth, even if symptoms are not evident on yam crops.

Chemical analysis of the plant tissue provides an additional diagnostic tool, which, when available, can be very valuable for confirming a tentative diagnosis based on visible symptoms, or identifying a suspected problem when symptoms are not visible. However, to interpret tissue analyses, both the concentrations expected in healthy tissue and the concentrations indicative of deficiency or toxicity need to be known. This must be determined separately for each species, and specified for the particular tissue sampled and the crop's stage of growth. Determining these standards for yams has been a central focus of the research presented in this book, and will be covered in greater detail below.

If a soil is low in several nutrients, the plant usually shows deficiency symptoms of the element that is most limiting to growth. If that nutrient is supplied, the growth rate will increase until it is limited by the next most scarce nutrient, and a new set of symptoms may develop. It is difficult to establish from plant symptoms or tissue composition which nutrients are likely to be deficient other than the one that is most limiting. Soil tests may provide some guidance, but they need to be calibrated for each crop and soil type before they can be interpreted with confidence.

One of the simplest and most reliable methods of discovering which nutrients are deficient in a soil is through small pot trials. In nutrient omission pot trials, each pot receives an adequate supply of all the mineral nutrients (control, or 'All' treatment), or 'All' minus one. Thus, in each omission treatment, the plants depend on the soil for the supply of only the omitted nutrient, as all other nutrients are supplemented. Plants are grown for a short period (usually 4–6 weeks), and the dry weight of tops is compared with that of the 'All' treatment. Any nutrient whose omission results in a

significant decrease in weight is regarded as deficient. Usually, an indicator plant such as maize is used, which offers rapid and uniform establishment from seed, and well-characterised responses to nutrient deficiencies. However, nutrient levels that are deficient for one species may be adequate for another. Yams have been successfully grown in pot trials, but their high variability in establishment and growth rate means that success will require a higher than usual number of replicates and attention to detail in trial maintenance. The methodology for nutrient omission pot trials is explained in detail in Asher et al. (2002).

If a nutrient deficiency is suspected in a crop, the best way of confirming it is by observing a positive response to fertiliser containing that nutrient. When testing a fertiliser response, it is important to have an untreated area for comparison. Usually a test strip in the middle of the field is treated with fertiliser. Alternatively, fertiliser may be applied to the whole field, with the exception of a central strip, which would remain unfertilised. For yam, the fertilised area should be separated by several metres from the area regarded as unfertilised, because yam roots have an unusually long reach, commonly exceeding 3 m and possibly exceeding 5 m (Melteras et al. 2008; O'Sullivan 2008).

Another useful technique for confirming deficiencies of micronutrients is leaf painting. By carefully painting half of an affected leaf with a dilute solution of the suspected nutrient, the response can be seen by comparing the colour or expansion of the painted half with the unpainted half. Leaf painting has been used successfully to diagnose deficiencies of Fe, Mn, Zn, Cu and Mo in yam. Details are given in the text for each of these deficiencies.

Interpreting visible symptoms

Due to the different role played by each nutrient in the plant, each nutritional disorder tends to produce its own characteristic symptoms. Visible symptoms provide a useful diagnostic tool that is not dependent on costly laboratory equipment or time-consuming chemical analyses. However, some disorders produce rather similar symptoms or no symptoms at all, and the effects of insect pests and diseases may produce symptoms similar to those of nutritional disorders. Environmental conditions (e.g. moisture supply, temperature, light) may affect the appearance and severity of nutrient disorders. Cultivars may also differ in their expression of symptoms. Nevertheless, there are often distinct patterns, and a careful observer can usually reduce the number of possible causes to a few, if not to a single suspect. Tentative diagnoses can then be confirmed by using fertiliser test strips, soil tests, leaf painting or plant tissue analyses.

Visible symptoms often take the form of 'chlorosis', the reduction of green colour (chlorophyll pigment) in the leaves. Chlorotic tissue may be light green, yellow or whitish. Tissue furthest from the veins is often the most severely affected, as it is last in the supply line. Hence, chlorosis patterns are frequently described as 'interveinal' if the tissue on and adjacent to the veins retains a darker colour than the remainder of the leaf. To what degree the minor veins retain their colour in addition to the major veins, and the distance over which the colour change is graduated, are additional features that aid diagnosis. If the chlorosis affects the whole leaf blade uniformly, it is referred to 'general'. 'Vein clearing'—when the veins become paler than the rest of the blade—is more often a symptom of viral infection than of a nutritional disorder.

'Necrosis' is the death of tissue. It may occur following chlorosis as part of a progressive degradation, or it may arise in localised zones of the leaf due to a sudden dysfunction. The location, shape and size of necrotic lesions are useful discriminators, as are the colour and texture of the dead tissue.

Other types of symptoms include changes in the shape or dimensions of plant parts, such as thickening, cupping or curling of the leaf blade, size reduction of the blade, deformities causing irregularly shaped or incomplete leaf blades, or shortening of internodes in the stem.

In addition to the appearance of a particular symptom and the speed with which it develops, the position or location of that symptom on the plant must be noted. Symptoms are often not apparent early in crop development (while the shoot is dependent on the mother tuber), but may intensify as the seed reserves are exhausted, or as the demands of the vine overtake the capacity of the roots to supply them. Often, it is the youngest leaves and shoot tip that show greatest stress.

In most plants, several of the macronutrients can be remobilised from older leaves to supply the shoot tip, and in this case the symptoms appear on the oldest leaves in the form of premature senescence. This is normally the case for N, P, K and Mg, and to a varying extent, for S. An unusual feature of yams, compared with other plants, is that they appear to have little tendency to remobilise these nutrients in response to a deficiency in the shoot. This is particularly the case for P deficiency, where acute symptoms commonly appear on the youngest leaves. Symptoms of N, K and Mg deficiency tend to be distributed throughout the plant, and some remobilisation may occur. After the onset of tuber development, plants may respond to the tubers' demands for nutrients by remobilising nutrients from the oldest leaves to tubers. Deficiencies tend to cause

vines to senesce earlier, or conversely, fertilisation is often observed to cause vines to stay green and active for longer.

Elements taken up in excess of plant requirements usually continue to be accumulated during the life of a leaf. Thus, there will be a tendency for toxicity symptoms to appear first on the older leaves where accumulation has been occurring for the longest time. However, when toxicities damage roots and limit the uptake of other nutrients, younger leaf symptoms may develop in response to micronutrient deficiencies (particularly Fe deficiency) induced by the toxicity.

Interpreting tissue analyses

Chemical analysis of plant tissue is also an important technique in the diagnosis of nutritional disorders. Due to the time delay in sending samples for analysis, the result may be too late to help the current crop, but can confirm the cause of a particular symptom and will inform the management of future crops.

The interpretation of tissue analyses is based on established relationships between crop yield and nutrient concentrations in plant tissue (Figure 1). Critical concentrations are those which separate the sufficient (healthy) range from the deficient or toxic range. For practical purposes, critical concentrations are defined as those concentrations associated with 90% of maximum yield (Ulrich and Hills 1973). Because the relationship between nutrient concentration and growth rate is not a rigid one, there is variability in the concentration associated with 90% of maximum yield, so many workers prefer to define a critical range. The probability that plant growth is limited by undersupply or oversupply of a nutrient is high if that nutrient is below a critical range for deficiency or above the range for toxicity. Within the critical range, the probability that plant growth is altered varies from high to moderately low. In the adequate range, there is a low probability that the supply of the nutrient is growth-limiting.

The relationship between crop yield and concentration of a particular nutrient in plant tissue may be determined by means of nutrient solution culture experiments, glasshouse pot experiments or field experiments. Generally, field experiments are considered the best (Bates 1971), but are considerably more expensive than solution culture and pot experiments. They also depend on the availability of sites that are deficient in each of the nutrients to be studied. The values given in this book have been derived from solution culture experiments. Where possible, their reliability has been validated under field conditions.

Selecting tissue for sampling

Different parts of a plant have different structure and function, and consequently different concentrations of nutrients. Therefore, the way we sample plant tissue affects the nutrient concentrations we find in them. As it is not practical to sample whole plants, a certain part of the plant is usually specified for sampling. This is referred to as the 'index tissue', and the concentrations listed as representative of deficiency or toxicity are specific for this tissue.

Leaves are usually considered the most satisfactory parts for sampling. Because leaves often change their nutrient composition with age, it is important that leaves of the same physiological age are compared.

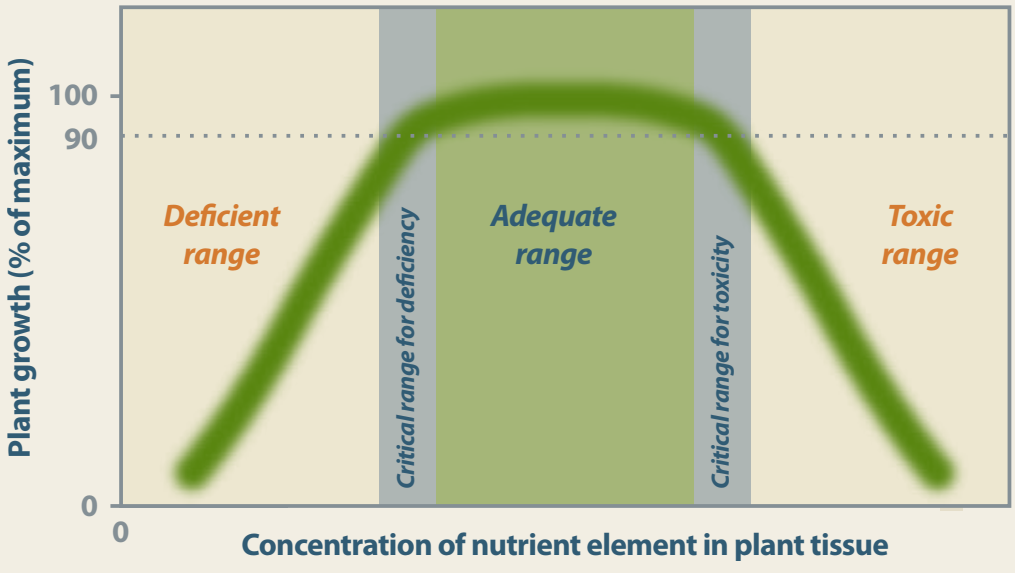


Figure 1. Schematic relationship between the concentration of a nutrient element in plant tissue and plant growth or yield, assuming other requirements for growth are not limiting.

In many annual crops, the blade of the youngest fully expanded leaf is selected as the index tissue for analysis. However, yam leaves may continue to expand throughout much of their life, so their physiological maturity cannot be judged easily on the basis of full expansion. Various researchers have collected leaves using different criteria, and it is difficult to compare the nutrient concentrations they have quoted.

Frequently, researchers recommend different tissue for the measurement of different nutrients. For instance, petioles (leaf stalks) are often preferred for assessment of K status, as their K concentrations are higher and more responsive to K supply than the concentrations in leaf blades (e.g. Obigbesan and Agboola 1978). However, this is a matter of degree, and does not warrant the complication of defining a range of different index tissues for different purposes. As long as the reference concentrations are calibrated for the specified tissue, it is not critical whether this tissue is the ideal choice for a particular nutrient.

For the work described in this book (which is the original work of the author), index leaves were defined by counting the nodes from the first open leaves of a vine tip. Open leaves are defined as those that have flexed back so their upper surface faces away from the vine (Figure 2). The first node is the one with the youngest open leaves, and nodes are counted back down the vine (regardless of whether there are one or two leaves at each node).

For *D. alata* and *D. rotundata*, leaf blades from the fifth and sixth nodes were found to be satisfactory index leaves. They were sufficiently mature that nutrient concentrations were not rapidly changing with age, and not too far from the tip to make counting difficult. Leaves may not be fully expanded until 10 or more nodes from the tip, but at this point they may be entangled in the vine mass and it is difficult to trace the vine back.

In *D. esculenta*, leaves tend to remain small and covered densely in hairs for some distance from the tip. The fifth and sixth nodes were often still in this immature stage, but leaves at the seventh and eighth nodes were usually more mature, although not fully expanded. Immature leaves are not ideal for analysis because of the rapid changes in nutrient concentration with leaf position. Their hairiness is also undesirable, as it makes representative sampling of dried and ground tissue difficult because the hairs tend to separate in clumps. Therefore, the seventh and eighth leaves of *D. esculenta* were chosen as the index tissue (see Figure 3). However, with only one leaf at each node in this species, internode distances tended to be shorter, so the distance from the tip to the index leaves was no greater than in *D. alata*.

Figure 2. Index leaves for sampling are identified by counting nodes from an active tip. The first node counted is the youngest bearing 'open' leaves, which are tilted away from the stem (bottom pair of leaves pictured). Those still pointing toward the tip are not counted (top pair of leaves).

Figure 3. A vine tip of D. esculenta *showing the first six open leaves, beside mature leaves from the middle section of the vine. Rapid expansion begins at about the fifth leaf on actively growing vines. By the seventh leaf, leaves lose most of their hairiness and are well expanded.*

Table 3 gives the estimated values for critical range for each disorder in *D. alata* (see Appendix for details). Our data indicate that similar values apply for *D. rotundata* and *D. esculenta*, with the exception of likely lower critical ranges for K and Ca in both species, and for N in *D. esculenta*. Insufficient evidence has been collected relating to N deficiency in *D. rotundata*. Indicative critical ranges for these deficiencies have been added to Table 3; however, nutrient rate experiments have

Table 3. Critical nutrient concentrations for deficiency and toxicity of mineral nutrients for *D. alata*, *D. rotundata* and *D. esculenta*

		D. alata	*D. rotundata*	*D. esculenta*
		(leaves from 5th and 6th nodes)		(7th and 8th leaves)
Disorder	Unit	Critical range	Indicative range where different from *D. alata*	
Deficiency of:				
Nitrogen	%	2.9–4.0	Possibly lower	2.0–2.6
Phosphorus	%	0.21–0.37	Similar	Similar
Potassium	%	2.1–3.9	2.2–2.8	2.1–2.6
Calcium	%	1.0–1.5	0.5–0.9	0.5–0.9
Magnesium	%	0.10–0.14	Similar	Similar
Sulfur	%	0.10–0.14	Similar	Similar
Iron	mg/kg	25–45	Similar	Similar
Boron	mg/kg	9–20	Similar	Similar
Manganese	mg/kg	10–15	Similar	Similar
Zinc	mg/kg	15–35	Similar	4–6
Copper	mg/kg	2.0–3.6	Similar	Similar
Molybdenum	mg/kg	<0.8	Possibly lower	Possibly lower
Toxicity of:				
Sodium (salinity)	mg/kg	400	Not tested	Not tested
Boron	mg/kg	220–300	Similar	Not tested
Manganese	mg/kg	5,000–7,000	Similar	Not tested
Zinc	mg/kg	280–400	Similar	Not tested
Copper	mg/kg	20–30	Similar	Not tested

kg = kilogram; mg = milligram

Note: *D. alata* data were obtained from experiments in solution culture, and were measured in the leaf blades from the fifth and sixth nodes bearing open leaves from the shoot tip, sampled around 70 days from sprouting. Evidence from *D. rotundata* and *D. esculenta* , including samples from solution culture, sand culture and field experiments, suggest similar responses for most disorders, but indicative ranges are suggested for those disorders where species differences are evident. Disorders marked 'lower' apparently have a lower critical concentration than in *D. alata*, but evidence is insufficient to specify a range.

not been conducted to confirm these estimates. See Appendix for more detail on the derivation and discussion of these critical values.

Apart from the physiological age of the leaf, as indicated by its position on the plant, tissue composition may vary with the age or stage of development of the crop. For instance, in some crops the critical concentration for N deficiency is found to decline with crop age. Caution should therefore be exercised in applying the critical concentrations established for young plants to tissue taken from older crops. The critical concentrations quoted in Table 3 refer to young plants, around 2–3 months after emergence, while vine tips are still growing and before the onset of rapid tuber filling.

Environmental conditions may further affect the concentrations of nutrients found in leaves. The concept of critical nutrient concentration requires that the nutrient of interest is the only growth-limiting factor when the plant material is sampled. It has been shown that water stress can change the nutrient concentrations in leaves. Plants take some time to recover their normal nutrient concentrations after restoration of adequate water supply (Reuter and Robinson 1986). For example, to establish the P status of *Stylosanthes humilis*, Fisher (1980) recommended that a period of several weeks without water stress should precede the sampling of tissue. This is not practical in many situations, but users should be mindful of this potential source of error.

Collecting and preparing leaves for analysis

To collect leaf samples, the blades are removed without the petiole. The laboratory should be consulted to ask what quantity of material is required per sample. Generally three to five leaves will suffice, but including more leaves per sample reduces the potential for random variability.

When sampling a crop, it is best to take a composite sample of leaves from several plants that are equally affected by the symptom of concern. If the crop is not uniformly affected, several samples could be taken, each from small, uniform areas of the crop, from the most to the least affected. The observed symptoms and level of severity should be recorded for each sample, and the samples clearly labelled. It is preferable to number the samples sequentially and to keep a record of all sample details against each number before sending them to the laboratory for analysis.

It is important to sample leaves that have not been contaminated with soil. If the leaves are dusty, they may be gently rinsed and blotted dry, but extended immersion in water and rubbing should be avoided. Only distilled or deionised water should be used.

Samples should be dried as soon as possible after sampling, using gentle heat (e.g. 60–70 °C for 48 hours) or microwaving, until they are crisp. Sundrying is acceptable if conditions are good for rapid drying. If samples must be stored for more than a few hours before drying, it is preferable to keep them cool (e.g. in an ice box) to minimise the weight loss due to respiration of the living tissue. Well-dried leaves will still be green after drying. Those that have degraded before drying, or have been dried at too high a temperature, may be brown to black. Their nutrient concentrations may not be representative of the original tissue.

Soil analysis

The total amount of a nutrient in the soil does not generally reflect the quantity available for uptake by plant roots. Soil extraction and analysis methods have been developed (and continue to be developed) to estimate the quantity of a nutrient that is available to the plant. The method must provide a good estimate of nutrient availability in a defined range of soil types and soil analysis methods must be rapid, accurate and reproducible before being accepted for routine use in soil-testing laboratories.

The results of soil analyses are interpreted on the basis of previously established relationships between crop yield and soil test. These relationships may be established by means of glasshouse pot experiments or field experiments. In either case, they are specific to both the soil type and the crop species (and to some extent, the cultivar) used in the experiments, and can be applied to other crops or soils only with a degree of caution and uncertainty. As of 2009, very little research had been done to document relative yield or fertiliser response of yam species in relation to soil tests for specific nutrients.

One advantage of soil analyses is that they can be conducted before a crop is planted, allowing for the application of appropriate fertiliser. Disadvantages of soil analyses include (Melsted and Peck 1973):

- difficulties in selecting a testing method that is suited to a variety of soil types
- problems in sampling due to soil variation across a field
- problems in estimating the likely effects of environmental conditions in the forthcoming season.

Correcting nutritional disorders

The approach taken to improving crop nutrition will depend on the grower's situation. Where fertilisers and water are readily available and relatively inexpensive, growers may aim to maximise the crop's potential by eliminating any nutritional stress. Where fertilisers are unavailable or too expensive, or where water stress or disease load is likely to limit crop potential, the aim may be to optimise use of resources in the agroecosystem in order to gain an adequate and sustainable reward for the grower's labour. The rate of cropping that is sustainable depends on the extent of nutrient recycling from the crop the back to the soil as well as the time required for soil reserves to be mobilised or organic material to accumulate to replenish the nutrients and biological functions of the soil.

At whatever level of operation, it is important to recognise the limitations of the resource base. A traditional cropping system may become unsustainable through intensification, whether by increasing the number of crop cycles between fallows or shortening the fallow period. Intensification is frequently paralleled by a shift from subsistence to cash cropping. There are two important implications of this shift. Firstly, there is a reduction in nutrient cycling from the crop back to the soil, as crop products are less likely to be consumed locally. Secondly, an increase in cash income, meaning that purchased inputs, such as fertilisers, may become accessible and profitable for farmers.

Various aspects of managing crop nutrition and soil fertility are discussed in the next chapter. Measures for the correction of specific nutritional disorders are discussed in the section for the particular disorder.

Managing soil fertility

A fertile soil is one that allows a plant to grow and develop to the maximum extent possible, given the genetic background of the plant and the environmental influence of temperature, moisture and sunlight.

Fertile soil provides all the mineral nutrients in appropriate quantities to meet plant needs. However, there is much more to fertile soil than its nutrient content. It must also have an appropriate chemical environment (i.e. not too acidic or alkaline), so that the nutrients present are also available to plants and to avoid some toxic effects that occur at extremes of pH. Fertile soil must be able to hold a lot of water, to continue sustaining plant growth over short dry periods. However, it must also have plenty of air spaces, so that the roots can breathe. Fertile soils also support a diverse ecology of micro-organisms and small animals that contribute to crop health in a variety of ways.

Fertile soil has nutrients that are readily available to plants, but also has substantial stores of nutrients that are released slowly to replace those taken up by the crop. In this way, the soil supports crop growth and removal of harvests over several years or decades. This ability to provide a steady environment, despite nutrient removal or other changes, is called 'buffering'. However, every soil has a limited buffering capacity—even the most fertile soils would eventually be depleted if crops are continuously removed, taking mineral nutrients with them, and nothing added to replace the nutrients.

Organic matter

Fertile soil usually contains a lot of organic matter. This is the decomposed remains of plants and animals that have become part of the soil. When plant leaves or roots die, they become invaded by microscopic organisms (mainly fungi and bacteria) that eat them and break them down. Most of the material is used to provide energy for these organisms, but some of it is hard to digest and remains in the soil for a long time. This microscopic and molecular-scale organic matter is referred to as humus, and gives well-developed soil its black colour.

The organic material improves soil fertility because it can:

- provide nutrient reserves that are steadily released
- hold a lot of water for its weight
- support a healthy diversity of micro-organisms
- improve the physical structure of the soil, allowing better penetration of air, water and plant roots.

When soil is tilled and crops are grown and removed, the soil's organic matter is not replaced as fast as it is broken down, so it becomes depleted. Traditionally, the land is fallowed to restore its organic matter content. Fertilisers can be used to replace fallowing for a period of time by replenishing nutrient supplies, but organic matter decline may gradually reduce fertility through deteriorating soil structure, buffering capacity and ecological balance. Improved farming techniques can allow continuous cropping without depleting organic matter, but they may not replace all the beneficial effects that fallows provide.

Tillage and soil preparation

Yams prefer a light-textured, well-aerated soil. Tillage reduces the density of the soil, and generally increases yields unless soils are naturally loose and well structured (Lugo et al. 1993). In traditional systems, tillage is localised at the planting station for each plant. Compacted soil limits development of the tubers, so a hole is generally dug to the full depth that tubers are expected to grow, and back-filled with loose, stone-free soil. The planting sett is placed on top of the loose soil, and a mound is formed by gathering surrounding topsoil. Where mechanical tillage is used, the soil is normally ridged. The benefit of ridging or mounding depends on the soil texture and drainage—free-draining soil may yield equally well without mounding (Maduakor et al. 1984, Lugo et al. 1993). However, mounding may also be used to prevent the developing tubers being exposed at the soil surface. Agbede (2005) found that soil bulk density was negatively correlated with tuber length, leaf nutrient concentration and yield.

Fallows and auxiliary crops

Fallows play a very important role in traditional farming in the tropics. During the fallow, the land is 'rested' in order to recover its fertility. Natural vegetation is allowed to grow. In a good fallow, some of those plants are legumes, which are able to fix nitrogen (N) from the air, so that the soil N supply is gradually restored through the natural composting of the leaves and roots from the legumes. Trees and other deep-rooting plants take up nutrients from deep layers of the soil where crop roots cannot reach them. In this way, they can help restore nutrient availability for the subsequent crop, when these nutrients are returned to the topsoil by the decay or burning of the trees.

During the fallow, pests and diseases that damage the crop may also be reduced. This is because they do not have appropriate host plants to feed on or because of the increase in other organisms that may eat them or compete with them. For yams, it is particularly important that the populations of plant-parasitic nematodes are reduced. Other beneficial organisms may also build up in the soil, such as mycorrhizae. These fungi help plants capture nutrients from the soil in return for some of the 'food' plants make through photosynthesis. Yam crops are usually heavily infected with mycorrhizae and have probably come to depend on these fungi to extract nutrients from the soil, since yams have relatively few fine roots.

Many traditional farmers burn the fallow vegetation when they are ready to plant crops. Burning releases the nutrients in the vegetation quickly, so that initial crop growth is lush. However, there are some problems associated with this process. Some of the most important nutrients, especially N and sulfur (S), are lost into the air during burning. Other nutrients may be more easily leached or eroded away by heavy rainfall because the soil surface is exposed during the establishment phase of the crop. An alternative method is to allow the fallow vegetation to rot naturally. This gives a slower release of nutrients, but allows almost all the nutrients to be recycled back into the soil. However, an advantage of burning is that it may also have a role in reducing the incidence of pests and diseases. In these situations, other management practices may be needed to control pest problems in a no-burn cropping system.

As land becomes scarce due to population growth or increased competition between food crops and cash crops, the first response is usually to shorten the fallow period. In many places, fallows that were once more than 10 years are now only 1–3 years. This is not enough time for forest species to become established and produce seeds for the next generation. Short fallows become dominated by grasses and woody shrubs. Although grass roots are good at restoring soil texture, they are not as good at restoring the balance of nutrients and micro-organisms.

'Improved' fallows or 'planted' fallows are short fallows where the farmer deliberately plants particular species at the end of the crop cycle to increase the efficiency of the fallow. Improved fallow species may be:

- legumes to build up N
- deep rooting to capture potassium (K), S and boron (B) from deep soil layers
- chosen for their ability to suppress crop pests and diseases
- able to provide other services, such as pole timber for fencing or staking yams
- pruned or ring-barked to provide live stakes.

A planted fallow of Gliricidia sepium*, in the Bogia district of Papua New Guinea. (Photo: James Ernest)*

A planted fallow of Gliricidia sepium*, like the one visible in the background, was used to suppress grass before the establishment of this* D. esculenta *garden on former grassland, in the Bogia district of Papua New Guinea. (Photo: James Ernest)*

'Cover cropping' involves the growth of a crop, usually a legume, to improve soil conditions for subsequent crop growth. Benefits include conserving soil moisture, reducing soil temperature, reducing weed competition, and improving soil physical and chemical properties (Obiagwu 1997a). Cover crops may be intercropped, relay planted or planted in sequence with the main crop. The cover crop may produce an economic yield of grain or the biomass produced by the cover crop may be only used for mulch. Thus, some cover crops may be regarded as intercrops or rotations, and others as improved fallows. Examples of the use of legumes in yam cropping systems are reported by Obiagwu (1995 and 1997b) and Obiagwu and Agbede (1996).

Mulch is the term used for plant material (either fresh or waste material from crop processing) placed on the soil surface. It is an effective method of increasing soil organic matter gradually over a period of years. It also has immediate benefits in retaining soil moisture and reducing soil temperature. The cooler, moister conditions can significantly increase yam emergence and early growth, and hence yield (Maduakor et al. 1984; Olasantan 1999). Mulch suppresses weeds, reduces erosion and is a source of nutrients for the crop. The yield advantage of mulch is greater in drier climates (Lebot 2009), but in wet climates a management advantage may be gained if the mulching system is not too laborious.

*A cover crop of velvet bean (*Mucuna pruriens*) in Papua New Guinea. (Photo: James Ernest)*

Fertilisers and soil amendments

Fallowing and cover crops alone may not be enough to fully restore a soil that has been cropped several times or to make a naturally poor soil fertile. Fertilisers may be needed when the supply of a nutrient is deficient, even after fallowing. The type and amount of fertiliser required depends on the soil and the crop.

Nutrient deficiencies are alleviated by increasing the supply of the deficient nutrient. Applying inorganic fertilisers is one way of doing this. Another may be to add organic material, such as animal manure, if it contains an appropriate balance of the required nutrients. Other approaches aim to change the soil properties in order to increase the availability of nutrients already present or to reduce the supply of elements causing toxicity. The pH of acid soils may be increased by adding lime (calcium carbonate [$CaCO_3$]) or dolomite (calcium magnesium carbonate [$CaMg(CO_3)_2$]). Gypsum (calcium sulfate [$CaSO_4$-$2(H_2O]$]) may be used to correct problems of soil surface crusting and poor permeability in saline and sodic soils. In soils prone to waterlogging, improved drainage may be necessary to reduce both denitrification and the production of toxic forms of manganese (Mn), or simply to ensure that the roots receive enough oxygen to function well.

The timing and placement of nutrient applications are important issues. Forms of nutrients and amendments that are relatively insoluble, or which need to be well distributed to optimise root function, are usually applied before planting. During land preparation, lime, gypsum, Mg or B supplements, or manures can be mixed through the soil. In the case of phosphorus (P), it is usually better to confine the fertiliser to a narrow band or a localised zone around each planting station, as less P will be bound up by the soil if it is localised at high concentrations than if it is dispersed at low concentrations.

Soluble nutrients do not need to be incorporated, so they can be added later. They also have a greater potential to be lost from the soil if applied too early (i.e. before the crop is ready to use them). This applies particularly to N sources, but also to K on light-textured soils. These may be applied in one to three doses at intervals after the crop has established. Regular applications of fresh plant mulch also provide a steady release of these nutrients.

Where micronutrient deficiencies occur, it is often because of the high potential of the soil to bind them, so additions to the soil may be ineffective. Foliar sprays may be needed, and may be required several times through the growing season.

The planting system for yams influences the placement of fertiliser. The most common planting system involves digging a hole large enough to accommodate the tubers that are expected to form, and then back-filling the hole with loosened soil (with any rocks or roots removed). The planting sett is placed near the natural ground level and then soil is mounded up over it. Where mechanical tillage is used, yams are usually planted in ridges.

When fertilisers are applied at planting, they are often incorporated into the loosened soil in the planting hole. If they are applied after crop establishment, they

Women planting a yam garden on newly cleared land, Banks Islands, Vanuatu. (Photo: Oniel Dalesa)

Farmer applying fertiliser in a groove around the mound, showing evidence of root disturbance. (Photo: James Ernest)

are usually placed in a shallow furrow or groove around the base of the mound, or along the base of the ridge, and covered with 3–4 cm of soil.

Burying the fertiliser reduces losses of N by the release of ammonia or N oxides into the air. It may also ensure greater access to roots, as the soil remains moister and at a more stable temperature away from the surface. However, it is laborious and risks damaging the yam roots. Yam roots radiate from the crown of the plant and remain just under the soil surface for some distance before branching and descending (Melteras et al. 2008; O'Sullivan 2008). By using an implement to cut a furrow around the mound, there is a danger of severing or damaging a high proportion of the roots near their base. This damage may be responsible for the negative response to fertilisation reported in several studies. A furrow along a ridge is less damaging, as a smaller proportion of roots may be intercepted. Placing the groove higher up on the mound or ridge reduces the chance of root damage, but may reduce the accessibility of the fertiliser to roots if this soil is inclined to dry out between rainfalls. A preferred method of burying fertiliser may be to insert it into a series of stake holes in the side of the ridge or mound.

The excavated root system of a young plant of D. esculenta *(11 weeks after planting), showing shallow seminal roots radiating from the crown, with relatively few and short branches. By 20 weeks, most seminal roots exceeded 2 m in length and some exceeded 4 m. (Photo: Marie Melteras)*

On sandy soils, Nwinyi and Enwezor (1985) found that broadcasting of fertiliser was equally as effective as banded or ring placement, and therefore preferable as it required much less labour. When fertiliser was applied on the soil surface in the furrows between the ridges, yield improvement was usually less, which they attributed to higher levels of leaching in furrows on sandy soils. Furrow application gave the highest yield when the application was followed by a dry period (so that leaching was reduced) and when fertiliser applied on ridges was probably less available to the plants due to the drying of the soil. As these studies demonstrate, yam root activity is not confined to mounds or ridges, but is equally high beneath the furrows.

More research is needed on fertiliser application methods in varying climates and soil textures. For top dressings of N or K fertilisers, broadcasting may be a preferred strategy, if it is soon followed by rain or if applied immediately before applying a layer of mulch. Broadcasting is not recommended for superphosphate, which should be kept in a concentrated zone to prevent fixation. For mounded planting, the recommended method for superphosphate is to apply it in a ring (of about a 15 cm radius) around the sett before mounding up. For ridge plantings, banding along the sides of ridges before or soon after planting is recommended. For K, deep placement has been shown to improve responses in some crops, but has not been investigated in yam. Applying a proportion of the K to the soil in the planting hole may be preferable to top dressing all of it. Soil texture should influence the proportion of K applied at planting—on very sandy soils, where high levels of leaching are expected, top dressing in

several doses might be advised. On heavier soils, where leaching losses are less likely, between one-half and the complete dose could be applied at planting.

The optimum timing and placement for different nutrients should be considered when deciding on the type of fertiliser to use. Best control of fertilisation is achieved by using separate fertilisers for each of the nutrients required. However, this requires a greater level of understanding by farmers. Farmers are commonly encouraged to use a compound fertiliser, containing N, P, K and possibly Mg, and a range of micronutrients, mixed into a single product. With these products, compromises must be made to the ideal treatment of individual nutrients. In general, the application should be guided by the optimum timing for N, which is in two or three doses applied 2–4 months after planting. However, the placement may need to take into consideration the crop's requirement for P and the P-fixing potential of the soil. Banding or multiple-spot applications would be preferred over broadcasting, except on soils where P fixation is known to be low.

Selection of crop genotypes

Plant species, and even cultivars within species, differ in their sensitivity to extreme nutrient levels in the soil. They may vary in their ability to take up nutrients when they are scarce, or in their requirement for a particular nutrient so that they maintain their yield despite its scarcity. They may vary in their tolerance of toxic concentrations of elements. Therefore, the selection of appropriate crop genotypes is also a useful strategy for addressing nutritional problems.

For some crop species, agricultural scientists have developed cultivars that are resistant to particular nutrient problems, such as sunflower cultivars tolerant of low B supply (Blamey et al. 1984) and barley cultivars resistant to B toxicity. In sweetpotato, there is evidence of regional adaptations conferring tolerance to low N (Jones and Bouwkamp 1992) and possibly to low B (D'Souza and Bourke 1986). Researchers have identified sweetpotato cultivars that are tolerant of aluminium (Al) (e.g. Ritchey et al. 1991), or of salinity and B toxicity (Chávez et al. 1995). To date, yams have not been selected for tolerance to specific soil conditions. Abruna-Rodriguez et al. (1982) noted that varieties of *D. alata* vary somewhat in their tolerance of soil acidity, but no systematic work to identify tolerant varieties has been reported.

Nutrient requirements of yams

It is common for papers reporting fertiliser trials to state their aim was to 'determine the fertiliser requirement of yams' or to announce that 'nitrogen is the most important nutrient for yam'. It is not useful, however, to regard fertiliser requirements in these terms. The requirement for any crop at any site depends on the soil's ability to supply the nutrient and on the crop's potential to use it.

There are two components of the soil's ability to supply a nutrient. They are:

- the concentration of the nutrient in the soil solution, or the readily available pool which may include loosely bound nutrients as well as those in solution
- the total quantity of the nutrient in mobilisable pools.

This latter component may include chemical forms bound to soil particles or incorporated in organic material. Thus, there are different effects of intensity and quantity. A soil with a high binding capacity for a nutrient may have large reserves, but may maintain very low concentrations in the soil solution. Many crops may respond to fertilisation on these soils, even though there is enough of the nutrient in the soil. Crops tolerant of low external concentrations may not respond to fertiliser on the same soil. In contrast, on a soil with low binding capacity for a nutrient, the initial concentration may be adequate, but the mobilisable pool may be quickly depleted so that crop yield is limited before the end of the season. Even crops tolerant of low nutrient concentrations will respond to fertilisation, because they are unable to obtain the quantity they need from the soil.

Yams have long been regarded as requiring high soil fertility, because yields decline quickly when crops are grown repeatedly on the same soil or if fallow periods are reduced. However, their low response to fertilisation suggests that they are quite tolerant of low soil nutrient concentrations and that the observed yield decline may be due to other factors.

Despite their tolerance of low nutrient concentrations, yields will be reduced if the crop is unable to take up the quantities of nutrients it needs. Most of the nutrients taken up by a yam crop are removed from the site when the crop is harvested. As the vines senesce, a large proportion of their nutrient content is recycled into the tubers, so little is returned to the soil from the vines. Depending on the extent of nutrient reserves in the soil, the harvest loss may be incurred only once or several times before yields of subsequent crops suffer from nutrient deficiency.

The quantity of each nutrient removed by the crop depends on the yield and on the nutritional status of the crop. Table 4 lists the range of nutrients contained in tubers from an average 1-ha crop. These quantities

are measured from samples taken from farmers' fields and markets, and are not necessarily from healthy crops. Well-nourished crops may be assumed to contain quantities at the upper end of the range for each nutrient, with the exception of sodium (Na), where the higher values may be indicative of salinity stress. For a yam crop to reach its yield potential (greater than 60 t/ha), its nutrient requirements may be more than four times those given in Table 4.

The quantity of nutrients removed by a crop is often used as a first estimation of the fertiliser requirement of the crop. For N, P and K, which are the nutrients most likely to be depleted by repeated cropping, this is a logical strategy to maintain fertility in the long term. However, consideration should also be given to the rates of losses by denitrification, leaching, erosion or fixation in the soil.

Table 4. Quantities of nutrients removed from the field, in 15 tonnes of harvested tubers

Element	Removal in 15 t of tubers
Macronutrients	*Kilograms*
Calcium	0.5–3.3
Magnesium	1.0–4.5
Nitrogen	30–76
Phosphorus	0.7–8.7
Potassium	26–78
Sodium	0.2–21.0
Sulfur	1.5–2.7
Micronutrients	*Grams*
Boron	10–14
Copper	7.5–57.0
Iron	21–270
Manganese	2.9–115.0
Zinc	36–95

t = tonne

Note: This equates to removal per hectare for crops yielding 15 t/ha, the average for the Pacific region. Data are based on the range of composition of tubers published by various authors, collated by Bradbury and Holloway (1988). Data from *D. alata*, *D. esculenta* and *D. rotundata* have been combined, as the range was similar for all species for each nutrient. Quantities given are not the total uptake by the crop, but only the nutrients removed in the harvested product. It is assumed that vines are not removed from the field and that nutrients contained in them will be returned to the soil.

For the other nutrients, most soils have abundant reserves to supply many crop cycles, so it is not necessary to supply them routinely to replace those removed. However, although they are less commonly deficient, they are no less important. When they are deficient, the quantity needed to restore their availability may greatly exceed the amount removed by the crop, in order to restore both bound and plant-available pools in the soil, or to restore healthy ratios with other soil components. But lower doses may be adequate to maintain fertility in subsequent years.

Many factors limit the availability of fertiliser nutrients to plants. Even for N, P and K, the quantities removed by the crop may not bear much relationship to the crop's response to fertilisation rates in a particular season. In practice, it is more common to base fertiliser recommendations on regional fertiliser rate trials. If they are done at a sufficient number of sites over several seasons, these trials can be used to calibrate soil tests so that site-specific fertiliser recommendations can be based on a soil test before planting. This is the approach generally applied to production of major crops in industrialised countries.

For yam, the information from regional trials is usually limited to advising which nutrients appear to be yield limiting or not limiting in a particular soil type, and the application rate associated with greatest response in that environment. It is more difficult to anticipate when a nutrient may become limiting as cropping intensity increases. Several papers have compared fertiliser responses on sites with different cropping history. They have generally found little or no response to fertilisers on well-fallowed land, and although N (and often P or K) may increase yields on cropped land, fertilisation is rarely able to restore yields to the level found on newly cleared land.

Since most reports from yam fertiliser trials contain little information on soil or plant nutrient levels, and often contain inadequate information on the trial layout and fertiliser application methods, it is difficult to draw conclusions from them. There is much yet to be learned about the relationship of yams to soil fertility.

Yield determination in yam crops

Yam farmers in different places and cultures have different priorities for yam production. Some seek to maximise yield in a given area of land, while others prefer to use a lower planting density to maximise the yield from a limited amount of planting material. Some want to grow the largest size tubers possible and may be willing to use very large planting setts and intensive management to achieve this. Others prefer to grow a wide diversity of genotypes, using a range of cultural practices adapted for each genotype, to ensure an extended supply of yams rather than the maximum quantity harvested at one time. All farmers make compromises according to the resources available to them. Therefore, there is no ideal system to optimise yam production.

Many research papers have been published on the growth pattern of yams and on the influence of various agronomic practices on yam production. However, much of this literature is difficult to access and even more difficult to interpret, given the inconsistencies in results and limited information on the circumstances relating to individual trials. This chapter attempts to review this literature, and to present a general understanding of the yam crop and the factors influencing it. All these factors interact with the crop's response to soil fertility and to fertilisers. Hence, an understanding of these influences is important in researching and managing crop nutrition.

Planting material

Yams are traditionally grown from tubers or pieces of tuber from the previous crop. The planting piece is called a 'sett' or 'mother tuber'. The size of sett used varies, from around 100 g to 500 g or more, with 300 g being a fairly typical size. Depending on plant spacing, seed rates may range from 2–6 t or more per ha. Thus a large quantity of planting material is needed, and since it consists of tubers that may otherwise be eaten, this requirement reduces the net yield of food available from a yam crop. Farmers typically use between 10% and 40% of their yield as planting material for the following season.

In comparison, sweetpotato and cassava are grown from tip or stem cuttings, which do not compete with the food yield. If necessary, many cuttings can be taken from each plant so a particular variety can be multiplied quickly. This is not true of yams, where farmers struggle to maintain the germplasm of preferred varieties in a bad year and new varieties can spread only slowly.

The low multiplication ratio of yams greatly limits the dissemination of new cultivars. Techniques have been developed for the rapid multiplication of yams using minisetts (tuber pieces around 30 g) (Ng 1992; Bakang 1998), from vine cuttings (Quamina et al. 1981; Vander Zaag and Fox 1981; Viana and Felippe 1988; Singh et al. 1991) and from true seed (Wilson 1982; Okezie et al. 1986). These techniques are not relevant to the production of the food crop, as the tubers produced by such plants are generally small and suited mainly for planting material.

Many studies have been done on the effect of sett size on yam yield. There is no doubt that larger setts produce larger, more vigorous plants that yield larger tubers. This is apparently due to earlier germination, and quicker growth of roots and vines in the earliest phase of crop development, which will be discussed in more detail below.

In addition to size, the part of the mother tuber that is used for a sett also affects the timing and strength of initial growth. 'Head setts', from the top of the tuber, sprout most strongly, followed by middle and tail setts. However, the influence on final yield has not been well studied. Small whole tubers are comparable or superior to head setts, and are preferred if available.

Although larger setts increase final tuber size, the increase is not proportional to the increase in sett size. For example, doubling the sett size from 125g to 250 g may only increase tuber yield by 20–30% (Lyonga et al. 1973). Consequently, the 'multiplication ratio' (the weight of harvested tubers divided by the weight of the planting material) is greater for smaller setts. However, the additional yield from larger setts is usually greater than the additional weight of planting material, so

larger setts usually give greater net yield (the weight of harvested tubers minus the weight of planting material) than smaller setts (Onwueme 1978). Hence, smaller setts are generally used to multiply planting material, but larger setts are preferred for production.

The effect of nutritional status of seed tubers is an important question for future research. It is likely that tubers from plants deficient in nitrogen (N), phosphorus (P) or zinc (Zn), for example, may be slower in their establishment and thus have a lower yield potential than those from well-nourished parent plants. If this is the case, they may also have a lower response to fertilisers, despite their deficiency, due to this limit on their yield potential. The full benefit of fertiliser regimes may be better revealed by multiseason trials, in which the seed for each treatment is sourced from the same treatment in the previous year. This is speculative, but worthy of investigation.

Seed yams carefully suspended for storage during dormancy in Mele Island, Vanuatu. (Photo: Grahame Jackson)

Growth pattern

Yam growth may be separated into four distinct phases, characterised by shifts in source and sink relationships between plant parts.

Phase 1

The first phase of yam growth is dependent on the mother tuber (or sett) as the primary source of energy and nutrients. A corm-like growth of meristematic tissue, referred to as the primary nodal complex, forms either at the proximal (top) end of the tuber or by spontaneous differentiation of cells at any point in the cambial layer, just under the skin of the tuber. Root and shoot buds form on the primary nodal complex. Root growth is very vigorous and may precede stem emergence, with primary roots typically radiating outward within the top 10 cm of soil (Oyolu 1982; Njoku et al. 1984; Budelman 1990a; Melteras et al. 2008). Stems grow strongly upward. Those of *D. cayenensis-rotundata* initially lack normal leaves, baring only small leaf bracts at each node.

The height before leaf development and the length of internodes depends on both the size of the mother tuber and the light intensity. Once leaves develop, the vine becomes more twining and the plant's photosynthesis steadily takes over from the mother tuber as the main source of energy. The period of dependence on the mother tuber lasts 6–10 weeks (Nwoke and Okonkwo 1978; Nwoke et al. 1983; Njoku et al. 1984).

Phase 2

The second phase is characterised by the rapid growth of the vine and leaf canopy. Development of the root system is slowing down and ceases around the time that tubers start to develop. Tuber initiation means different things in different species: in *D. alata*, the primary nodal complex evolves into the tuber, so it may be said to be present from germination (Ferguson 1973), although clear differentiation of this tissue is generally between 2 and 3 months after germination. In *D. esculenta*, tubers are formed at the end of short stolons, and may be said to be initiated when stolons emerge. In genotypes that produce multiple tubers, tuber number increases during this phase, but tuber weight develops only slowly. Timing of tuber initiation, and duration from tuber initiation to tuber bulking, differs among species. Tuber initiation is influenced by shortening daylength (photoperiod) (Shiwachi et al. 2002), a response that tends to synchronise tuber development irrespective of planting date or rate of early development.

The start of tuber bulking is reported to be earlier with larger planting setts (Ferguson 1973, presumably in response to greater carbohydrate supply from a larger leaf area. Earlier commencement in turn means a longer period is available for tuber bulking. However, Nwoke et al. (1983) found no effect of sett size on timing of tuber initiation or bulking. Flowering occurs around the time of tuber initiation in those genotypes that produce flowers (Kpeglo et al. 1982).

Phase 3

The onset of rapid tuber bulking occurs several weeks after tuber initiation and coincides approximately with the cessation of vine growth (Chapman 1965; Sobulo 1972a; Okoli 1980; Melteras et al. 2008). Although vine tips become inactive, leaf area and mass continue to increase for around 3 weeks as young leaves expand to maturity (Nwoke et al. 1983). From this point, vines gradually senesce while tuber bulking continues.

Initially, tubers increase rapidly in size and weight, but have a relatively low dry-matter content. They are building the cells in which starch will be stored. The dry-matter content of tubers gradually increases as these cells are filled with starch, with maximum dry-matter yield reached when vine senescence is virtually complete (Melteras et al. 2008). Immature tubers have a pale tip where new tissue is still developing.

At maturity, the dark bark of the tuber extends across the tip. However, this reference to immaturity refers only to the potential for further growth. Okoli (1980) observed that tubers harvested at the start of the tuber bulking stage are capable of sprouting and concluded yam tubers are 'mature' almost as soon as they are formed.

Phase 4

After complete senescence of the vine, the tubers are dormant for a period of 1–5 months, depending on species and storage conditions. Tubers harvested earlier than full maturation of the crop have an extended dormancy period (i.e. they sprout at the same time as tubers harvested at a later time) (Okoli 1980). Dark, well-ventilated conditions are preferred for storage of dormant tubers.

During this period, the dry-matter content of the tubers gradually declines due to respiration. Nitrogen fertilisation of N-deficient yams has been reported to promote earlier sprouting, but P and potassium (K) fertilisation tended to suppress sprouting and thus enhance storability (Kpelgo et al. 1981). Fertilisers, or tuber nutrient status, did not change the rate of weight loss during storage (Kpelgo et al. 1981; Okwuowulu et al. 1995).

Dormancy is prolonged by temperatures below 15 °C (Lebot 2009). Sprouting may be promoted and synchronised by incubation at constant warm temperatures, between 25 °C and 30 °C. In Tonga, a common practice is to place prepared planting setts in a pit covered with banana leaves and soil, so that their respiration raises the temperature. The setts are incubated for 3–4 weeks before planting. The high temperature and humidity also promotes sealing of cut surfaces on the setts (S. Halavatau, pers. comm.). Elsewhere, farmers wait until buds form naturally before planting setts. After dormancy is broken, the tubers lose weight faster than they do during dormancy, due to increased respiration rates. This limits the time that tubers can be stored for food, although removing the buds as they form can slow the deterioration of tubers.

Yield determination

Tuber yield, on a per-plant basis, appears to be most closely related to the 'leaf area duration', which is a cumulative measure of the leaf area across the whole growth cycle of the crop. On a crop basis, leaf area duration is expressed on the basis of leaf area index (leaf area per unit land area) (Chapman 1965; Enyi 1972a, b).

As there is a limited time for vine development between sprouting and tuber formation, the speed of early growth is very important. Larger sett size leads to larger plants with larger leaf area. The leaf area at the end of the sett-dependent phase of growth is only around one-tenth of the final leaf area achieved (Chowdhury 1998; Melteras et al. 2008). Nevertheless, Enyi (1972a) showed that the advantage of large setts was established at this time, as the relative growth rate of plants from all sett sizes was subsequently similar, but the head start given by larger setts translated into a much larger final leaf area.

The maximum leaf area index reached is highly influential on the tuber-bulking rate (Enyi 1972a), plateauing at maximum light interception (Rodriguez-Montero et al. 2001). Thus, the vine growth achieved during the second growth phase is vital to yield, but seems to be largely predetermined at the end of phase 1. However, the relative growth rate in phase 2 can be increased by staking, which improves the light interception of the developing canopy (Enyi 1972b) and by fertilisation, which increases photosynthetic efficiency (but only when this is limited by low nutrient supply in the soil).

The duration of the tuber-bulking phase may also be important, although it is not clear to what extent it is programmed or if it is variable in response to agronomic conditions. Reports differ on whether staking or fertilisation may result in earlier tuber initiation or bulking. Fertilisation has been observed to prolong vine senescence, probably by reducing the competition between tubers and leaves for the nutrients whose supply is limiting growth. A dry end to the growing season may also shorten the bulking period, as well as reducing gas exchange and photosynthesis rate in the leaves, compared with growth in a continuously moist environment. Leaf diseases, particularly anthracnose (*Colletotrichum gloeosporioides*) in *D. alata*, also reduce the photosynthesis rate and time to complete vine senescence.

In addition to accelerating canopy development, large setts may influence yield through the development of a more extensive root system and by development of a larger primary nodal complex from which tubers are initiated (Ferguson 1973). However, the contributions

of these factors have not been studied and are difficult to separate from the influence on vine growth.

The importance of leaf area duration may be specific for certain genotypes grown under varying agronomic conditions such as sett size, plant spacing, staking and fertilisation. When comparing genotypes grown in similar conditions, Chowdhury (1998) concluded that partitioning of dry matter (harvest index) was more important than total crop growth rate or leaf area duration. Conversely, Okoli (1980) observed that a higher proportion of dry matter was allocated to tubers in lower yielding than in higher yielding cultivars.

Sett size and plant spacing

The impact of sett size is influenced by the spacing of plants (or plant population density). The advantage of large setts is greatest at wide plant spacing (Kayode 1984). A number of studies have compared sett size and spacing, but few have selected treatments that are comparable on the basis of seed rate (weight of setts per ha). An exception is the study of Rodriguez-Monero et al. (2001), who showed that yield increased with seed rate, with little difference in total yield between small setts at high density and large setts at lower density, at the same seed rate. They showed that higher seed rate resulted in earlier achievement of maximum leaf area index; hence, greater use of sunlight over the growth cycle. However, tuber size was greatly influenced by plant density, so that the weight of marketable tubers was much greater for large setts at low density.

The plant population density used in the Rodrizuez-Monero et al. (2001) study ranged from 20,000–95,000 plants per ha, much higher than those used by growers in Africa and the Pacific region. Typically, these regions have a plant population density of 10,000 plants per ha (one per square metre) or lower. In Asia and the Caribbean, densities from 10,000–35,000 plants per ha are more common and sett sizes are correspondingly smaller. In contrast to Rodriguez-Monero et al. (2001), Kayode (1984) found a considerable benefit of increasing sett size from 300 g to 400 g, either at the same spacing or at the same seed rate, with plant populations ranging from 7,000 to 11,000 plants per ha.

The effect of plant spacing on size of harvested tubers appears to diminish beyond 10,000 plants per ha (1 m × 1 m spacing) and be negligible above 4,444 plants per ha (1.5 m × 1.5 m spacing) (King and Risimeri 1992). However, very large setts may respond to wider spacings.

The extra labour required to establish and harvest a crop at higher plant populations further increases the cost of high seed rates. Suja et al. (2003) found that profit was greatest for large setts planted at low density (ranging in this case from 12,000–28,000 plants per ha), although total and net yield were highest for large setts planted at high density. Both the labour saving and a higher ratio of marketable to undersize tubers contributed to the profit margin.

Competition, weeds and intercropping

Yams are recognised as poor competitors with weeds, and yield can be severely reduced if weeds are not controlled in the early phase of the crop. Intensification of cropping usually increases weed intensity and this is seen as a barrier to yam production in continuous cropping systems (Dumont 1973).

Akobundu (1981) found that yams were most sensitive to weed competition between 8 and 16 weeks after planting, coinciding with phase 2—the period of rapid vine growth. Unamma and Akobundu (1989) demonstrated that at least half of the reduced yam yield due to weeds was a result of allelopathy. Allelopathy refers to the situation where one plant suppresses the growth of another nearby plant by releasing inhibitory chemical compounds into the root environment. When root zones of weeds and yam were separated, no yield reduction was observed in yam as a result of above-ground competition. When leachate from the weed zone was applied to weed-free yams, yield depression was observed. The contribution of different weed species to this effect was not studied.

Yam crops usually require weeding approximately four times in the season and can represent a high proportion of the production cost. Akobundu (1981) estimated that weeding required 5 person-days per ha every time weeding was needed. This translates into 20 person-days for four weedings or approximately 30% of the labour requirement for the crop (a similar proportion to harvesting). Oyolu (1982) reported the weeding requirement at 64 person-days per ha for a season in typical Nigerian production conditions.

Mulching is an effective means of reducing weed intensity (Singh et al. 1986). Herbicides may also be cost-effective for many growers. Chikoye et al. (2006) found that a single application of the herbicide glyphosate (1 kg active ingredient [ai] per ha applied at 4 weeks after planting) was highly cost-effective—giving higher yam yields, better weed control and lower input cost than plots weeded by hoeing four times during the season. The herbicide fluazifop-P-butyl was inferior to hoeing. Akobundu (1981) reported greatest control using a pre-emergence application of fluometuron with metolachlor (2 kg ai per ha of each), but glyphosate was not among the herbicides tested. The most effective herbicide is likely to depend on the species composition of weeds in any situation.

Intercropping also challenges the yam crop with competition, but when well managed it can reduce weed loads. Short-season crops, such as maize and melon, may be planted alongside yam and harvested during the early-bulking phase of the yam crop. Kolo (1995) reported that yam (*D. rotundata*) and melon (*Citrullus lanatus*) can be grown together without noticably affecting the yield of either crop, while reducing weeds by about 50%.

Trellis or pyramid staking of yam is better for the intercrop than individual staking. Anuebunwa (1992) successfully intercropped yam with cassava (*Manihot esculenta*), maize (*Zea mays*) and melon, but found that yam competed poorly in random arrangements. It performed better in alternate row or double row arrangements. However, Odoemena (1997) found that intercropping yam and 'Egusi' melon (*Colocynthis vulgaris*) reduced yam yields in all planting arrangements, while increasing melon yields. Variable results may be influenced by water availability, as competition for water is more intense under intercropping (Ghuman and Lal 1991).

Singh et al. (1986) found intercropping *D. floribunda* with cowpea (*Vigna unguiculata*) and blackgram (*V. mungo*) equally effective in suppressing weeds. The value of the grain yield using blackgram made this treatment most profitable.

Obiagwu (1997b) employed grain legumes as intercrops to supplement N to other crops. On a sandy river basin soil in Nigeria, yam responded positively to NPK (ratio of 15:15:15) applied at 30–90 kg/ha, and to intercropping with cowpea or yam bean (*Sphenostylis stenocarpa*). This intercropping was equivalent to applying 48 and 26 kg/ha of NPK, respectively. Cowpea also gave the greatest improvement in maize yield, equivalent to applying 37 kg/ha of NPK. Intercropping stimulated nodule growth in the legumes, although it reduced their grain yield. Biomass of the legumes was not reduced when intercropped with yam, but was reduced when intercropped with maize or cassava. Common bean (*Phaseolus vulgaris*) had higher N fixation, leaf nutrient levels and biomass than the other legumes, but was slower to gain groundcover. It also had lower grain yield, meaning more N stayed in the field. Therefore, Obiagwu recommended common bean as a rotation crop rather than intercrop. Lima bean (*Phaseolus lunatus*) with a long growth cycle could also be used in an improved fallow.

There is evidence that the stimulation of nodulation by close association of roots of legume and non-legume species indicates a direct transfer of N compounds to the non-legume species (van Noordwijk and Dommergues 1990).

Nedunchezhiyan et al. (2006) found intercropping of unstaked *D. alata* improved yields due to an increase in the vertical profile of the yam canopy and resulting reduction in anthracnose severity. Maize performed better than redgram (*Cajanus cajan*) or sorghum (*Sorghum bicolor*) in this system. The use of maize or sorghum intercrops in place of stakes is also increasingly popular in the savannah zone of Nigeria, due to the shortage of staking materials (Agbaje and Adegbite 2006).

Pests and diseases

This section will not attempt to give a detailed overview of pests and diseases of yams. A recent review can be found in Lebot (2009). Emphasis is given in this section to their relationship with crop nutrition and to their role in yield decline resulting from increased cropping intensity.

Crop nutrition is widely recognised to affect severity of a range of pests and diseases (Engelhard 1989). Yam crops under nutritional stress are likely to have increased susceptibility to infection, and appropriate fertilisation may be an effective disease-control measure. However, the emphasis should be on the nutritional status of the crop, not on the fertiliser as a potential treatment for disease.

Anthracnose

The foliar disease anthracnose, caused by the fungus *Colletotrichum gloeosporioides*, is present in all yam-growing regions and most severely affects *D. alata*. It is by far the most important foliar disease of yams. It causes black lesions and premature dieback of the foliage, which may significantly shorten the growing season. In areas of high humidity, production of *D. alata* is often limited by anthracnose prevalence.

Spread of anthracnose is fastest where large areas of yam monocrop exist in close proximity. Hence, the problem has grown with increased cropping intensity and has reduced *D. alata* to a minor crop in areas where it was previously dominant (i.e. when gardens were relatively small and surrounded by forested fallow land). The identification of anthracnose-resistant cultivars has improved production potential. Hepperly and Vazquez (1989) recommended an integrated approach to controlling anthracnose—combining seed treatment, crop rotation, intercropping, foliar fungicide and the use of resistant cultivars.

No studies have been reported on the effects of yam nutritional status or fertilisation on anthracnose severity.

A necrotic lesion caused by the anthracnose fungus Colletotrichum gloeosporioides *on* D. alata.

Nematodes

Plant-parasitic nematodes are microscopic roundworms that invade the roots and tubers. The yam nematode, *Scutellonema bradys*, is the most damaging species in West Africa and the Americas, and has also been recorded in the Pacific region and India. It causes 'dry rot' of yams in storage. Lesions form in the tissue just below the skin; the affected tissue becomes blackened and dry. As a result, moisture loss from the whole tuber is increased and secondary infection by fungi or bacteria can lead to a wet rot that destroys the tubers. Lesion nematodes, *Pratylenchus* spp., especially *Pratylenchus coffeae*, are present in the West Indies and Pacific region, and cause similar damage to the yam nematode. These migratory endoparasites are believed to cause little damage to the fibrous roots, as infestation does not affect vine weight or tuber number (Bridge 1982; Baimey 2005), but tuber weight is reduced (Baimey 2005).

Root knot nematodes, of the genus *Meloidogyne*, are widespread and have a wide host range. Damage is usually greatest when yams are grown together with, or immediately after, another susceptible crop, including many vegetable species. Infection causes galls to form on the roots and tubers, resulting in deformed tubers. Plant growth and yield are also stunted by *Meloidogyne* infestation, presumably due to fibrous root damage. Genotypes vary in their susceptibility.

The severity of nematode damage is generally proportional to the nematode population. Nematode populations build up in the soil if yams are grown in the same place in successive seasons. This is recognised as a considerable barrier to continuous cultivation of yams (Dumont 1973). During a fallow, nematode populations decline through both the lack of appropriate host plants and by direct antagonism from other soil organisms. This may have a greater influence on yam yield decline following reduced fallows, than does soil mineral fertility. The primary source of infection is often the seed tuber, but in most cases nematodes have to migrate through the soil in order to infect the new season's tubers (Bridge 1982). A soil with a low population of parasitic nematodes is likely to have a healthy population of nematode antagonists, and may therefore reduce the rate of infection even from seed-borne eggs.

Natural bush fallows may contain a variety of hosts for nematodes and therefore provide limited control (Bridge 1982). Selection of nonhost cover crops or improved fallow species may reduce nematode populations faster. Cover crops that may have nematode control potential include African marigold (*Tagetes* spp.), kudzu (*Pueraria phaseoloides*), velvet bean (*Mucuna pruriens*) and porcupine jointvetch (*Aeschynomene histrix*) (Lebot 2009). However, the porcupine jointvetch is susceptible to anthracnose (Cook et al. 2005) and would potentially exacerbate anthracnose problems. More research is needed to identify and evaluate break crops in different agroecological conditions.

Dry rot under the skin of D. rotundata *caused by the yam nematode* Scutellenema bradys. *(Photo: Lawrence Kenyon)*

*Root knot nematode (*Meloidogyne *spp.) symptoms on* D. rotundata *tubers in West Africa. (Photo: Lawrence Kenyon)*

*Galls caused by root knot nematodes (*Meloidogyne spp.*) on the tubers of* D. esculenta *in Vanuatu. (Photo: Colin Asher)*

Reported effects of fertilisation on nematode damage are inconsistent. Obigbesan and Adesiyan (1981) reported that N fertilisation markedly increased infection rates and population density of S. bradys. Phosphorus had no effect on its own, but it enhanced the effect of N. However, Adesiyan and Adeniji (1976) and Baimey et al. (2006) found that fertilisers reduced nematode densities in tubers at harvest. In contrast, Baimey et al. (2006) observed that N fertilisation increased the rate of nematodes breeding in stored tubers.

These conflicting reports result from the complex interaction of nutrition with both the parasite and the plant, as well as with other soil biota that may antagonise nematodes. Nutritional deficiency often increases the plant's susceptibility to the nematodes and thus increases nematode damage. However, the same deficiency may reduce the population and reproduction of nematodes, as they in turn are less well nourished. Conversely, fertilisation may increase plant tolerance, but also increase nematode populations (Bell 1989). Arbuscular mycorrhizal fungi are also known to increase crop tolerance to nematodes, both by improving the crop's P nutrition and by direct antagonism to nematodes. Phosphorus fertilisers have been found to increase tolerance of cotton to root knot nematodes in severely deficient soils. However, P fertilisers increased nematode damage in soils that contained moderate levels of P, possibly by reducing the plant–mycorrhizal association (Bell 1989).

Viruses

Viruses are an invariable feature of vegetatively propagated plants. About 15 viruses have been described in yams and virtually all crops are infected with at least one. The low multiplication rate of yams limits the potential for virus-free planting material programs, such as those that exist for potato and, in some places, sweetpotato. Although viruses evidently reduce vegetative growth and tuber

White yam mosaic virus on D. rotundata. *(Photo: Lawrence Kenyon)*

Severe stunting and leaf deformity caused by shoestring virus disease in D. rotundata. *(Photo: Lawrence Kenyon)*

size, the magnitude of this effect and its dependence on environmental conditions are not well documented. No information is available on the influence of plant nutrition on virus impacts.

Insect pests

Insect pests are the problems most commonly cited by farmers, as their presence and the damage they cause are most easily observed. In some regions, their damage is indeed severe. In West Africa, yam tuber

Tubers of D. rotundata *showing tunnels formed by the yam beetle* Heteroligus meles *in Ghana. (Photo: Lawrence Kenyon)*

Termite infestation in D. rotundata *tuber in Ghana. (Photo: Lawrence Kenyon)*

beetles (particularly *Heteroligus meles*) are serious pests, making numerous large feeding holes in the tubers. Taro beetles (*Papuana* spp.) cause similar damage in Pacific island countries.

In some drier savannah areas, termites (*Amitermes* spp. and *Microtermes* spp.) are serious pests, attacking both the seed tubers after planting, and the new tubers before or after harvest. They form colonies inside the tubers, creating extensive cavities and tunnel networks. For both beetles and termites, most damage generally occurs shortly before harvest, and delayed harvesting can greatly increase damage.

Atu (1993) found that fertilisation reduced the incidence of termite damage on tubers, although it was not clear which components of the fertilisers tested were most effective. The termite reduction was not correlated with an increase in yield (the highest yielding fertiliser mix gave little termite reduction), so the effect cannot be attributed to improved nutritional status of the plant.

Scale insects (*Aspidiella hartii*) and mealy bugs (*Phenacoccus gossypii*, *Geococcus coffeae*, *Planococcus citri*) feed on the sap of roots and tubers. They sometimes feed on the leaves and stem, but the damage here is minor. Most damage occurs on tubers in storage. Infested tubers shrivel and are more prone to fungal rots. Sprouting of tubers may be suppressed, and the shoot weakened or killed by insect feeding. They are usually controlled by brushing off before storage and before planting. Dipping planting material in hot water is also an effective control.

No information is available on the effect of yam nutritional status or fertilisation on the severity of insect damage. In other crops, K deficiency is widely known to increase foliar and sucking insect damage by reducing cuticle formation and reducing the plant's chemical defences against insect feeding.

Stakes

Most yam genotypes, in most production environments, yield better when the vines are provided with support than when they are not. Staking appears to perform two functions—to increase the light interception of the leaf canopy and to increase ventilation around the leaves. Ventilation is particularly important in humid environments where high humidity in the canopy can increase the incidence of fungal leaf diseases, especially anthracnose. Staking also facilitates weeding, especially with thorny varieties (King and Risimeri 1992). However, the cost of staking can be high, and staking materials are becoming increasingly scarce in many production areas as land use intensifies. Obiazi (1995) reported that the average Nigerian farmer spends 60 person-days per ha in procuring and installing stakes. Irizzary et al. (1995) reported that construction of trellises was the highest input cost for yams in Puerto Rico.

In some situations, yams are successfully produced without staking. *Dioscorea opposita* is typically not staked in Japanese commercial crops. In Puerto Rico, Irizzary and Rivera (1993, 1997) and Irizzary et al.

A tuber of D. rotundata *infested with mealy bugs. (Photo: Lawrence Kenyon)*

The pyramid staking system used in a germplasm collection in Vanuatu. (Photo: Lawrence Kenyon)

Canopy development of D. esculenta *on shared stakes (one stake per four plants). (Photo: James Ernest)*

Yam stakes for sale on Kiriwina Island, Papua New Guinea. When the price per stake is greater than the price of a kilogram of yam, stakes become a considerable expense for land-poor farmers in low-yielding environments. (Photo: James Ernest)

(1995) reported *D. alata* yields up to 70 t/ha without staking, and no significant advantage of staking when anthracnose-resistant cultivars are selected. In Tonga, stakes are generally not provided for *D. alata*, although twiggy debris from fallow clearing may be heaped in rows for vines to climb on and raise them off the ground. This custom probably results from a low availability of staking materials, but the relatively low humidity and high light intensity on these small islands may also reduce the benefit of staking.

In the East Sepik region of Papua New Guinea, two distinct subspecies of *D. esculenta* are cultivated. Genotypes similar to those grown elsewhere in the Pacific region are known as 'mami' and are normally staked, but a group referred to as 'asakua' (belonging to a proposed subspecies *D. esculenta* var. *spinosa*; Burkhill 1951) is never staked (Quin 1984).

In yam vines, there is typically a strong gravitational influence on apical dominance. While a vine tip actively grows upwards, it suppresses the development of lateral branches. It may grow for up to 2 m beyond support, but progressively moves from vertical to horizontal and finally hangs down when it is too large to support itself. As soon as the tip is no longer the highest point on the vine, its dominance is lost and branches form at the highest nodes. Typically, the hanging tip becomes inactive and the new branches become dominant.

The dependence of yam genotypes on staking may relate to their strength of apical dominance and their tendency to branch. Those that are slow to initiate branches may develop best on tall stakes, where the vital early growth of the vine is uninterrupted. Those with less apical dominance and greater branchiness may be less assisted by staking.

The system of staking may depend on local conditions and available materials. A typical method is to provide one vertical stake per stand. Frequently, where stakes are less available, one stake may be provided for 2–6 stands. Conversely, diligent farmers have been known to provide a stake for each of the shoots emerging from the crown. Ndegwe et al. (1990) and Ndegwe (1992) found that yield of *D. rotundata* increased with stake density (two stands per stake was the highest number tested), but that the increased yield may not justify the increased cost.

Pyramid staking, where stakes from three or more mounds are bound together at the top, provides a more sturdy support where staking materials are weak or where tropical storms commonly bring down single stakes. The resulting canopy development is

similar to that on shared stakes and yield is generally less than on single-staked plants. However, risk and weed management may justify the choice, and the yield effect may not be consistent from year to year (Kolo 1995). Trellising, where relatively few poles are spanned by horizontal wires or lighter timber, is common in the Caribbean and India, and also used by some traditional farmers in Melanesia and Micronesia. Trellises allow very good canopy development, but usually require a greater investment of materials and effort. The benefit of very tall stakes appears to depend on the yield potential of individual plants (Okigbo 1973). King and Risimeri (1992) compared planting density of *D. esculenta* at 2,500 (2 m × 2 m), 4,444 (1.5 m × 1.5 m) and 10,000 (1 m × 1 m) plants per ha, and no staking compared with stakes 1.5 m and 3 m in height. Staking increased yield at all densities, but higher stakes were only beneficial at low plant density, where yield per plant was greatest. However, net yield was greater at the medium or high plant densities, and thus did not require tall stakes.

Obiazi (1995) reviewed the need for staking, shortage of stakes and on-farm stake production options, including bamboo and tree legume plots, and live stakes. He listed a range of species and suitability criteria.

Onwueme (1982) recommended a no-staking system to reduce the labour requirement of yam production. However, he acknowledged that, while high yields were possible by combining no staking with closer spacing and smaller setts, the preference of many communities for large tuber size reduced the acceptability of this system.

Live-staking with *Gliricidia sepium*

Land shortages and deforestation often result in a shortage of staking materials for yams. Some farmers in West Africa have used living trees to support yams for many years (Budelman 1991). In the Pacific region, *Dioscorea nummularia* is commonly grown on existing trees at the edge of gardens, but the yam species used for staple foods are less tolerant of shade. Nevertheless, in Pohnpei, Micronesia, certain genotypes of *D. alata* are commonly trained on living breadfruit trees by twine from the canopy to assist the vines to reach the light (Raynor et al. 1992). Kenyan farmers have recently adopted live-staking of yams using an indigenous tree, *Commiphora zimmermannii* (Getahun and Njanga 1990; Obiazi 1995).

Recent research in West Africa and the Pacific region has helped develop a system of live-staking for yam. Budelman (1990a, b) compared three leguminous trees—*Leucaena leucocephala*, *Gliricidia sepium* (gliricidia) and *Flemingia macrophylla*—for their suitability as live stakes for *D. alata* in Ivory Coast. Gliricidia was found to have suitable architecture of both tops and roots, providing sturdy support without excessive shading and minimising competition within the crop root zone. Otu and Agboola (1994) subsequently reported positive results using gliricidia live-staking of *D. rotundata*. Ernest and O'Sullivan (2004) successfully used gliricidia to stake *D. esculenta* and *D. rotundata* in Papua New Guinea. The tree is widely distributed throughout the tropics. Because it is planted from large pole cuttings, it is easily established, even among grasses.

Farmers that harvest yams benefit from softer soils and partial shading provided by live-stake gliricidia trees. (Photo: James Ernest)

Continued overleaf

Two planting systems have been characterised. The West African studies have used alley cropping, with gliricidia planted as a row between alternate yam rows. In Papua New Guinea, trees were planted on a 2 m × 2 m grid system, with one tree for every four yam mounds, so that the spacing of yam plants was the same as for normal staking (1 per m^2). The latter system is described in more detail below.

The trees are planted using large poles, 2–2.5 m tall, 8–10 months before planting yams (generally at the start of the wet season). They can be established in grassland, as their canopy develops at the top of the pole and does not have to compete with the grass. Alternatively, the land is cleared before planting the trees, and a cover crop of a herbaceous legume, such as *Mucuna cochinchinensis* or *Dolichos lablab*, is planted to suppress weeds and to provide additional mulch for the yam crop.

At the start of the following wet season, the groundcover is removed and yams are planted as normal, at 1 m × 1 m spacing with four mounds around each pole. The removed vegetation can then be returned to the plot as mulch. Once the majority of setts have sprouted and are ready to train onto stakes, the trees are pruned, removing all branches near their base. Prunings are left in the plot as mulch. Four branches per tree are stripped and turned upside-down (so they don't take root) from each mound to the pole, and yam shoots are guided onto the branches.

Every 2 months during the growing season, tree branches are pruned wherever they extend beyond the yam canopy. In the final stages of senescence of the vines, the trees are allowed to grow.

If nematode build-up is not a problem at the site, a second crop of yam can be grown on the same trees. Alternatively, secondary crops can be planted at the start of the following season. The trees can be ringbarked, so they shed their leaves gradually, progressively reducing the shade for the establishing crop plants and providing nutrients from the fallen leaves.

Trial results indicate that regular pruning is crucial, as shading can reduce yields when trees are not kept in check. However, when regularly pruned, the trees do not negatively compete with the crop, and yield is improved on the least fertile sites due to the nutrient contribution of the leaf mulch. Establishment of yams is improved due to the partial shading of the trees. The system can also reduce labour inputs for weeding and staking. Further benefits to farmers include softer soil texture, and shading of workers at planting and harvest. Live-staking may alleviate many of the problems associated with shortened fallows, including weed intensity, decline in soil nutrient availability and organic matter content, and shortage of staking materials.

Leaf mulch provided by pruning gliricidia supplies plant-available nutrients and increases soil moisture retention, an important factor, particularly on atolls. (Photo: James Ernest)

A live-staking demonstration plot. The picture shows that very good yam canopy development and light exposure are possible when the trees are well managed. (Photo: James Ernest)

Nutrient deficiencies: nitrogen

Nitrogen deficiency

Nitrogen (N) is needed to build many components of plants, but the most abundant component requiring N is protein. In leaves, proteins form much of the machinery needed for photosynthesis. The chlorophyll pigments, which give leaves their green colour and allow them to capture energy from sunlight, also contain N. The photosynthetic proteins and pigments are more thinly spread in N-deficient plants, causing a paler coloured plant that grows more slowly.

Plants can respond to N deficiency by increasing the growth of roots relative to tops. By doing this, they increase the volume of soil they can explore to help supply more N. In root crops, such as yam, this may also promote the growth of tubers. Yam plants that are N deficient may initiate tubers earlier, but generally have reduced yield because they have reduced leaf area and a lower photosynthetic rate. But mild N deficiency may be offset by the greater tendency to direct photosynthate to tubers, so that the reduction in tuber yield is less than the impact on top growth. However, the protein content of these tubers will be lower than tubers from well-nourished plants. Research has not yet established the level of N nutrition needed to optimise tuber yield, but it is evident that yams are quite efficient scavengers of N.

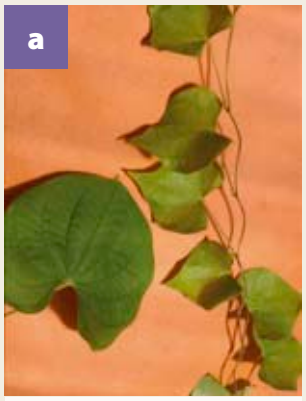
Occurrence

Nitrogen is needed in large amounts by plants, but it is normally scarce in soil minerals. Most of the air we breathe is N gas, but in this form it is not usable by plants or animals. A small number of micro-organism species have the ability to transform this N into usable forms (a process known as biological N fixation). Most traditional agriculture depends on biological N fixation by the *Rhizobium* bacteria, which live in the root nodules of leguminous plants. Nitrogen fixation requires a lot of energy and the legume supplies energy to the bacteria in return for the N. There are some other bacteria that can fix N without legumes, but the amounts of N fixed are so small that they offer little benefit to agriculture. Other plants obtain N when the legume leaves or roots rot in the soil, or from wastes produced by animals that eat the legumes. At the end of a long fallow, N has built up in all the plant material, as well as in the organic material in the soil. However, if the fallow vegetation is burnt, much of the N is lost back into the air.

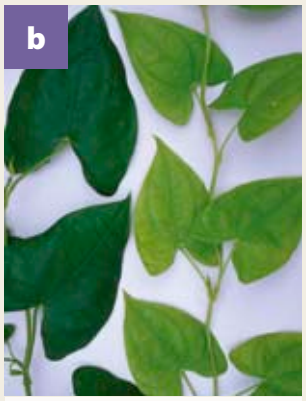
Nearly all natural ecosystems and traditional farming systems have below-optimal supplies of N. Biological N fixation never raises N availability to an ample level, because legumes will not expend their energy on N fixation unless they require the N more than the energy itself. If legumes are supplied with high N, they will not fix N. Only by transferring biologically fixed N from a larger area to a smaller area (such as in animal manure, which is derived from fodder gathered from a large area) can N stress be removed and crop growth potential realised.

Atmospheric N can be fixed by a chemical process to make a synthetic N fertiliser. The use of synthetic N fertilisers, particularly on cereal crops, expanded greatly from the 1950s onward as part of the Green Revolution. Modern agriculture has come to rely on it to a large extent. It is unlikely that the current global human population could be supported without it.

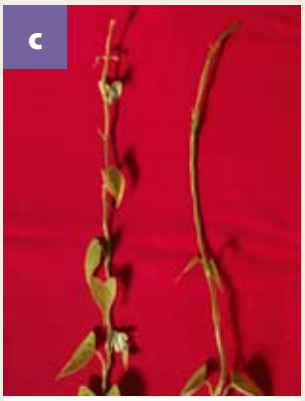
However, yams are rarely grown as a commercial crop and most yam farmers can not justify the cost of purchased inputs such as N fertiliser. Organic fertilisers, particularly animal manures, are useful sources of N, but contain much lower concentrations than inorganic fertilisers. If the fertiliser N requirement is in the range of 50–100 kg N/ha, this would require application of 100–200 kg/ha of urea, or 2–20 t of manure (depending on its composition). This poses two challenges for subsistence farmers—the ability to carry such large quantities to their fields and the lack of sufficient manure. Another impact of land scarcity for many communities is the reduction in livestock ownership.



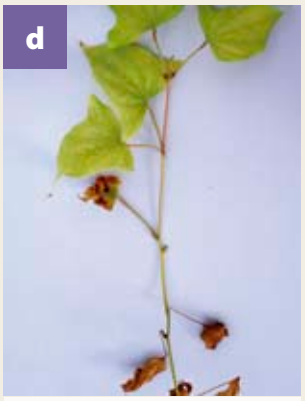
D. esculenta: greatly reduced leaf size and mild general chlorosis (right), compared with a leaf from a well-nourished plant (left).



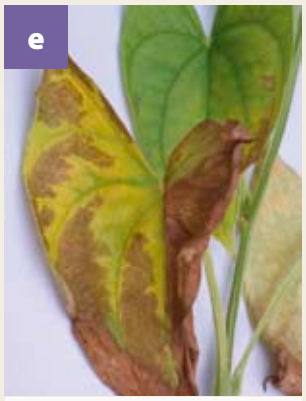
D. alata: comparison of healthy leaves (left) with those of an N-deficient plant (right).



D. alata: tip of an N-deficient plant (left) showing short internodes and small leaf size, compared with stronger tip and longer internodes on a healthy plant (right).



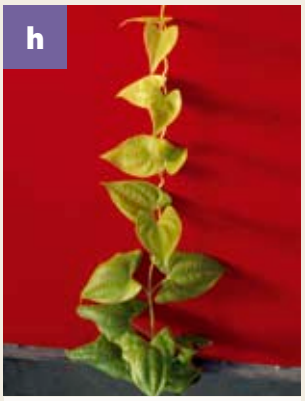
D. rotundata: severe N deficiency resulting in an inactive shoot tip and senescence of the older leaves.



D. alata: necrosis preceded by yellowing, spreading into interveinal areas on the oldest leaves on the vine.

D. alata: necrosis spreading into interveinal areas on leaves in the lower midsection of the vine.

D. esculenta: small brown spots near the margins of an older leaf from an N-deficient plant.



D. alata: a severely N-deficient plant, with chlorosis increasing toward the youngest leaves, but no senescence of oldest leaves.

N = nitrogen

Figure 4. Symptoms of nitrogen deficiency in yam plants.

Symptoms

The primary symptom of N deficiency is a dull, light-green colour of the foliage. The colour may be uniform (Figure 4a), but commonly shows a weakly interveinal pattern, with slightly darker green on and around the main veins of the leaf (Figure 4b). The size of mature leaves is also reduced (Figure 4a–b). Tip growth is slowed and internodes are shortened, so leaves behind the tip will be more mature, if smaller, than leaves at an equivalent position on healthy plants (Figure 4c). N-deficient plants tend to have relatively few branches. All of these symptoms are difficult to assess in the field, without healthy plants for comparison.

The oldest leaves on the vine may shrivel and drop off earlier than normal (Figure 4d). Often, they turn yellow before they dry up (Figure 4e), but sometimes there is little yellowing ahead of the spreading dead tissue (Figure 4f). The dead tissue tends to be light brown and supple. In *D. esculenta*, small necrotic lesions on older leaves have been observed, before the onset of any spreading necrosis or leaf shedding (Figure 4g). Senescence of the oldest leaves is a common symptom of N deficiency in plants, but is less pronounced in yams. It may not be present during the vegetative growth phase and healthy yams also show senescence of oldest leaves toward the end of their growth cycle.

Therefore, it may be difficult to assess whether N deficiency has promoted or accelerated the death of oldest leaves.

Severely N-deficient yams may become increasingly pale from mature to youngest leaves (Figure 4h). This is an unusual symptom and suggests that yams are less able than most plants to move N from older leaves to supply the new leaves. Again, the symptom is difficult to identify in the field, as the young leaves of healthy yam plants are naturally pale and take some time to develop their full colour.

Diagnostic tests

In leaves of *D. alata*, a critical concentration range of 2.9–4.0% was estimated for leaf blades of the fifth and sixth youngest nodes. This wide range reflects both the variability in N concentration among plants (for leaves at the same position) and the variation with leaf position. Younger leaves tend to have higher N concentration than older ones. The leaves at any particular node may vary in age, depending on the rate of growth of the vine tip. Consequently, factors that change the rate of vine growth, including stage of crop growth and environmental conditions such as temperature, light and water availability, may change the absolute age of leaves sampled and hence their N content. The critical range is therefore a guide. Samples with N concentration below the range are likely to respond to N fertilisation, while those within the range may benefit.

The response of *D. rotundata* to N supply has not been studied in detail, but when grown together, *D. alata* and *D. rotundata* leaves contained similar N concentrations and plants responded to varying N amounts similarly. The critical range for *D. alata* may be taken as indicative of that for *D. rotundata*.

The critical concentration for *D. esculenta* appears to be lower than that in *D. alata*. In sand culture, apparently healthy growth was associated with a concentration of 2.2% in leaves of the seventh and eighth nodes, but the N supply may not have been optimal. Where both *D. esculenta* and *D. alata* were both sampled from the same location in field surveys, *D. alata* leaves invariably contained higher N concentrations. A tentative critical range for *D. esculenta* of 2.0–2.6% is suggested.

In the field, fertiliser test strips may be used to confirm a deficiency of N and to distinguish N from sulfur (S) deficiency. For example, urea (containing only N) and sulfate of ammonia (containing both N and S) can be applied to separate strips of one or two rows, at a rate of about 50 kg N/ha (e.g. 5 g N per mound, at 1 m × 1 m spacing of mounds). If plants green up equally with either sulfate of ammonia or urea, it can be concluded that they were suffering from N deficiency. If only the sulfate of ammonia produces a response, the problem would be S deficiency. If neither is effective, another problem may be present, and testing the soil pH would be a suitable starting point (see 'Aluminium toxicity').

Soil N measurements are difficult to interpret, as sources of N with differing availability to plants are not distinguished. As a rough indication, concentrations below 0.1% N (Kjeldahl method) are regarded as very low and concentrations of 0.5–1.0% N may be adequate for maximum crop growth (Landon 1991, quoting Metson 1961).

Kayode (1985) reviewed reported fertiliser responses of yams in West Africa and concluded that a small response to N was usually obtained on previously cropped sites with soil N < 0.1%, but not on newly cleared sites with soil N > 0.3%. Irizarry et al. (1995) recorded no response of *D. alata* to fertiliser on a site with soil N measurements in the range of 0.18–0.22%, despite a very high yield (58 t/ha fresh weight tuber) and removal by the crop of 214 kg/ha of N. However, the very narrow plots used may not have prevented root access of fertiliser between treatments. A similar experiment on the same soil using *D. rotundata* (Irizzary and Rivera 1985) recorded a significant response to high application rates of combined fertiliser (containing 224 kg/ha N), using wider plots separated by ditches. For a discussion of yam root length in relation to field trial design, see O'Sullivan (2008).

Management

Each yam crop removes a considerable amount of N from the soil and this must be replaced to maintain soil fertility. Irizarry et al. (1995) estimated a total removal of 25 kg N for each tonne of edible dry matter in a well-nourished crop of *D. alata*. Estimates of removal by *D. rotundata* include 11 kg N/t (Irizarry and Rivera 1985), 12 kg N/t (Obigbesan and Agboola 1978) and 20 kg N/t (Sobulo 1972b). These removal rates correspond to around 150–250 kg N/ha for high-yielding crops. The lost N can be replaced by planting legumes on the site, applying plant material or animal manures from outside the site, or applying chemical fertilisers. Not all yam farmers will be able to justify the expense of N fertilisers.

Nitrogen-containing fertilisers include urea, ammonium nitrate, ammonium sulfate or NPK (nitrogen, phosphorus, potassium) compound fertilisers. Nitrogen applied in fertiliser is readily lost by release of ammonia into the air (if fertiliser is not buried), conversion of nitrate by soil microbes into gaseous forms or by leaching in excessive rain or

irrigation. Therefore, it is best applied when the plants are ready to take it up. It is recommended to give a first application after the crop has established and again during the period of rapid vine growth. The fertiliser should be buried in a shallow furrow or broadcast immediately before rain. Application rates most commonly applied are between 50 and 200 kg N/ha, depending on the yield potential expected at the site. If two applications are to be made, only half the intended amount is applied at each application.

Studies of yam response to fertilisation have frequently recorded no response to N applications. The lack of response may be difficult to interpret, as often no details of the soil or plant N levels are given. However, in many published experiments, plot sizes have been too small to ensure good separation of treatments, as yam roots are now known to reach over several metres (Melteras et al. 2008; O'Sullivan 2008). Consequently, little advice is available for farmers on yam responses to N fertilisers.

A large proportion of the N in vegetation is lost by burning, so farmers should be discouraged from burning fallow vegetation when N deficiency is evident.

Animal manures are a good source of N, but their availability to yam farmers is usually limited. Nitrogen supply can also be improved by including more legumes in the farming system. This may be achieved by growing:

- or encouraging certain species in fallows
- leguminous crops (i.e. peanuts or pigeon peas) in the crop rotation
- a cover crop of herbaceous legumes between crops
- leguminous trees as hedge rows, live fences or live stakes.

Prunings from leguminous trees can be used to mulch yam crops. In addition to supplying N and other nutrients to the crop, mulches help retain soil moisture, minimise extremes of soil temperature and suppress weeds (see box 'Live-staking with Gliricidia sepium' on pp. 39–40).

Nutrient deficiencies: phosphorus

Phosphorus deficiency

It is difficult to estimate the extent to which yam yields are reduced by phosphorus (P) deficiency on a global scale. Field symptoms have not been described and the majority of published fertiliser experiments found no yield response to P fertilisation. It appears that yams are good scavengers of P and cope well with low-P soils. Many plant species form a symbiotic association with soil fungi (mycorrhizae), which help them to capture soil nutrients, especially P. Yam roots are usually heavily infected with mycorrhizal fungi, and their tolerance of low soil P may be attributable to this association. Nevertheless, it is possible that the problem is under-reported, as symptoms are not apparent. In many instances, the lack of fertiliser response may have been due to inadequate trial design. In Tonga, P fertilisation consistently improved yields by 20–100% on volcanic ash soils, which bind P strongly (limiting its availability to plants).

Phosphorus is particularly needed by plants for energy-transfer processes and to build membranes. Because the requirement is more for function than for structure, P deficiency can greatly reduce plant growth without changing the appearance of the plant. When symptoms finally do appear, the deficiency is quite severe by that point.

Phosphorus is regarded as a mobile nutrient—if it is in short supply, plants can move it from less important parts to wherever it is most needed. Typically, plants sacrifice their oldest leaves in order to release mobile nutrients for the shoot tip and young leaves. Therefore, we expect to see symptoms of P deficiency in the oldest leaves. However, yams appear to be the exception; they do not readily remobilise P to supply the shoot tip. Rather, severe P-deficiency symptoms appear in the young leaves. During tuber filling, senescing leaves do release P, which is remobilised to the tubers. Irizarry et al. (1995) estimated that one-third of the P in tubers comes from senescing leaves.

Occurrence

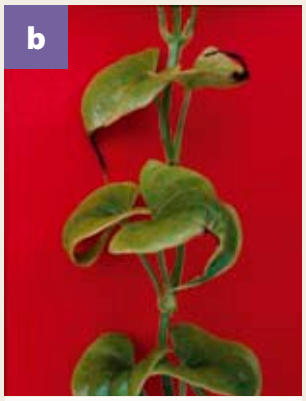
Plants need P in much smaller quantities than nitrogen (N), but the P in soils is often very tightly bound and difficult for plants to take up. Most volcanic soils and acidic soils have low P availability. In acidic soils, P may be adsorbed by iron (Fe) or aluminium (Al) oxides, and various clay minerals. Many of the most fertile and productive soils in tropical zones are derived from volcanic material containing allophane minerals, which have a large P-fixing capacity. Phosphorus deficiency is often the major limitation to crop growth on these soils, particularly where previous cropping has caused a depletion of soil organic matter and increased acidification. In alkaline, calcareous soils, P may be adsorbed by calcium carbonate or precipitated as calcium phosphate. Phosphorus deficiency is also common on highly weathered tropical soils and siliceous sands. In fact, few soils are naturally well endowed with this nutrient. For this reason, P deficiency is very common, and often limits plant growth more than N deficiency. Increased cropping intensity, which reduces soil organic matter content, may induce or exacerbate P deficiency by reducing activity of mycorrhizal fungi, as well as reducing the pool of plant-available P supplied through decomposition.

Symptoms

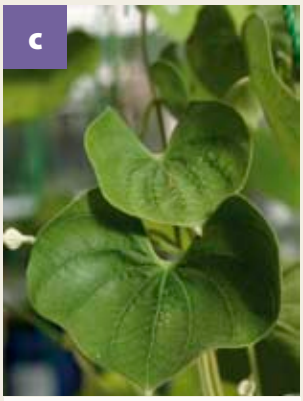
Moderate P deficiency causes growth reduction with no apparent symptoms. Foliage may be even darker green than in healthy plants. Tuber yield may be adversely affected before symptoms are visible.

As P deficiency intensifies, specific symptoms appear in the young leaves. Initially, the internodes are shortened and leaves are thicker and stiffer than normal, and don't expand to their full size (Figure 5a). They may be curled down towards the tip of the blade (*D. alata*) (Figure 5b) or gathered along the main veins, indicating uneven expansion (*D. esculenta*) (Figure 5c). The leaves may be light green to yellow (Figure 5a), or develop bleached white zones between the main veins (Figure 5d). However, in some cases, the normal

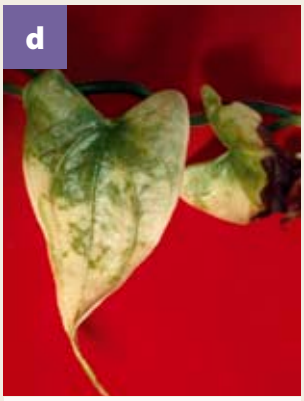
D. alata: tip region showing short internodes, and pale young leaves that are stiff and curled downwards.



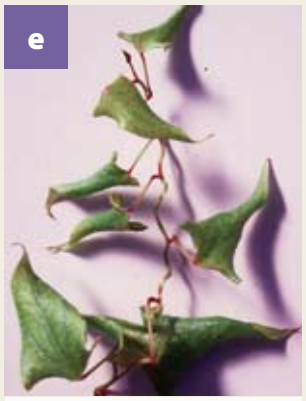
D. alata: young mature leaves that are small, stiff and curled down at the tip.



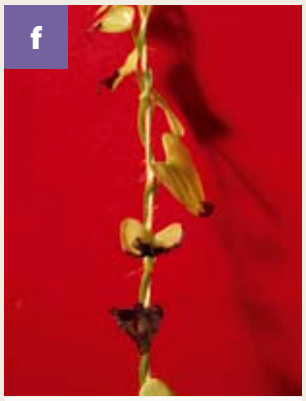
D. esculenta: young leaves showing puckering along the main veins, and slight upward cupping, due to uneven expansion of the leaf blades.



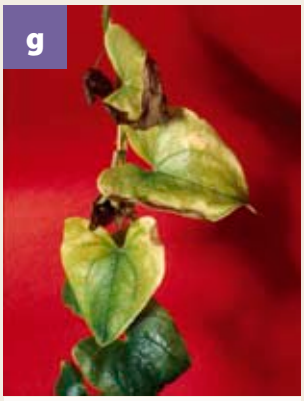
D. alata: young leaves showing bleaching of tissue between veins, and dark necrosis spreading from the leaf tip.



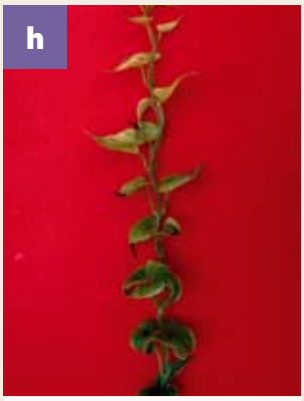
D. alata: tip has become inactive and barely extends past the youngest leaves, which are small despite being quite mature. Leaves are stiff and curled down at the margins.



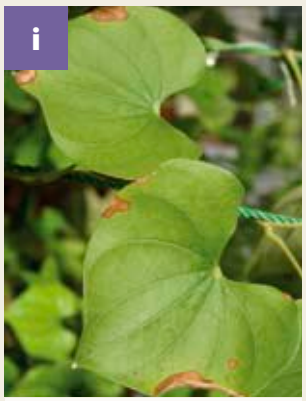
D. alata: young leaves becoming necrotic from the tip of the blade.



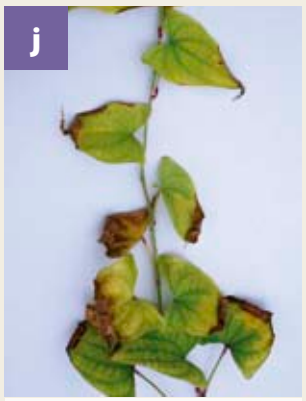
D. alata: young leaves showing a rapid deterioration from green, well-expanded leaves (lowest, older leaf) to blades that die before expanding (top, younger leaf).



D. alata: symptoms progressing from dark green leaves that are small and curled down, to dead tips on blades, to very pale and small youngest leaves.

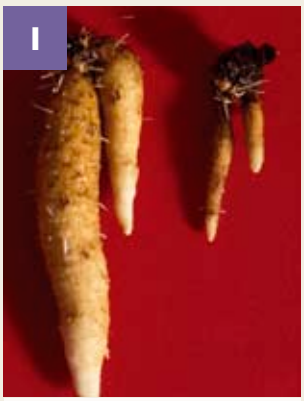


D. esculenta: patches of necrosis along the margins of young mature leaves.



D. alata: oldest leaves showing progression of chlorosis and necrosis spreading from leaf tips.

D. rotundata: dark necrotic lesions forming on older leaves, appearing as watery, stained areas on the lower surface.



D. alata: tubers from a well-nourished plant (left) and a P-deficient plant (right), after 9 weeks growth.

P = phosphorus

Figure 5. Symptoms of phosphorus deficiency in yam plants.

dark green colour is retained (Figure 5c). The shoot tip may become inactive, which can be observed by the relative maturity of first leaves (Figure 5e). As severity increases, leaf blades become necrotic at the tip or margins, and the whole blade may dry up (Figure 5f–h). In *D. alata*, the dead tissue is generally dark and brittle. In *D. esculenta*, patches of brown marginal necrosis may be observed on leaves before the onset of deformities, but do not spread (Figure 5i).

Older leaves may senesce prematurely (Figure 5j), but this is not a consistent or conspicuous symptom of P deficiency in the vegetative stage of yam growth. In *D. rotundata*, dark necrotic lesions may be observed on older leaves, but these do not rapidly progress to full senescence of the leaves (Figure 5k).

Phosphorus deficiency strongly reduces the growth of tubers (Figure 5l).

Diagnostic tests

In *D. alata*, a critical concentration range of 0.21–0.37% was estimated for the leaf blades sampled from the fifth and sixth youngest nodes during the rapid vine growth phase. Leaf P concentration tends to decline with leaf age (i.e. position on the vine), but remains fairly stable throughout the growing season (Irizarry et al. 1995; author's data, see Appendix). Both *D. esculenta* and *D. rotundata* appear to have similar foliar P concentrations to *D. alata* when sampled at the same location at both fertile and P-deficient sites. Therefore, the critical range for *D. alata* may be used as indicative of deficiency in these species also.

Little work has yet been done to calibrate soil tests for predicting yield response of yam to applied P, but it would appear that yams are very efficient at using P at low concentrations in the soil (Vander Zaag et al. 1980). Most fertiliser response trials have not recorded any response of yams to P fertilisation. Vander Zaag et al. (1980) tested several varieties each of *D. alata*, *D. rotundata* and *D. esculenta* for response to P application. The authors used a soil with a soil-solution P concentration of 0.005 parts per million (ppm) before fertilisation. Only the highest yielding varieties of *D. alata* responded to additional P, up to a soil solution concentration of 0.02 ppm.

Olsen's extraction of soil is the most commonly used test for soil P (Rayment and Higginson 1992). Bingham (1962) suggested that available P levels in the range of 5–7 ppm (using Olsen's method) correspond to the threshold for deficiency in crops with a low P requirement, such as yam. Using Olsen's method, S. Halavatau (unpublished) recorded a positive response to P fertilisation of *D. alata* on a soil testing 8 ppm P, but not on soils testing 18 ppm P or above. It should be noted that these measurements include only part of the P in soil organic matter, which may represent a considerable proportion of the P available to the crop in some soils.

Measurements of P-binding capacity, in addition to plant-available P, have been used to estimate the quantity of P fertiliser required on P-fixing soils. Phosphate binding can be estimated using P-sorption isotherms (Fox and Kamprath 1970) or P retention (Saunders 1974). These methods have been described by Rayment and Higginson (1992).

Management

Phosphorus deficiency can be corrected by broadcast, band or spot application of soluble P sources, such as single or triple superphosphate, ammonium phosphate or mixed fertilisers (containing N, P and potassium (K), with or without other nutrients). Band or spot application of P fertilisers is recommended on strongly P-fixing soils.

Rock phosphate is a relatively cheap alternative to more soluble fertilisers. Rock phosphate should be well incorporated into the soil. It is usually only effective on acidic soils, due to its very low solubility at neutral to high pH.

Single superphosphate (10% P) also contains sulfur (S) and calcium (Ca), and is recommended in soils where these nutrients are also low. Triple superphosphate (TSP, 24% P) also contains Ca, but not S.

Application rates of P fertilisation depend on the P-binding capacity of the soil. The amount of P removed by the crop is around 1.3–2.2 kg P/t of edible dry matter, equivalent to 12–25 kg/ha of P (Sobulo 1972b; Obigbesan and Agboola 1978; Irizarry and Rivera 1985; Kabeerathumma et al. 1991; Irizarry et al. 1995). However, on P-binding soils, 50–100 kg/ha of P may be needed to maximise the yield response when P is placed in a concentrated band in the mound (S. Halavatau, unpublished data). Higher application rates, up to 400 kg/ha, are required if P fertiliser is incorporated throughout the soil (such as with rock phosphate), but a greater residual effect will be gained in subsequent years.

Adding organic matter, in the form of either plant or animal manures, provides P and improves the microbial activity in the soil, which may improve P capture by mycorrhizae.

Nutrient deficiencies: potassium

Potassium deficiency

Occurrence

Potassium (K) is often fairly abundant in the rocks and minerals that form soils, but after repeated cropping, or on soils that are heavily leached by high rainfall, K levels run low. Potassium deficiency occurs most commonly on sandy soils, which have a low cation-exchange capacity (CEC), and on Oxisols and Ultisols with low base status. Some volcanic-ash soils have large K reserves, while others may have a low CEC. A low CEC means a low availability of K, and a poor ability to retain added K.

Plants need about as much K as nitrogen (N). Crops that supply vegetative materials or 'wet' products (i.e. root crops and fruits, compared with 'dry' cereals, pulses and nuts) have much more K in the harvested product. Gardens that are dominated by root crops are very often deficient in K because it has been removed over many years by crops.

In traditional subsistence systems, where the crop is consumed locally, and human and animal manures are retained in the system, K losses are less than in modern commercial cropping systems. Even so, K deficiency is probably the primary limiting factor in many subsistence farming communities, from West Africa to Papua New Guinea. In surveys of yam crops across three provinces of Papua New Guinea, K deficiency was the most common and most severe nutrient deficiency encountered.

Symptoms

Potassium-deficient crops generally are a lighter shade of green than healthy crops, but specific symptoms may not be present. Young mature leaves usually show chlorosis symptoms most distinctly. In mildly deficient plants, the paler interveinal tissue is usually finely divided by the network of greener veins (Figure 6a–c). However, chlorosis patterns may be diffusely interveinal (gradually fading with distance from the major veins) (Figure 6d) or more general (with veins barely greener than interveins) (Figure 6e) as severity increases.

Premature senescence of the oldest leaves is usually characteristic of K deficiency, but in yams, this may not be evident until the onset of tuber filling. At this stage, the lowest leaves may rapidly develop a light-brown necrosis, spreading from the tips and margins of the blades (Figure 6f–g). The necrosis may be preceded by yellowing, but this is often limited to a yellow strip at the leading edge of the dead zone.

Growth of the vine tip is generally slowed and internodes shortened. The vine tip may become prematurely inactive, which is evident from the maturity of leaves immediately behind the tip (Figure 6h).

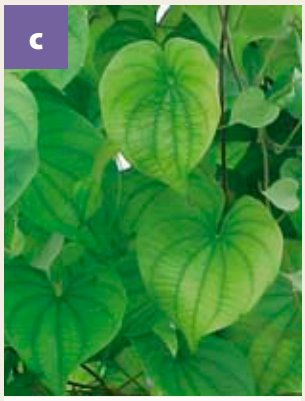
Potassium deficiency may make plants wilt more easily in dry weather, and be more susceptible to diseases and pests.

Diagnostic tests

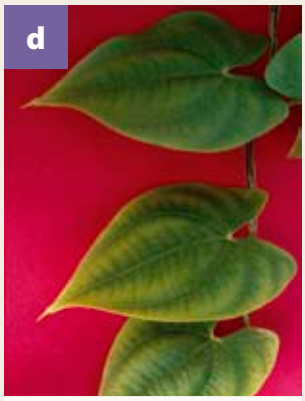
In *D. alata*, a critical concentration range of 2.1–3.9% was determined for the blades of leaves sampled from the fifth and sixth youngest nodes of actively growing vines. This wide range reflects both the variability in K concentration among plants (for leaves at the same position) and the variation with leaf position. Younger leaves tend to have higher K concentration than older leaves. The leaves at any particular node may vary in age, depending on the rate of growth of the vine tip. Consequently, factors that change the rate of vine growth, including stage of crop growth and environmental conditions (i.e. temperature, light and water availability) may change the absolute age of leaves sampled, and hence their K content. In addition, the availability of sodium (Na) in the soil may affect the response to K, as Na can substitute for part of the K requirement in plants that are K deficient. The critical range is therefore only a guide. Samples with a K concentration below the critical range are likely to respond to K fertilisation, while those within the range may benefit.

D. alata: mid leaves showing interveinal chlorosis between a network of greener veins.

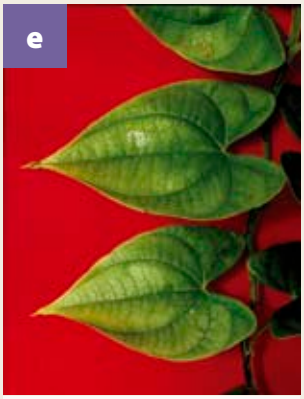
D. alata: distinct interveinal chlorosis on a mature leaf.



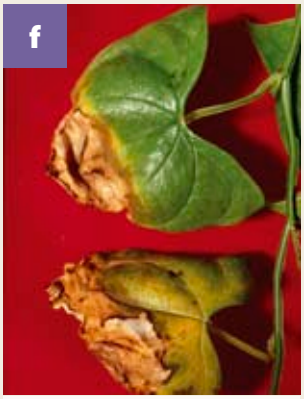
D. esculenta: a K-deficient crop in Papua New Guinea showing interveinal chlorosis on young mature leaves, finely divided by greener veins.



D. alata: mid leaves showing a more diffuse interveinal chlorosis.

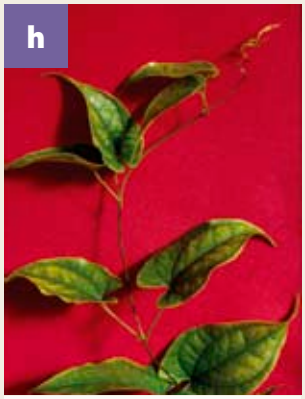


D. alata: young mature leaves with a general chlorosis, slightly greener on veins.



D. alata: older leaves with necrosis spreading from the tip. Before necrosis, yellowing may be general (as on the lower leaf), limited to a narrow band (as on the upper leaf) or absent.

D. rotundata: leaves near the base of the vine, with necrosis spreading from tips and margins. Several nodes have already lost leaves.



D. rotundata: low activity of the vine tip, evident by relatively mature first leaves. All leaves display a diffuse interveinal chlorosis.

K = potassium

Figure 6. Symptoms of potassium deficiency in yam plants.

Both *D. rotundata* and *D. esculenta* leaves have been noted to contain less K than *D. alata* when grown on the same site (Obigbesan and Agboola 1978; Vander Zaag et al. 1980; author's data, see Appendix). This may be related to the lower water content (higher dry-matter content) of their foliage. However, the difference between *D. alata* and *D. rotundata* is inconsistent and may be a result of differential Na uptake. On a site with greater Na availability, *D. rotundata* had lower K and higher Na than *D. alata*. However, on a site with low Na availability, the two species contained similar K concentrations. The critical concentration for *D. alata* was 3.3%, but for *D. esculenta*, it appeared to be in the vicinity of 2.5% (O'Sullivan and Ernest 2007). In *D. esculenta*, an index leaf concentration of 1.8% K was associated with growth reduction by almost one-half when compared to well-nourished plants. It is suggested that a tentative critical range for *D. esculenta* is 2.1–2.6%, and that a similar range is likely to apply to *D. rotundata*.

Soil exchangeable-K measurements are frequently used to predict the K status of crops. This does not reflect the soil's reserves of potentially available K, which may be released over a period of time. Crop responses to K fertilisation are generally expected at exchangeable

K values in the range 0.2–0.6 centimoles of positive charge [cmol(+)]/kg soil, although this relationship depends on the soil texture and total CEC. Sandy soils may respond only in the range 0.05–0.25 cmol(+)/kg (Landon 1991). Ekpete (1978) concluded that yams appeared tolerant of marginal soil K levels, compared with other crops. However, soil tests have not been calibrated for yam response to K.

Management

The amount of K removed from the soil by a yam crop is similar to the amount of N—estimates range from 12–25 kg K/t of edible dry matter or 150–250 kg/ha of K for high-yielding crops (Sobulo 1972b; Obigbesan and Agboola 1978; Kabeerathumma et al. 1991; Irizarry and Rivera 1985; Irizarry et al. 1995).

Potassium can be added to the soil either in the form of inorganic fertiliser, or in organic mulches and composts. The most common form of fertiliser is muriate of potash (otherwise known as potassium chloride). Potassium nitrate is also used in compound fertilisers. Recommendations for fertiliser additions range from 80–200 kg K/ha, roughly corresponding to the expected removal by the crop. Because K is easily leached from light-textured soils, split applications are recommended on these soils—one-half incorporated in the soil in the planting hole at planting and one-half broadcast during the period of rapid vine growth. On soils with higher clay content, a single dose at planting is adequate.

Organic mulches are much more bulky than inorganic fertilisers, therefore requiring more labour, but the efficiency of nutrient use by the crop may be higher. Generally, fresh plant material contains much more K than animal manure or bedding straw. Rates of up to 20 t/ha of plant mulches have been recommended. They may be applied at intervals during the growing season, such as by periodic pruning of leguminous trees grown for the purpose of mulching.

Deep-rooted trees may be able to access K from the subsoil, which shallow-rooted crops such as yam can not reach. Long fallows help to return K to the topsoil, when the vegetation is burnt or rots away. Using leaves or other by-products from trees as mulch gives crops access to some of this deep-soil K (see box 'Live-staking with *Gliricidia sepium*', on pp. 39–40).

Excessive application of K may lead to magnesium (Mg) or calcium (Ca) deficiency, due to reduced uptake of these elements (Spear et al. 1978). High levels of K may reduce Mg and Ca uptake by competing with these nutrients for uptake sites on the roots. On sandy soils in particular, Mg and Ca applications may be necessary in addition to K to prevent induced deficiencies (Landon 1991). On heavier soils, K additions may make the clay more sticky and weaker in texture, reducing drainage. Calcium (and to a lesser extent Mg) adhering to the surface of clay particles helps the particles clump together, producing a desirable crumb texture. By displacing Ca on the surface of clay particles, K weakens the bonds between the particles. On these soils, it may be beneficial to add Ca (in the form of gypsum) to maintain soil texture.

Nutrient deficiencies: calcium

Calcium deficiency

Occurrence

Calcium (Ca) is usually an abundant element in clays. It is also a major constituent of coral and limestone. However, in soils high in silica sand (formed on granitic rock or sandy river sediments) it can be in short supply. High levels of potassium (K) or magnesium (Mg) may reduce Ca uptake by competing with Ca for uptake sites on the roots. Therefore, K fertilisers can make Ca deficiencies worse.

The process of soil acidification results in low availability of Ca, as well as increasing the concentrations of soluble aluminium (Al) species. Aluminium damages plant root tips (root pruning) and consequently reduces the plant's ability to take up Ca. The root pruning caused by Al toxicity reduces uptake of all nutrients, but Ca is mainly absorbed through young root tissue just behind growing tips. Therefore, Ca absorption is more affected by Al toxicity. In these situations, Ca deficiency may be better regarded as a symptom of soil acidity. However, since the treatment of acidity generally requires addition of calcium carbonate (lime), the distinction is hardly necessary.

Calcium is taken up into the shoot with the flow of water and is not actively transported by the plant from one tissue to another. Plant parts such as the shoot tips and developing fruits, which do not lose much water and therefore do not get much Ca inflow, are particularly sensitive to Ca deficiency. In many crop species, deformities of the young leaves are common in Ca deficiency, but this has not been observed in yams. Hot, dry, windy weather, which causes the leaves to shut down and reduce water flow, can cause Ca-deficiency symptoms in new leaves even when soil Ca levels are adequate. Plants recover when normal weather returns, but the affected leaves may not.

Symptoms

Calcium deficiency mostly affects the growth of new tissue—at the vine, root and tuber tips. The earliest apparent symptom may be premature inactivity of the vine tips (Figure 7a–b). This is evident by the relative maturity of leaves just behind the tip. The vine is typically thin and internodes are shorter than usual, and the tip does not extend far beyond the first open leaves. In severe cases, the tip and youngest leaves may die (Figure 7c), or the youngest leaves die while the tip remains green. The inactivity of the shoot tip may stimulate axillary shoots to develop at the upper nodes, but these generally only produce one or two leaves before also becoming inactive (Figure 7d).

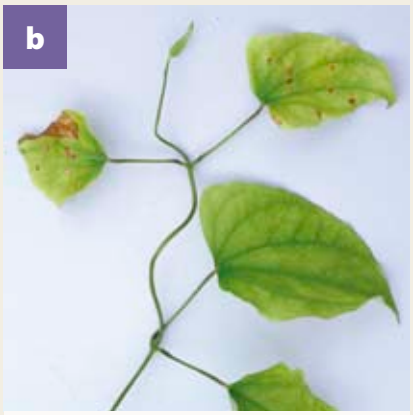
Young leaves may also be paler than normal, with either a uniform light-green to cream colour, or an interveinal pattern becoming gradually greener towards the main veins (Figure 7a–b). This is generally the case with *D. alata*, but *D. esculenta* and *D. rotundata* often show no chlorosis. On all species, young mature leaves often develop dark necrotic spots, which can be scattered on interveinal tissue, or form a more regular arc around the petiole attachment (Figure 7e–f). Mid leaves sometimes show necrosis on the veins on the underside of the leaf (Figure 7g). In contrast to sulfur (S) deficiency, this necrosis usually extends to the petiole attachment point. Petioles may also bear necrotic lesions.

Root growth is particularly affected by Ca deficiency. Root tips may die, resulting in a cluster of branching just behind the tip (Figure 7h–i). The growing tip of the tuber is affected and tubers may be blunt-ended and short, or have constrictions (Figure 7i).

Diagnostic tests

In *D. alata*, the critical tissue concentration range for Ca deficiency has been estimated to be 1.0–1.5% in leaf blades sampled from the fifth and sixth youngest nodes from the tip. Calcium concentration increases with leaf age, so older leaves will have higher critical concentrations.

D. alata: the top of a C-deficient vine, with an inactive tip evident by the maturity of first leaves. Young leaves are chlorotic and young mature leaves show scattered dark spots.

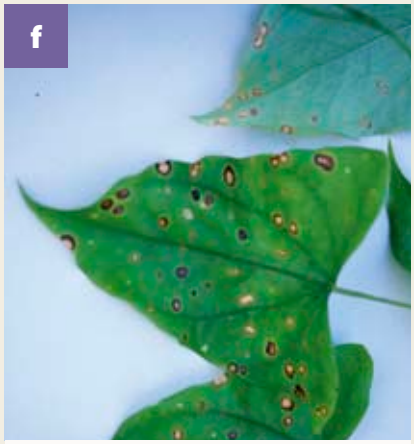


D. rotundata: an inactive tip and chlorotic young leaves showing necrotic spots.

D. alata: the shoot tip and first leaf have died due to severe Ca deficiency.

D. esculenta: axillary shoots on a Ca-deficient plant, each with one or two mature leaves and an inactive tip.

D. alata: dark necrotic spots on young mature leaves, generally forming an arc around the petiole attachment.



D. rotundata: in this species, necrotic spots on young mature leaves tend to have a pale centre.

D. alata: necrosis of main veins on the underside of young mature leaves.

D. alata: root tips affected by Ca deficiency, with short secondary branches behind dead tips.

D. rotundata: a blunt-ended tuber showing constrictions and roots with short branches clustered behind dead tips.

Ca = calcium

Figure 7. Symptoms of calcuim deficiency in yam plants.

Dioscorea rotundata appears to have a greater tolerance to low tissue-Ca levels, showing less growth reduction despite lower tissue concentrations than *D. alata* when grown at deficient Ca levels. *Dioscorea esculenta* also tended to have lower Ca levels than *D. alata* when grown at the same site, and concentrations as low as 0.95% were associated with healthy growth (O'Sullivan and Ernest 2007). A critical range of 0.5–0.9% is suggested for these species when sampling leaves from the fifth and sixth nodes for *D. rotundata* and the seventh and eighth nodes for *D. esculenta*.

Attempts to measure plant-available Ca in the soil are generally unreliable, since the availability is dependent on a number of factors. Exchangeable Ca levels less than 0.2 centimoles of positive charge [cmol(+)]/kg soil indicate that Ca deficiency is likely (Landon 1991). Very high availability of K (through heavy K fertilisation) or sodium (Na; sodic soils) may cause Ca to be deficient to plants even though the exchangeable Ca levels may be in what would normally be considered an adequate range.

Management

Addition of lime (calcium carbonate, 40% Ca) has the dual effect of providing Ca and raising the soil pH. Lime is poorly soluble and has low mobility in the soil, so it should be broadcast and incorporated thoroughly into the soil before planting the crop. Application rates for lime are high (generally 1–4 t/ha), but will be effective for several years. The appropriate rate should be calculated by a soil analytical laboratory on the basis of the pH and buffering capacity of the soil.

If Ca deficiency is not associated with soil acidity, gypsum (calcium sulfate, 22% Ca) may be used. It is usually also incorporated into the soil, although it is more soluble than lime. Single superphosphate and triple superphosphate also contain Ca (23% and 16% Ca, respectively) and may be suitable sources where both phosporus (P) and Ca are in short supply.

Applications of Ca (particularly as gypsum) may intensify deficiencies of Mg or K. It may be necessary to add these nutrients in conjunction with Ca, so that deficiencies of these nutrients are not induced.

Nutrient deficiencies: magnesium

Magnesium deficiency

Occurrence

Magnesium (Mg) deficiency may result either from low Mg content in the soil or from an overabundance of potassium (K) or calcium (Ca), which inhibits Mg uptake by the crop. Therefore, the disorder is most likely to occur on sandy soils that have a low cation-exchange capacity (CEC), volcanic ash soils with high K status or some calcareous soils. Overfertilisation with K may also induce Mg deficiency. In strongly acidic soils, Mg deficiency may be induced by the presence of toxic concentrations of aluminium (Al) in the root environment, which inhibit root growth and Mg uptake by the plant (see 'Aluminium toxicity').

Symptoms

The crop appears light green, with an interveinal pattern of chlorosis most pronounced on young mature leaves. Vine tips and stems generally appear healthy. Leaves are generally a healthy size, and have a normal soft texture and a light sheen. Leaves in full sun are likely to be paler than those in the shade, as the yellowing results from photobleaching of the green chlorophyll pigment. The pattern of chlorosis varies with variety. Usually, there is a margin of green tissue either side of the main veins, but the minor veins are less defined (Figure 8a). The leaf margin may also remain green. In some cases, the chlorosis is most pronounced in a band on either side of the main veins (Figure 8b). In others, the yellowing is more uniform across the leaf, contrasting with the greener network of veins (Figure 8c).

Older leaves develop necrotic lesions that spread from irregular interveinal spots or from the leaf tip (Figure 8d–e). The dead tissue is pale to medium tan in colour, but often has a dark edge. Young leaves that are severely bleached may also develop scattered necrotic spots, but these rarely spread (Figure 8f).

Commonly, the surface of the leaf becomes stained light brown over the interveinal regions. This symptom does not appear to be directly related to the development of necrotic lesions. It has been observed on both *D. alata* and *D. esculenta*, both in experimental conditions (Figure 8g–h) and in the field (Figure 8i).

Diagnostic tests

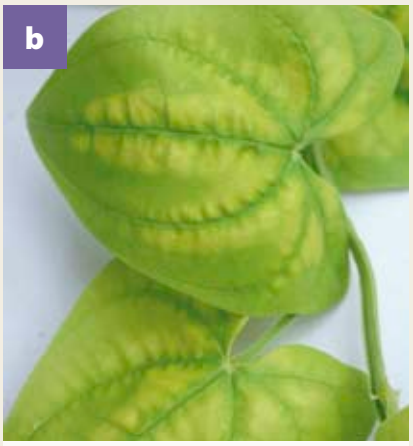
In *D. alata*, the critical range for Mg deficiency was estimated to be 0.10–0.14% in leaf blades sampled from the fifth and sixth youngest nodes on actively growing vines. A similar range appears to apply to *D. esculenta* and *D. rotundata*, and all have similar Mg concentrations when grown at the same site.

Soil tests have not been calibrated for yam response to Mg. For other field crops, extraction of soil using neutral 1 M ammonium acetate is a standard procedure and Mg levels of less than 100–200 mg Mg/kg are generally considered to have a risk of Mg deficiency. It is also recommended that the K:Mg ratio should be ≤ 5:1, on a weight-of-element basis (Doll and Lucas 1973).

Management

Magnesium deficiency may be corrected by incorporation of dolomitic lime or magnesium oxide into acid soils (20–50 kg Mg/ha), or by band application of kieserite or fertiliser-grade magnesium sulfate (10–40 kg Mg/ha). Magnesium sulfate (also known as epsom salts) is the most soluble of these sources and it is the preferred source where it is necessary to correct an observed Mg deficiency in an established crop. However, this is often a more expensive option. If top dressing of the established crop is difficult, magnesium sulfate may be applied as a foliar spray or dissolved in irrigation water.

D. alata: interveinal chlorosis—both the main veins and leaf margins remain green. Lower leaves develop brown interveinal lesions.



D. alata: chlorosis is sometimes more pronounced in a band on either side of main veins.

D. esculenta: young mature leaves showing distinct interveinal chlorosis, which becomes less distinct on older leaves.

D. alata: older leaves develop necrotic lesions, either from the tip extending into interveinal zones or spreading from irregular interveinal spots.

D. rotundata: older leaves showing interveinal chlorosis and pale necrosis spreading from margins or interveinal lesions.

D. alata: when lesions form on younger leaves, they may take the form of numerous small spots.

D. esculenta: staining on the upper surface of older leaves, extending in a fragmented pattern from the petiole attachment.

D. alata: a brown stain on interveinal areas of upper or lower leaf surface, preceding the development of lesions.

D. esculenta: symptoms including strong interveinal chlorosis and staining of interveinal areas due to Mg deficiency in the Kimbe area of Papua New Guinea. (Photo: Mike Bourke)

Mg = magnesium

Figure 8. Symptoms of magnesium deficiency in yam plants.

Nutrient deficiencies: sulfur

Sulfur deficiency

Occurrence

Sulfur (S) is very soluble and is easily washed out of soils entirely, or out of the topsoil into the subsoil. This is especially the case on sandy acidic soils and if organic matter content in the soil is low. Sulfur is also lost into the air when vegetation is burnt. Areas that have experienced frequent burning, such as many tropical grasslands, are often depleted in S. In coastal areas, S may be replenished by sea spray, but may not be sufficient to counteract leaching and burning, as S deficiency has been reported even on small islands. Young volcanic ash generally has good supplies of S, but a combination of high rainfall and frequent burning may produce S deficiency even on volcanic soils. Deep-rooted plants may get enough S from the subsoil, but shallow-rooted crops, such as yam, suffer from deficiency.

Symptoms

Plants are generally a light-green colour all over, but the younger leaves are palest. Veins may be slightly greener than the interveinal tissue (Figure 9a), but often the colour is uniform across the whole leaf. Plants grow slowly and leaf size is reduced. The vine tip may become inactive, which may be evident from the maturity of the first leaves and the short distance from the first leaves to the tip (Figure 9b). These symptoms are similar to those of nitrogen (N) deficiency, but in contrast to N deficiency, leaves tend to be slightly stiffened and may be shiny.

In severely deficient plants, expanding leaves may develop white bleached zones in the interveinal tissue or near the tip (Figure 9c). The leaf tips may become brown and the necrosis may spread to the whole leaf blade, producing a zone of dead leaves below the vine tip.

Necrotic lesions may also occur on the stem (Figure 9d) or on veins under the leaf (Figure 9e). These symptoms are most commonly seen on mature leaves in the middle of the vine.

Commonly, mature leaves develop scattered spots, which appear faintly bruised and stained but generally don't become fully necrotic (Figure 9f). They may be surrounded by a yellow halo.

Diagnostic tests

In *D. alata*, a critical concentration range of 0.10–0.14% S was estimated in leaf blades sampled from the fifth and sixth youngest nodes from actively growing tips. Growth reduction was steep when tissue S concentrations dropped to below 0.10%. Similar concentrations appear to apply for *D. rotundata* and *D. esculenta* (O'Sullivan and Ernest 2007). All have similar tissue concentrations when grown at the same sites.

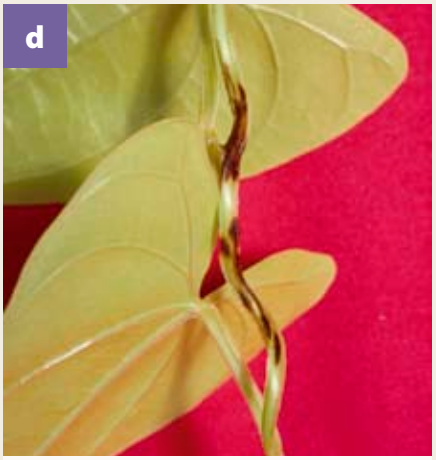
The chemistry of S in soils is complex. There is no reliable measure of plant-available S that can be applied over a wide range of soil conditions. Total S measurements may be related to crop response to S fertiliser only when the soil S reserves are very low. Calcium phosphate extraction is used to estimate the soluble plus adsorbed sulfate fraction (Rayment and Higginson 1992). This may be used to predict S deficiency in soils with a low organic matter content. However, in most humid tropical soils, S is predominantly supplied from the degradation of organic material (Landon 1991). Landon quoted approximate critical levels of 200 mg/kg total S or 6–12 mg/kg extractable S. Soils with a low organic matter content are likely to have S concentrations below these amounts.

In the field, fertiliser test strips may be used to distinguish S deficiency from N deficiency. A row of plants may be fertilised with sulfate of ammonia and another row with urea. There must be several untreated rows left between the fertiliser strips, as yam roots may extend over several metres (O'Sullivan 2008). The plants would likely have been suffering

D. alata: indistinct interveinal chlorosis on young mature leaves.

D. rotundata: interveinal chlorosis on young leaves and an inactive vine tip.

D. alata: white bleached zones on expanding leaves, developing into necrosis.



D. alata: lesions on the vine stem.

D. esculenta: necrosis on the veins under mature leaves.

D. esculenta: spots of bruised or stained tissue with a yellow halo on mature leaves.

S = sulfur

Figure 9. Symptoms of sulfur deficiency in yam plants.

from S deficiency if they became greener in the strip containing sulfate of ammonium, but not urea (when compared with the rest of the field). If both treatments were equally effective, the problem would be N deficiency. If neither is effective, another problem may be present, and testing the soil pH would be useful (see 'Aluminium toxicity').

Management

Maintaining a high organic matter content in the soil will increase the availability of S to the roots and decrease the rate of nutrient leaching. Burning crop and fallow residues leads to direct losses of S to the air and loss of organic matter inputs to the soil. Burning should be especially discouraged where S supply is poor.

As for potassium (K), trees may be able to get S from the subsoil, which crop plants can not reach. Tree prunings from fallows, living fences or hedgerows can be used to provide leaves for mulching the garden.

Sulfur deficiency may be corrected by the addition of an S-containing fertiliser. The fertiliser chosen may be primarily for supplying S, such as gypsum (calcium sulfate) or elemental S. Alternatively, S may be added as a constituent of fertilisers intended to supply other nutrients, such as ammonium sulfate (24% S, also containing N) or single superphosphate (11% S, also containing phosphorus (P). It should be noted that many 'high-analysis' fertilisers, such as triple superphosphate, monoammonium phosphate, diammonium phosphate and urea, contain only trace amounts of S.

Nutrient deficiencies: iron

Iron deficiency

Occurrence

Iron (Fe) is usually fairly abundant in soil minerals, but not very soluble. Iron oxides give brown and red soils their colour. Deficiencies usually occur in soils with high pH (alkaline), such as those formed on coral or limestone. At a high pH, very little iron is soluble for plants to absorb. Symptoms of Fe deficiency are very common on atolls and coastal soils affected by lime. In these situations, Fe deficiency may often be associated with deficiencies of other micronutrients, such as manganese (Mn), copper (Cu) and zinc (Zn), whose availability is also pH-dependent.

Heavy applications of lime or phosphorus (P) fertilisers can induce Fe deficiency. Iron deficiency may also be expected on soils lacking in clay minerals, such as sandy soils and organic soils. A number of other disorders that impair root function can inhibit Fe uptake and induce symptoms of Fe deficiency in the leaves. These may include toxicities of Mn or aluminium (Al)—common complications of acid soils—or deficiencies of calcium (Ca) or boron (B).

In all cases of Fe deficiency, care should be taken to determine the conditions responsible for the disorder. Iron deficiency is one disorder where visible symptoms are obvious when crops are only mildly affected.

Symptoms

The young leaves become chlorotic, initially yellowish green with darker green veins (Figure 10a). Young mature leaves may be the first to show distinctive symptoms and generally display a detailed network of greener veins on a pale leaf (Figure 10b–c). However, on younger leaves, the minor veins may be indistinct. Generally, leaf venation is more distinct on *D. alata* and *D. esculenta* than on *D. rotundata*. Leaves in full sun are affected more than those in the shade.

As the deficiency intensifies, young leaves of *D. alata* may become completely bleached white (Figure 10d). In purple-tipped varieties, the shoot tip becomes pink (Figure 10e). The bleached leaves tend to become necrotic, with dead tissue spreading from the leaf margins or from scattered spots on the leaf blade (Figure 10d–e). The shoot tip may die in severe cases, but usually the tip, stem and petioles remain alive, even when the blades of young leaves are dead (Figure 10f). In *D. esculenta*, bleaching was not observed in response to Fe deficiency, but the young leaves shrivelled before full expansion. In contrast to other species, *D. esculenta* showed extreme bleaching of young leaves that was caused by Mn deficiency. In all species, the shoot tip may become weak and thin, with short internodes (Figure 10f). Axillary branches may show the symptoms more strongly than leaves on the main vine (Figure 10g).

Diagnostic tests

In *D. alata*, a critical range for Fe deficiency of 25–45 mg/kg Fe has been estimated for leaf blades sampled from the fifth and sixth youngest nodes. Leaves from healthy plants typically contain 60–400 mg/kg Fe. Iron deficiency is not well characterised in *D. rotundata* and *D. esculenta*, but all three species contain similar concentrations when grown at the same site.

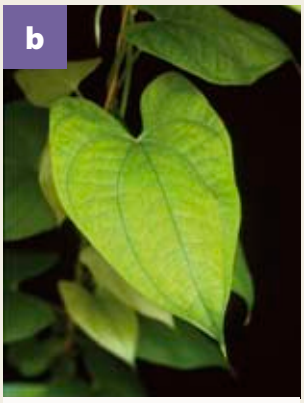
Leaf painting is a very useful technique to confirm Fe deficiency (Figure 10h). A 1% solution of ferric ammonium sulfate is carefully painted onto one-half of a chlorotic leaf. It is important to clearly label the painted leaf so that it can be identified on later inspection. The leaf should be labelled before painting to avoid handling when it is wet. After 4–7 days, regreening should be evident if Fe deficiency is present.

Due to the large number of factors that affect the availability of soil Fe to plants, soil measurements are not generally reliable for diagnosing Fe deficiency.

Management

On high pH soils, application of Fe compounds as a soil fertiliser is likely to give a poor response, as the

D. alata: interveinal chlorosis on young leaves due to Fe deficiency.

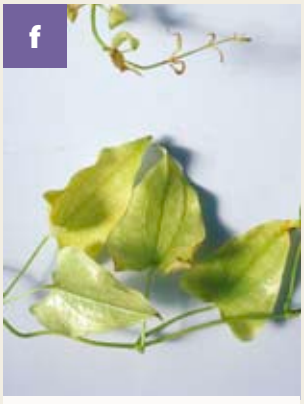


D. alata: detailed veinal pattern on a mature leaf that has developed chlorosis.

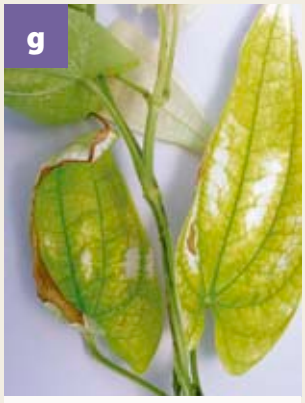
D. esculenta: mature leaves showing interveinal chlorosis with strong contrast between veins and interveinal tissue.

D. alata: young leaves bleached white and becoming necrotic, with lesions spreading from the margins.

D. alata: a purple-tipped variety showing pink pigmentation of the tip and bleached young leaves developing necrotic spots.



D. rotundata: young mature leaves that are chlorotic and reduced in size and a weak shoot tip whose youngest leaves have died early in their development.



D. alata: chlorosis on young mature leaves and an axillary shoot baring bleached white leaves.

D. alata: the right-hand side of a bleached leaf was painted with ferrous ammonium sulfate while it was still expanding. A week later, dramatic greening and increased expansion are evident on the painted side.

Fe = iron

Figure 10. Symptoms of iron deficiency in yam plants.

added Fe will be precipitated and become unavailable to plants. Treatment of an Fe-deficient crop is best achieved by a foliar spray of chelated Fe or 1–2% ammonium ferric sulfate solution. Burying small pieces of scrap iron (i.e. nails and steel food cans) in the mound at planting can also be effective in reducing Fe deficiency, but care should be taken not to place them where they will interfere with tuber growth. Soaking cans in sea water before burying accelerates rusting and has been successful in increasing their effectiveness as an Fe supplement on calcareous atoll soils (Cable 1992).

Traditionally, atoll farmers have managed lime-induced deficiencies by building up high organic-matter levels, such as in compost pits. Organic matter is the key to nutrient availability in these soils, which have multiple nutrient deficits.

If Fe deficiency occurs on an acidic soil, it may be a secondary effect of another nutritional disorder, such as Mn toxicity or Ca deficiency. In this case, liming may alleviate the Fe deficiency by eliminating the underlying problem.

Nutrient deficiencies: boron

Boron deficiency

Occurrence

Boron (B) deficiency is most likely on soils derived from acid igneous rocks and freshwater sediments (which are naturally low in B) or in acidic, sandy soils in high rainfall areas (from which B has been leached) (Bradford 1966). Dry or cold conditions, which restrict root development and the movement of water from roots to tops, seem to exacerbate B deficiency. Recovery may occur following rain or warmer weather.

Boron deficiency has not been reported as a problem in yam crops, but is quite common in other crops and may be unrecognised in yam. Some types of plants are more susceptible to B deficiency than others: those with white sap, such as sweetpotato and pawpaw, are particularly prone. If these are present in the vicinity of the yam crop, presence or absence of symptoms on them would aid diagnosis of the problem in the yams.

Symptoms

The primary symptom of B deficiency is deformity of the young leaves (Figure 11a–e). This commonly appears as crinkling along the veins, deflection of the leaf tip, cupping either upward or downward, or twisting—all due to uneven expansion of different parts of the leaf blade. Constricted tissue (often along veins or in a particular sector of the blade) may appear paler and may become necrotic—generally a dark-brown, brittle necrosis in irregular patches. Leaves are typically stiffer than normal. Leaves are also usually brittle and crack easily when bent (Figure 11f). Leaf deformity in *D. alata* characterised by wide, shortened leaf blades with curled tips. In *D. rotundata*, only mild deformities were seen, but necrotic spots developed on young mature leaves (Figure 11g).

Young mature leaves, even those lacking deformity, may be paler than normal, with a weakly interveinal, uneven or mottled pattern (Figure 11c). Stronger chlorosis is usually caused by iron (Fe) deficiency, induced by the restricted root growth resulting from B deficiency. This is commonly seen in B-deficient plants of *D. alata* and *D. rotundata*, but it is also possible to have severe B deficiency without chlorosis if Fe levels are sufficient. In the case of *D. esculenta*, chlorosis of young leaves was attributable to induced manganese (Mn) deficiency (Figure 11h).

Shoot tips may produce several leaves that fail to expand and then become necrotic (Figure 11i). The tip itself may die. Weakness or death of the shoot tip stimulates axillary branches, but these typically show stronger symptoms, with very small deformed leaves, often lacking lateral lobes (Figure 11b, 11j).

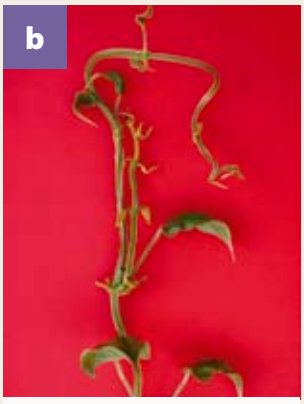
The root system of B-deficient plants is often restricted, as B is important for the elongation of root tips. Roots often show a cluster of short, thick branches around the tips of main roots and may have necrotic tips (Figure 11k). The tuber's growing tip may be arrested, causing blunt round or pear-shaped tubers, or irregular branching. Brown necrotic areas may occur in the flesh of tubers (Figure 11l).

Diagnostic tests

In *D. alata*, the critical concentration range for B deficiency has been estimated as 9–20 mg/kg in leaf blades sampled from the fifth and sixth youngest nodes. Boron deficiency has not been sufficiently characterised in *D. esculenta* or *D. rotundata* to provide a critical range. Crops sampled in regions where B deficiency is not uncommon and where B supply may have been suboptimal have frequently tested within this critical range without evidence of deficiency. However, severely deficient *D. esculenta* in sand culture had average concentrations of 10 mg/kg B in leaves of the seventh and eighth nodes (O'Sullivan and Ernest 2007).

There is no published information on soil B in relation to B deficiency in yams. Critical concentrations quoted in the literature for a wide range of crops mostly lie in the range of 0.3–0.5 mg/kg of B (extractable by

D. alata: deformed young leaves, showing crinkling along the veins and sections of paler or necrotic tissue that has failed to develop and expand normally.



D. alata: small, stiff, deformed young leaves with reduced lateral lobes and downward cupping. The weak tip has promoted axillary shoots to grow, but these have produced only tiny leaves and their tips have died.

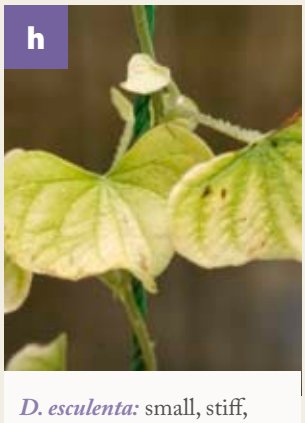
D. alata: small cupped and crinkled leaves characteristic of B deficiency, with interveinal chlorosis due to induced Fe deficiency.

D. alata: curled leaves and a dead shoot tip.

D. alata: irregular patches of necrosis contributing to the uneven expansion of young leaves.

D. alata: young mature leaves are stiffer and more brittle than normal, and crack easily when bent.

D. rotundata: mottled chlorosis and scattered necrotic spots on young mature leaves of a B-deficient plant.



D. esculenta: small, stiff, broad young leaves with twisted tips caused by B deficiency, and severe chlorosis due to induced Mn deficiency.

D. alata: shoot tips with dead, unexpanded leaves.

D. alata: axillary shoots baring tiny deformed leaves.

D. rotundata: root tips showing clusters of short, thick branches around necrotic root tips.

D. alata: a young tuber from a B-deficient plant, with irregular branching and breakdown of internal tissue.

B = boron; Fe = iron; Mn = manganese

Figure 11. Symptoms of boron deficiency in yam plants.

hot water), but may be up to 1 mg/kg for susceptible species and is possibly higher in alkaline soils than in acidic soils (Bradford 1966). The relationship between available B (extractable by hot water) and unavailable B is modified by a number of factors, including soil texture, pH and available calcium (Ca).

Management

Boron deficiency can be corrected by fertilising with borax or other borates (e.g. 'Solubor') and should be applied to the soil before planting. Recommended amounts are 1.0–1.5 kg B/ha on sandy, acidic soils or up to 4 kg B/ha on clay alkaline soils (von Stieglitz and Chippendale 1955). Overfertilisation may result in B toxicity, so it is best to aim for the lowest effective amount, which may be further reduced on subsequent crops due to persistence of the applied B in the soil.

On light-textured soils, building up soil organic matter will help. However, all plant material grown locally on the same soil type is also likely to have relatively low B concentrations, so the benefit may not be large.

Foliar application of B is often recommended for other crops, but its effectiveness for root crops is not established. Generally, B is not transported within the plant from vines to roots—except in some crops, such as apple (Brown and Shelp 1997). Therefore, while the tops may appear healthy after foliar spraying, symptoms may persist on the roots and tubers. Hence soil application is advised.

Nutrient deficiencies: manganese

Manganese deficiency

Occurrence

Manganese (Mn) is present in the soil as free Mn^{2+} (which is readily available to plants) and as oxides of low solubility. The proportion of Mn in various forms in the soil is dependent both on chemical reactions and on microbial activity. High soil pH greatly reduces the solubility of soil Mn. Therefore, Mn deficiency is most likely to occur in soils that are alkaline (such as coral atolls) or have been limed.

In very wet soil, the low oxygen status favours soluble Mn. In well-aerated soil, microbial activity results in its oxidation to insoluble forms. As a result, Mn deficiency may arise intermittently during drier periods or appear more severe in well-drained parts of the field. Cycles of Mn deficiency and recovery may result in symptoms normally associated with young leaves appearing only on a few adjacent mature leaves.

Dioscorea esculenta appears to be particularly susceptible to Mn deficiency. Symptoms are commonly seen in this species in coastal areas of Papua New Guinea, on alkaline soils formed on coral (Johnston 1996). However, because of the unusual presentation of symptoms in this species, they are often interpreted to be Fe deficiencies.

A large increase in yield was recorded after application of Mn to *D. alata* and *D. rotundata* on alkaline soils in Puerto Rico (Sotomayor-Ramirez et al. 2003).

Symptoms

Manganese deficiency appears to produce different symptoms in the three yam species studied. Symptoms in *D. alata* are typical of many plant species. The young expanding leaves first develop a fine interveinal chlorosis, in which small spots of tissue in between minor veins appear as pale, translucent spots (Figure 12a). These spots may be slightly sunken, giving the leaf surface a rough, rugous texture. Some or many spots then develop into necrotic lesions (Figure 12b). Necrosis also may develop on the stem wings in the upper part of the vine (Figure 12c). The youngest leaves are usually pale, but only develop spots as they expand (Figure 12d). The necrosis may cause some deformity of the expanding leaves. Older leaves also develop dark necrotic spots, but these are usually not preceded by pale translucent spots (Figure 12e). Initially, they are only apparent on the upper surface of the leaf. Affected leaves may then become yellow and die, but the dark spots remain evident in the paler necrotic tissue of the dead leaf (Figure 12f).

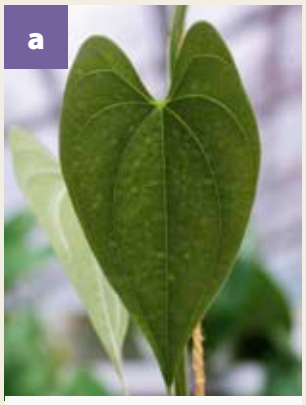
In *D. rotundata*, spots do not form as readily. Manganese deficiency causes considerable growth reduction before distinctive symptoms appear on the vines. Leaves may develop a rugous texture and mottled colour, and may be deformed with asymmetrical expansion or curled with wavy margins (Figure 12g). Young leaves may become chlorotic, particularly around the margins, and an increase in branching may produce a bushy growth habit (Figure 12h). Any severe bleaching of the young leaves is probably due to induced iron (Fe) deficiency resulting from poor root growth.

Young leaves of *D. esculenta* become pale, almost white, with main veins retaining a green margin (Figure 12i). Necrosis may spread on affected leaves as they reach full expansion (Figure 12j). A diffuse-edged interveinal chlorosis may extend to mid leaves. Older leaves may develop small, dark-brown spots in a similar manner to *D. alata*, except that spots remain small (Figure 12k). However, in contrast to *D. alata*, such spots are never observed on the young leaves.

The roots of Mn-deficient yams are finer and shorter than normal. Tuber growth is reduced and tubers may become necrotic at the growing tip.

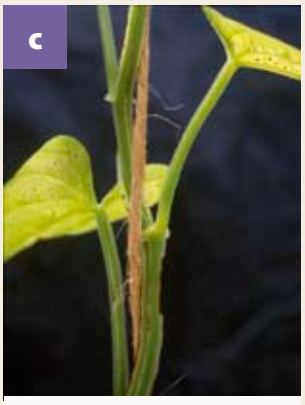
Diagnostic tests

In *D. alata*, a critical concentration range of 10–15 mg/kg Mn was determined in leaf blades sampled from the fifth and sixth youngest nodes. This



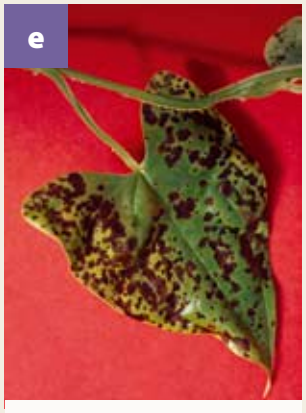
D. alata: a young expanding leaf showing early development of sunken, translucent spots.

D. alata: pale spots becoming necrotic lesions on an expanding leaf.



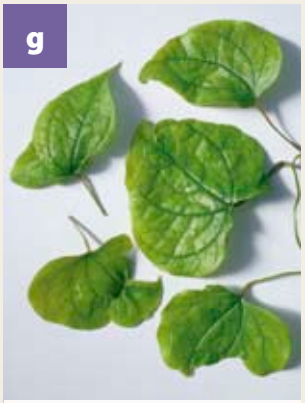
D. alata: necrosis on the wings of the stem, in the upper part of the vine.

D. alata: pale young leaves develop spots only as they expand. Necrosis on the stem may result in death of the shoot tip.



D. alata: dark necrotic spots developed on an older leaf due to Mn deficiency.

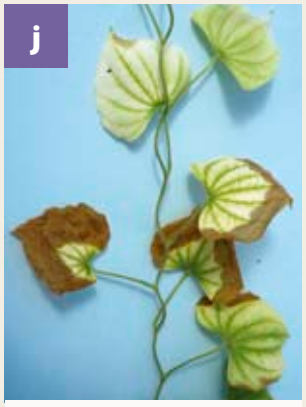
D. alata: older leaves senescing after developing dark spots. The spots are still visible in the necrotic tissue.



D. rotundata: deformities and mottled chlorosis on young mature leaves of an Mn-deficient plant.

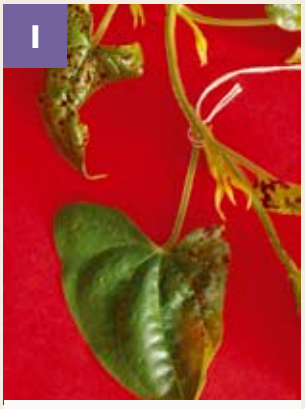
D. rotundata: despite the death of older leaves on the main stem, multiple branches still grew, producing small, pale leaves.

D. esculenta: young leaves bleached white on a crop growing on coral soil in Papua New Guinea. (Photo: James Ernest)



D. esculenta: the bleaching of young leaves and spreading necrosis as leaves reach full expansion.

D. esculenta: small necrotic spots developed on an older leaf.



D. alata: one-half of a leaf painted with manganese sulfate soon after opening, showing symptom development only on the unpainted side.

Mn = manganese

Figure 12. Symptoms of manganese deficiency in yam plants.

is consistent with concentrations recorded in healthy and deficient samples from *D. rotundata* (blades from the fifth and sixth nodes) and *D. esculenta* (blades from the seventh and eighth nodes).

Sotomayor-Ramirez et al. (2003) reported poor growth in yams in Puerto Rico that responded strongly to a foliar spray containing a mixture of micronutrients. They sampled leaves from the middle part of the vine on plants untreated with micronutrient foliar spray, and recorded concentrations of 32 and 25 mg/kg Mn in *D. alata* and *D. rotundata*, respectively. Treatment with the foliar spray caused a considerable increase in yield, as well as large increases in foliar Mn and zinc (Zn) concentrations. However, they did not establish the relative contributions of Mn or Zn deficiency to the poor growth and leaf symptoms observed.

Suspected cases of Mn deficiency can be confirmed by leaf painting with a 1% solution of manganese sulfate. Manganese application causes regreening of chlorotic tissue in *D. esculenta*. In young expanding leaves of *D. alata*, it arrests the development of interveinal pits and enhances expansion of the treated portion of the leaf blade (see Figure 12l).

Manganese availability in the soil may be estimated by extraction with a chelating agent such as diethylenetriaminepentaacetic acid (DTPA) (Rayment and Higginson 1992). Concentrations of DTPA-extractable Mn less than 4 mg/kg are considered potentially deficient for a range of root and vegetable crops (CFL 1983).

Management

On alkaline soils, Mn deficiency arises due to soil conditions that limit the availability of Mn to plants—not because there is insufficient Mn in the soil. Therefore, fertilisation of the soil with Mn may be ineffective, as the added Mn could become unavailable. Foliar sprays of 0.1% manganese sulfate or chelate, at 2–4 kg Mn/ha, may be effective (Tisdale et al. 1993; Weir and Cresswell 1993). Alternatively, the Mn-containing fungicide mancozeb can be applied if other sources of Mn are not available. Building up soil organic-matter content by mulching or composting will also help to improve the availability of Mn and other nutrients to the crop.

When deficiency occurs at neutral to acidic soil pH, Mn may be applied to the soil as either manganese sulfate or oxide. Volumes used for other crops are typically in the range of 10–20 kg Mn/ha. Soils low in Mn should not be limed if the soil pH is above 6.4 (as measured in water).

Nutrient deficiencies: zinc

Zinc deficiency

Occurrence

Zinc (Zn) deficiency may occur on acidic to neutral sandy soils with a low Zn content or on alkaline soils in which the solubility of Zn is reduced. Due to the declining availability of Zn with increasing soil pH, applying lime or dolomite to acid soils low in Zn may induce Zn deficiency. Applications of copper (Cu) fertiliser or large amounts of phosphorus (P) fertiliser may also exacerbate Zn deficiency (Olsen 1972).

Crops vary considerably in their sensitivity to Zn deficiency. Yams appear to be of moderate sensitivity; likely less susceptible than cassava or citrus. If these species are present in the vicinity of a yam crop suspected of Zn deficiency, they may be good indicators. They develop clear and distinctive symptoms in situations where symptoms on yams may be mild or not evident.

Symptoms

In the field, symptoms of Zn deficiency are conspicuous, in the form of smaller-than-normal leaves that are curled or wavy (Figure 13a). When less severe, the first symptom of Zn deficiency may be a mild interveinal chlorosis on mature leaves in the mid section of vines. The network of veins is usually clearly evident (Figure 13b). However, as this chlorosis intensifies at greater levels of deficiency, the darker green may be restricted to the main veins and the base of primary branches (Figure 13c). Necrotic lesions may develop at the margins or in interveinal patches (Figure 13c). In older leaves, a dark-purplish pigmentation may form in a mottled pattern across the leaf or predominantly over the main veins (Figure 13c, 13g).

Young leaves become smaller, generally narrower, and often twisted or curled (Figure 13d–e). They may also become pale or lightly bronzed, or they may retain a dark-green colour. Internodes are usually reduced in length. The young leaves may become necrotic, with lesions usually spreading from the tip (Figure 13f). Initially, the size reduction may be difficult to observe, but much more severe symptoms often appear on axillary branches (Figure 13c, 13g).

Dioscorea rotundata appears to be more sensitive to Zn deficiency than *D. alata*, but the symptoms are similar. Young leaves exhibit twisted forms and mottled chlorosis (Figure 13h). Older leaves may show distinct interveinal chlorosis and necrotic lesions (Figure 13i).

The same pattern is also seen in *D. esculenta*. Young leaves are reduced in size and develop wavy margins (Figure 13j). Interveinal chlorosis is most pronounced in young mature leaves (Figure 13k).

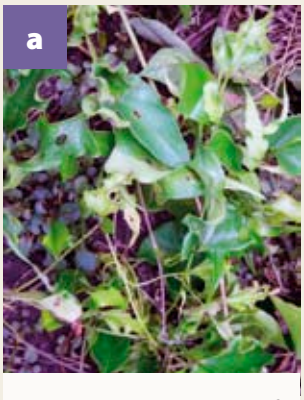
Tubers of Zn-deficient plants often have longitudinal cracks resulting in necrotic lesions.

Diagnostic tests

In *D. alata*, a critical concentration range of 15–35 mg/kg Zn was determined for leaf blades sampled from the fifth and sixth youngest nodes. *Dioscorea rotundata* appeared to respond in the same range as *D. alata*. An index leaf concentration of 13 mg/kg Zn was measured in a crop of *D. rotundata* displaying leaf symptoms of Zn deficiency (Figure 13a) and yield responded positively to application of Zn.

A lower concentration may apply for *D. esculenta*. In sand culture, healthy plants contained concentrations ranging from 7–10 mg/kg Zn, while 5 mg/kg was associated with mild deficiency (O'Sullivan and Ernest 2007). A critical range of 4–6 mg/kg Zn is suggested in leaves of the seventh and eighth youngest nodes.

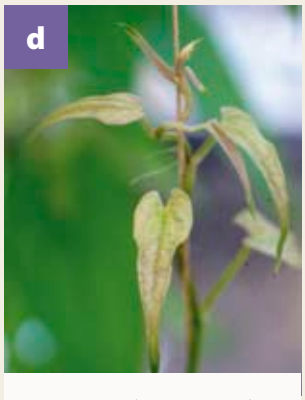
Sotomayor-Ramirez et al. (2003) recorded concentrations in leaves from the middle of the vine of 35 and 22 mg/kg Zn in *D. alata* and *D. rotundata*, respectively, on a site suspected of Zn deficiency. However, the contributions of deficiencies in Zn, manganese (Mn) and iron (Fe) to yield reduction were not established.



D. rotundata: symptoms of Zn deficiency in a crop in the Markham Valley, Papua New Guinea.

D. alata: young mature leaves of a mildly Zn-deficient plant, with mild interveinal chlorosis finely divided by a contrasting network of veins.

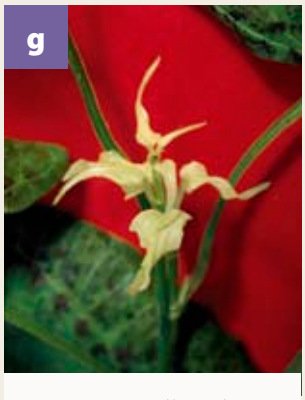
D. alata: older leaves of a Zn-deficient plant, showing interveinal chlorosis, marginal necrosis and purple pigmentation on veins. Axiliary shoots show severe bleaching and size reduction of leaves.



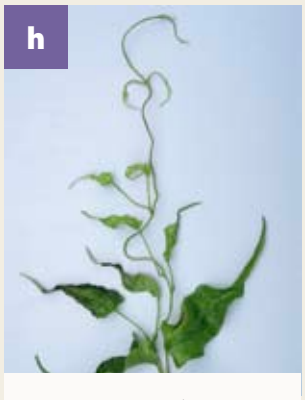
D. alata: a shoot tip with pale, narrow young leaves and short internodes.

D. alata: small, curled leaves and reduced internode length on a Zn-deficient shoot tip.

D. alata: a shoot tip with reduced leaf size and internode length, and curled leaves with mottled chlorosis and necrotic tips.



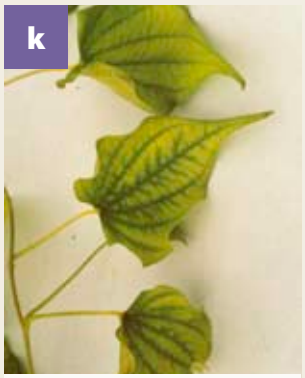
D. alata: an axillary shoot exhibiting severe symptoms of chlorosis, elongated and curled leaf shape, and reduced leaf size and internode length.



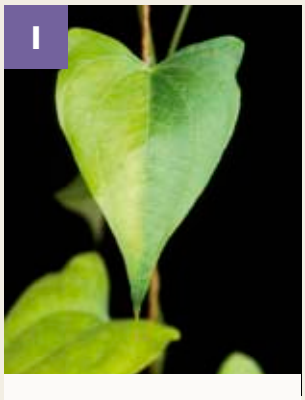
D. rotundata: a shoot tip showing curled leaf margins, mottled chlorosis and progressively reduced leaf size.

D. rotundata: interveinal chlorosis and necrotic lesions on mature leaves, and an axillary shoot showing severe leaf reduction and deformities.

D. esculenta: young leaves are reduced in size and wavy at the margins.



D. esculenta: interveinal chlorosis on young mature leaves.



D. alata: leaf painting on one-half of a young leaf with zinc sulfate has caused the tissue to regreen.

Zn = zinc

Figure 13. Symptoms of zinc deficiency in yam plants.

Suspected cases of Zn deficiency can be confirmed by a positive response to painting the leaf surface with a solution of 0.5% zinc sulfate and 0.25% calcium hydroxide. Normally, one-half of a leaf blade is painted, so the response can be compared directly with the untreated half. After a few days, this should result in regreening of chlorotic tissue on either mature or young leaves, and may increase expansion of the treated area of young leaves (see Figure 13l). It is important to label the painted leaf clearly so that it can be identified on later inspection.

Various extractants have been used to estimate plant-available Zn in soils, including hydrochloric acid, dithizone and diethylenetriaminepentaacetic acid (DTPA). These tests are influenced to varying degrees by the soil pH, free lime content and phosphate concentration, and reported critical concentrations for Zn in a range of crops vary widely (1.0–7.5 mg Zn/kg with hydrochloric acid, 0.3–2.3 mg Zn/kg with dithizone) (Landon 1991). An extractant containing 0.01 M ethylenediaminetetraacetic acid (EDTA) and 1 M ammonium carbonate has been found to be suitable over a range of soils, including alkaline, calcareous soils (Trierweiler and Lindsay 1969). Using this test, a critical concentration of 1.4 mg Zn/kg was determined for Zn in maize, a crop regarded as being sensitive to low Zn supply.

Management

Foliar spraying is probably the most convenient method of supplying Zn to a Zn-deficient crop and is particularly recommended on alkaline soils, where soil-applied Zn may have low availability. Amounts of fertiliser for yam have not been optimised, but a solution containing 1% zinc sulfate applied at about 8 kg/ha (2 kg Zn/ha) is a typical rate. This amount has been successful in alleviating symptoms and improving growth in Zn-deficient *D. rotundata* in Papua New Guinea.

On neutral and acidic soils where Zn deficiency is known to occur, soil application at or before planting is likely to be more effective than foliar sprays after crop establishment (Weir and Cresswell 1993). Soil application rates of 3–10 kg Zn/ha as zinc sulfate heptahydrate (23% Zn) or zinc oxide (60–80% Zn) are typical for vegetable crops. The lesser amount may suffice on light-textured acidic soils, whereas high-clay or high-pH soils may require the greater amount. Zinc oxide should be broadcast and incorporated into the soil before planting. Zinc sulfate heptahydrate is more soluble and band application at the time of planting is acceptable. Zinc applications may be effective for several years.

Burying small pieces of scrap galvanised iron in the mound or ridge may provide an effective source of Zn to the crop. This is a particularly useful strategy where Zn fertilisers are not available or are poorly effective due to high alkalinity of the soil. Keep them to the side of the planting sett, to avoid impeding tuber development.

Maintenance of a high soil organic matter content increases the availability of Zn to plants (Chapman 1966).

Nutrient deficiencies: copper

Copper deficiency

Occurrence

Copper (Cu) is often deficient in coral soils due to its insolubility at high pH, similar to iron (Fe), manganese (Mn) and zinc (Zn). It may also be deficient on leached sandy soils or on some peaty soils that have the ability to bind Cu tightly and therefore reduce its availability to plants.

Symptoms

In *D. alata*, the primary symptom of Cu deficiency is the appearance of small, deformed young leaves. These are typically crinkled along the veins, and cupped upward or curled under (Figure 14a). They often appear pinched at the tip, with a necrotic leaf tip (Figure 14b), or have torn away from a dead tip as they have expanded, producing a tattered margin (Figure 14c). However, this is not always the case, and in some instances, basal lobes or interveinal zones may be necrotic (a pattern similar to the symptoms of boron [B] deficiency) (Figure 14d). Leaves may be a normal, dark-green colour or paler, and are often shiny. Symptoms may develop quite suddenly, progressing from normal leaves to severely reduced leaves and dead shoot tips in only a few nodes of growth (Figure 14e). Dead or weak shoot tips stimulate the growth of axillary shoots, which grow with strong stems but very reduced leaves (Figure 14f–g). Increased branching towards the top of the vine may result.

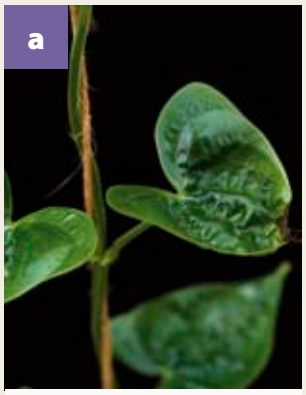
Copper deficiency has not been observed in *D. rotundata*. In *D. esculenta*, only a mild level of deficiency was induced in experimental conditions. This was accompanied by deformed young leaves with a tattered tip, similar to those seen in *D. alata* (Figure 14h). On coral-based soil in Kiriwina, Papua New Guinea, the common upward cupping or curling of leaves was associated with very low leaf Cu levels (Figure 14i).

Diagnostic tests

In *D. alata*, a critical concentration range of 2.0–3.6 mg/kg Cu was determined in leaf blades sampled from the fifth and sixth youngest nodes. This appears to be consistent with responses in *D. rotundata* and *D. esculenta*. *Dioscorea rotundata* and *D. alata* contained similar Cu concentrations in leaves of fifth and sixth nodes when grown together at deficient and normal Cu levels. In *D. esculenta*, a concentration of 2.6 mg/kg Cu was associated with mild symptoms but no significant growth reduction (O'Sullivan and Ernest 2007).

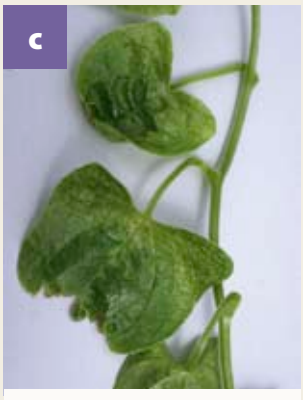
Leaf painting is an effective and inexpensive diagnostic test that may confirm the presence of Cu deficiency. Both surfaces of a very young leaf are painted with a dilute solution containing Cu (e.g. 0.25% $CuSO_4.5H_2O$ + 0.25% $Ca(OH)_2$). If Cu deficiency is the cause of the observed symptoms, the treated leaf will show increased expansion and reduced symptoms over the following week (see Figure 14j). It is important to clearly label the leaf so that it can be identified on later inspection. As the leaf should be painted at an early stage, and Cu-deficient leaves are very small, it is usually not practical to paint only one side of the leaf. However, in species with two leaves at each node, the paired leaf provides a direct comparison. A small amount of agricultural wetting agent or mild detergent may be added to the solution to ensure even wetting of the leaf surface, but this is not essential with yam, as the foliage wets relatively easily.

Soil extraction using ethylenediaminetetraacetic acid (EDTA) with ammonium bicarbonate has been recommended for evaluation of Cu status, particularly in alkaline, calcareous soils. Using this test, a critical concentration of 0.3–0.4 mg Cu/kg of air-dry soil was determined for wheat (Best et al. 1985). Soil tests have not been calibrated for Cu critical concentrations for yam.



D. alata: young expanding leaves showing typical deformities, including gathering along the veins and necrosis at the tip.

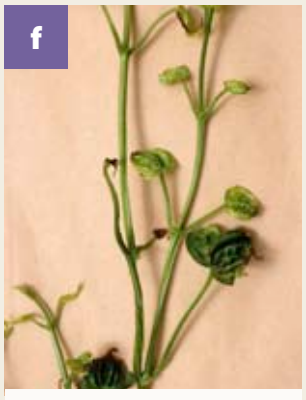
D. alata: typical deformities caused by Cu deficiency, usually including a 'pinched' tip.



D. alata: tattered margins on young leaves—they have torn away from a dead leaf tip as they expanded.

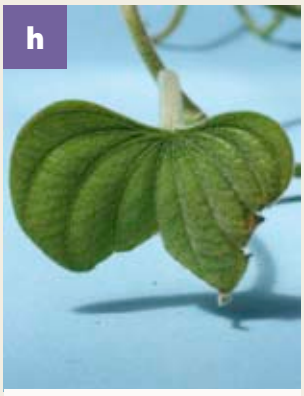
D. alata: shiny, deformed leaves developing necrosis in various parts, including basal lobes and interveinal sectors.

D. alata: progression of symptoms from normal leaves to severely deformed and reduced in size, to dead shoot tips, within a few nodes.

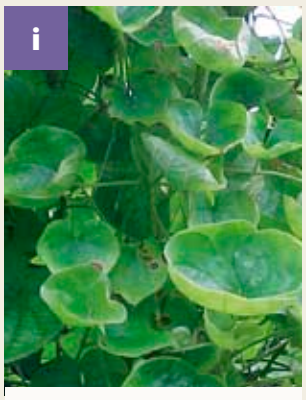


D. alata: axillary branches formed after the death of the original shoot tip, baring small, pale leaves.

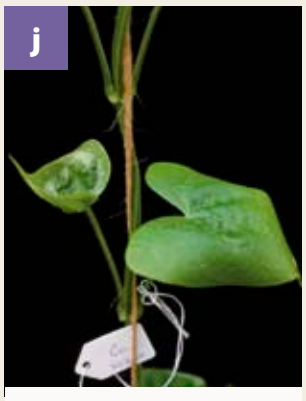
D. alata: multiple branches baring leaves at various levels of deformity and size reduction.



D. esculenta: a deformed young leaf with a torn margin.



D. esculenta: cupping of leaves due to Cu deficiency on a high-pH coral soil in Papua New Guinea. (Photo: James Ernest)



D. alata: a leaf that was painted with copper sulfate when just opened, showing increased expansion compared with its pair.

Cu = copper

Figure 14. Symptoms of copper deficiency in yam plants.

Management

Copper may be applied to the soil or as a foliar spray. On alkaline or organic soils, foliar sprays may be more effective due to the rapid immobilisation of soil-applied Cu. In general, however, soil application is considered preferable (Reuther and Labanauskas 1966). Rates of Cu fertiliser application for yam crops have not been tested. For other crops, soil applications of copper sulfate at 1 kg Cu/ha on acidic, sandy soils with low organic matter content, to 7 kg Cu/ha on alkaline, peaty or heavy-textured soils have been used. Overfertilisation with Cu can lead to Cu toxicity, so the minimum effective dose should be used. A single application of Cu may be effective for up to 10 years (Weir and Cresswell 1993).

For foliar application, doses as low as 0.25 kg Cu/ha have been sufficient for wheat. A convenient and widely available source of Cu is Bordeaux mixture (a mixture of copper sulfate and hydrated lime). A 1% solution (1 kg in 100 L) may be sprayed on leaves every couple of months, focusing particularly on the shoot tips. Bordeaux mixture is also used to control fungal diseases on leaves.

Nutrient deficiencies: molybdenum

Molybdenum deficiency

Occurrence

Molybdenum (Mo) is less available to plants at low soil pH, in contrast to many of the other micronutrients (that become less available at high soil pH). Thus, Mo deficiency is usually associated with acidic soils (pH < 5.5), particularly those that are geologically old and highly leached. Molybdenum deficiency has not been reported in yam crops to date. Soils that are low in Mo are often also low in phosphorus (P) and sulfur (S)—therefore, Mo deficiency may not become apparent unless P and S deficiencies have been corrected by fertilisation.

Molybdenum is required by plants in very small quantities. Its main (and possibly only) function in nonleguminous plants is as a component of the enzyme nitrate reductase. This enzyme is essential for the metabolism of nitrate, the main form of plant-available nitrogen (N) in most soils. Therefore, Mo-deficient plants may appear as if they are deficient in N, having general chlorosis and stunted growth. Additional symptoms (other than those of N deficiency) may occur as a result of nitrate accumulation in the tissue to the level where it is locally toxic—as the nitrate is not being reduced to a usable form.

Symptoms

It is anticipated that Mo-deficient yam crops will display symptoms resembling N deficiency, including a general light-green colour, small leaves and a reduced growth rate. Due to the difficulty in eliminating all sources of Mo contamination in experimental plant culture, the levels of Mo deficiency induced to date have been mild, and did not include significant reduction in growth. The symptoms described in the following paragraphs were observed in these plants, which were well supplied with N. The symptoms are probably related to the accumulation of nitrate in the plant tissue, rather than symptoms of poor N nutrition.

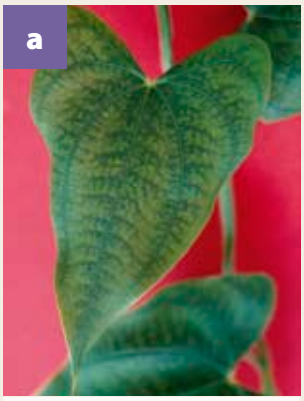
Mature to older leaves may develop a mild interveinal chlorosis (Figure 15a–b). In *D. alata* and *D. esculenta*, this is finely divided by the minor veins, but in *D. rotundata*, veins are less sharply delineated. In *D. esculenta*, some mature leaves may develop small pale lesions in the chlorotic tissue (Figure 15c). On older leaves of *D. alata*, small dark spots may develop on oldest leaves, which progress to become sunken necrotic lesions (Figure 15d). Alternatively, larger dark-grey or brown lesions may form on margins or interveinal tissue of older leaves without prior yellowing, but leaves may subsequently turn yellow and senesce fully (Figure 15e). The necrosis is confined to the margins in some instances in *D. alata* (Figure 15f), and in most cases in *D. rotundata* (Figure 15g).

Diagnostic tests

If interveinal chlorosis is present, leaf painting may be used to confirm the diagnosis. A solution containing 0.5% sodium molybdate may be painted on half of a chlorotic leaf. The leaf should be clearly labelled before painting, so that it can be identified at later inspection. If Mo deficiency is present, the painted portion should regreen after 5–7 days (see Figure 15h).

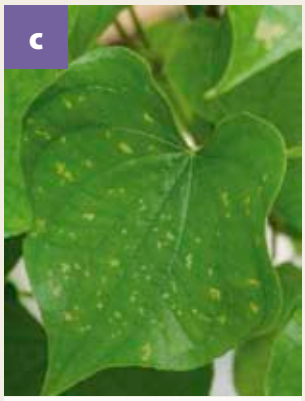
The critical concentration for Mo in yam tissue has not been well defined, and not all plant-tissue-testing laboratories have the ability to measure Mo accurately in the deficient range. From solution culture studies, a concentration of 0.8 mg/kg of Mo in leaf blades from the fifth and sixth nodes of *D. alata* was associated with symptom development, but no growth reduction was evident. In *D. esculenta*, the same concentration in blades from the seventh and eighth open leaves was associated with the onset of symptoms, but again growth reduction was not observed.

As Mo is required for the metabolism of nitrate, Mo-deficient plants accumulate nitrate in the plant tissues. Measurements of sap nitrate concentration have been used to distinguish Mo deficiency from N deficiency in a number of crops, including sunflower (McDonald 1978), potato (Ulrich 1993) and

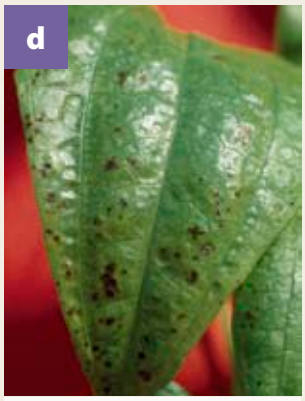


D. alata: finely divided interveinal chlorosis on a mature leaf in the lower part of the vine.

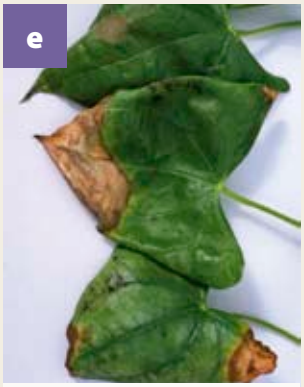
D. esculenta: finely divided interveinal chlorosis on a mature leaf.



D. esculenta: small pale lesions in interveinal tissue on a chlorotic leaf in the lower to mid section of the vine.



D. alata: small dark spots, many of which have become sunken lesions, on an older leaf.



D. alata: dark greyish-brown lesions spreading on marginal or interveinal tissue of oldest leaves.

D. alata: a narrow band of necrosis on the margins of older leaves.

D. rotundata: older leaves showing interveinal chlorosis and marginal necrosis.

D. esculenta: the response to leaf painting with sodium molybdate on one-half of a chlorotic leaf, seven days after painting. (Photo: James Ernest)

Figure 15. Symptoms of molybdenum deficiency in yam plants.

sweetpotato (O'Sullivan et al. 1997). The value of this approach is yet to be tested in yam.

Management

Molybdenum deficiency is relatively easily corrected, either by the application of small quantities of Mo to the soil or by raising the soil pH. Application of sodium molybdate or ammonium molybdate at doses of 0.2–0.3 kg Mo/ha should be sufficient to correct the disorder in most situations and may be effective for several years. Sodium molybdate may also be applied as a foliar spray. A solution of 50 g/100 L (sodium molybdate in water) has proven successful with other crops such as sunflower (Blamey et al. 1987). Some commercially available fertiliser mixtures also contain Mo.

Liming to raise the soil pH above 5.5 is usually effective in alleviating Mo deficiency. This may also improve conditions for crop growth in other ways, such as through better availability of P and alleviation of manganese or aluminium toxicity.

Mineral toxicities: salinity

Salinity

Occurrence

Salinity refers to the accumulation of soluble salts in the soil to the extent that the salt concentration in soil water is a problem for plants. Salts are minerals that, when dissolved, separate into positively charged and negatively charged chemical units (known as cations and anions, respectively). Salinity is measured by the electrical conductivity of the solution, which reflects the concentration of these electrically charged ions. However, it is not the electrical charge that affects plants, but the osmotic stress—salt attracts water from where it is less salty to where it is more salty. A salty root environment (more salt outside the roots than inside) makes it difficult for the plants to draw water out of the soil, so plants tend to wilt easily in warm, dry weather. Additionally, a high concentration of salt limits root growth, further exacerbating the difficulty that plants have in taking up sufficient water.

Almost invariably, the major cation associated with salinity is sodium (Na^+). Generally, the dominant anion is chloride (Cl^-), but sulfate, carbonate and bicarbonate will also be present in the solution. Saline soils are usually also alkaline (i.e. they have high pH), and the relative abundance of carbonate and bicarbonate determines how alkaline the soil is. The more alkaline it is, the more sodium dominates the soil solution. This is because carbonates of calcium (Ca) and magnesium (Mg) are much less soluble, and the solubility of potassium (K) is generally low due to other soil reactions.

The combination of Na^+ and Cl^- (sodium chloride) is referred to as 'common salt' and is the dominant salt in sea water. Sea water may indeed be the source of salinity, in coastal areas affected by seawater incursion or sea spray, but also in areas where buried sediments from past oceans underlie crop land, making the groundwater saline. Salts may accumulate in the surface soil when this groundwater is used for irrigation, or if excessive irrigation with fresh water causes the watertable to rise, bringing salts to the surface in low lying areas. Since irrigation water always contains some salt, salination of irrigated land is a risk wherever annual rainfall is insufficient to flush the salt away.

In addition to making the soil water salty, high sodium concentrations have detrimental effects on soil properties. The negatively charged surfaces of clay particles in the soil bind cations from the soil solution in a reversible way, and this is referred to as the cation-exchange capacity (CEC) of the soil. Most of the binding sites are usually occupied by Ca and Mg ions, and their strong electrical charge helps the particles stick together in clumps. This fine structure of clumps and channels is important for water drainage and air flow. Soils containing high levels of Na relative to Ca and Mg are termed 'sodic'. Sodium has a weaker charge than Ca and Mg, and the more Na that replaces Ca and Mg on the clay surfaces, the less they stick together. Sodic soils disburse when wet, becoming sticky and difficult to work. Unless they also have a low clay content, sodic soils suffer surface crusting, increased bulk density, poor aeration and waterlogging.

Sodicity and salinity are often closely related, but sodicity refers to the soil structural effects of sodium on the soil exchange sites, whereas salinity refers to the effects of high salt levels in the soil solution. Alkalinity is a third feature common to high-Na soils. Plants in saline soils may also be suffering effects of high soil pH, including low availability of the micronutrients iron (Fe), manganese (Mn), copper (Cu) and zinc (Zn).

Salinity impacts plants through the osmotic effect at the interface between the soil solution and the root, but also through toxic effects of excess Na or Cl taken into the plant. To a large extent, the toxicity of these elements is also due to osmotic effects inside the plant tissue.

When too much salt accumulates in the plant tissue, biochemical processes are disrupted and, when extreme, the tissue dies. This happens first at the edges and interveinal areas of older leaves—the areas at the end of the line for inflowing salt. Older leaves are also those that have been receiving high amounts of salt for the longest time. Different species and varieties of plants

have differing abilities to block the uptake of Na, and differing tolerance of salt concentrations in their tissues. A combination of these characteristics determines the salt tolerance of crop species and cultivars.

Yam is generally regarded as more sensitive to salinity than most other root crops.

Symptoms

Salt-affected yam plants tend to be pale, with a uniform light-green colour on young leaves becoming increasingly interveinal with leaf age (Figure 16a). Veins are typically not sharply defined—the green colour fades gradually with increasing distance from the main veins.

Leaves may hang more vertically on the vine or be curled down toward the tip, rather than angled up toward the light (Figure 16b).

The oldest leaves develop spreading necrotic lesions, starting from the tip, basal lobes or interveinal patches (Figure 16c). The necrosis quickly spreads across the entire leaf blade, so lower leaves may be entirely dead while those above are yet to show much necrosis (Figure 16d). Roots tend to be thin and finely branched, and may develop brown sections if salinity is severe.

Diagnostic tests

Electrical conductivity of the soil saturation extract (EC_e) is the most commonly quoted measure of soil salinity. Crop species vary widely in their salt tolerance, with an EC_e of 4 decisiemens (dS)/m corresponding to 50% yield reduction in sensitive crops, and over 10 dS/m for highly tolerant crops (Landon 1991). Yams are sensitive to salinity. In a solution culture experiment, *D. alata* suffered a 50% yield reduction at 4 dS/m, with significant growth decline at 1 dS/m. It is likely that yams in the field will respond to even lower conductivities, as the osmotic stress is greater in soil, with varying water content, than in solution culture.

Soil measurements of both exchangeable Na and exchangeable Na percentage (ESP) (ESP = 100 × exchangeable Na/CEC) are used to assess soil sodicity. Although a number of factors affect the amount of Na required to cause dispersion in a particular soil, as a rough guide soils, with exchangeable Na greater than 1 centimole of positive charge [cmol(+)]/kg soil or an ESP ≥ 15 may be regarded as potentially sodic (Landon 1991). In such soils, yam crops may suffer from both Na toxicity, and the deterioration of soil permeability and structure caused by high Na.

In leaf tissue, a critical concentration of around 400 mg/kg Na was determined for *D. alata* in blades of the fifth and sixth nodes. The relationship of dry-matter yield with Cl concentration was poorly defined. *Dioscorea alata* seems to show little exclusion of Na, accumulating levels over 10,000 mg/kg Na (1% of dry mass) under high-salt stress. This may contribute to its relatively low tolerance of salinity.

Management

Management depends on the source of salinity. Approaches include controlling groundwater rise by planting salt-tolerant trees and building up raised beds incorporating high organic-matter levels. Applying gypsum (calcium sulfate) to the soil can reduce the negative effects of Na on soil structure, and increase the amount of Na leached out of the soil by rainfall.

In areas where salinity is a widespread problem, yams are generally not grown. Other crops (i.e. sweetpotato), which have greater tolerance to salt, are available in these areas.

D. alata: interveinal chlorosis on mature leaves in the lower section of the vine.

D. alata: leaf presentation in a near-vertical position, with tips curled down.

D. alata: leaves near the base of the vine becoming necrotic, with lesions spreading from the tip into interveinal tissue.

D. alata: Leaves at the base of the vine are dead, but those above are only beginning to develop necrotic lesions.

Figure 16. Symptoms of salinity toxicity in yam plants.

Mineral toxicities: aluminium

Aluminium toxicity

Occurrence

Aluminium (Al) toxicity is the most common cause of growth reduction on strongly acidic soils. Aluminium is the most abundant metal in the earth's crust, but has very low solubility at neutral to alkaline pH. However, below a pH of approximately 5.3 (as measured in water), Al solubility increases and may reach toxic concentrations. In experimental conditions in the absence of Al, most plants will grow normally at pH values as low as 4.0. Therefore, in the field, crops probably encounter problems of Al toxicity before suffering any direct effects of low pH. Aluminium-sensitive species may suffer severe root growth reduction at concentrations of 10 micromolar (µM) Al or less, while more tolerant species may be unaffected up to concentrations of 25–40 µM (Blamey et al. 1987). Yam (*D. alata*) is very sensitive to soil acidity, in comparison with cassava, sweetpotato and taro, although some varieties are somewhat more tolerant than others (Abruna-Rodriguez et al. 1982).

Symptoms

The primary effect of Al is on the growth of root tips and root hairs. Roots appear short and thickened, with short laterals, and may be discoloured yellow to brown. Where the Al concentration increases with soil depth, the downward extension of the roots may be restricted, resulting in a very shallow root system.

The poor root system means that the plant cannot exploit the soil resources adequately. Plants grow poorly and appear stunted, with small leaves and weak tips. Any specific symptoms on the vine will depend on which soil-derived factor is most limiting for plant growth. Plants will suffer more readily from water stress. As Al in the soil solution inhibits the uptake of calcium (Ca) and magnesium (Mg) by roots, symptoms of Ca or Mg deficiency may develop. In addition, the solubility of phosphorus (P) is reduced in the presence of high concentrations of Al, so that P deficiency is often associated with Al toxicity. Symptoms of any of these disorders, together with general stunting, are indicative of Al toxicity.

Diagnostic tests

Aluminium toxicity is best diagnosed by testing the soil. Soils with a pH below 5.0 (as measured in a suspension of 1:5 soil and water) are at risk of Al toxicity. In soils below pH 4.5 (other than organic soils), Al is likely to severely reduce yam production. Tests for exchangeable Al and Al saturation may be useful. Abruna-Rodriguez et al. (1982) found that *D. alata* yields were significantly depressed when Al saturation was only 10% of the effective cation-exchange capacity (CEC) of the soil (at a pH of 5.1) and only 15–30% of maximum yield when Al saturation was 40% (at pH 4.8). In contrast, cassava did not show consistent yield reduction until Al saturation exceeded 70% (at pH 4.1–4.2). They recommended liming to pH 5.5 for yam production.

Little Al is taken up by plants into the foliage, so leaf analyses are not a useful test for Al toxicity. As even slight soil-dust contamination of the leaf samples can considerably elevate their apparent Al concentration, it is difficult to interpret leaf Al analyses with confidence.

Management

The soil pH can be increased by incorporating lime or dolomite into the soil. In addition, maintenance of high soil organic-matter levels through the return of crop residues, cover cropping or mulching will help as components in the organic matter are capable of binding free Al into nontoxic complexes. Organic matter also helps to slow the rate of acidification of the soil, which may result from sequential cropping. Choosing nitrate fertilisers instead of urea or ammonium fertilisers may also reduce acidification.

Phosphate forms insoluble complexes with Al. Some of the beneficial effect of adding P fertilisers to acidic volcanic ash soils appears to result from decreasing solution Al concentrations. However, this is not a recommended use for P fertilisers, as lime is much cheaper and P fertilisers will be more effective at correcting P deficiency after the soil pH is raised.

Mineral toxicities: boron

Boron toxicity

Occurrence

Boron (B) toxicity is most likely to arise on saline and alkaline soils, or following overfertilisation with B fertiliser, or following the application of irrigation water high in B.

The sensitivity of yam to salinity and sodicity makes it less likely that yams will be grown in areas where B toxicity occurs naturally. However, a temporary B toxicity may be encountered if B is oversupplied in response to a deficiency.

Yams were found to be fairly tolerant of B toxicity. However, this assessment was made on the basis of symptom development on young plants. The impact on tuber yield is not yet known.

Symptoms

Boron toxicity is one disorder where symptoms develop clearly before plant growth is appreciably reduced. In *D. alata*, a mottled interveinal chlorosis on mid to older leaves usually develops first (Figure 17a), with pale patches of tissue appearing in interveinal zones furthest from veins. In *D. rotundata*, the chlorosis may be more uniform or diffusely interveinal. Typically, small necrotic spots develop in interveinal zones (Figure 17b). In *D. alata*, these tend to be numerous and regularly distributed in the interveinal strips. They may be circular or angular in shape. A spreading necrosis usually follows, starting from the leaf tip and spreading across the entire blade (Figure 17c). The spots are usually still visible after they have been overtaken by general necrosis. In *D. rotundata*, spots are more scattered, and frequently have a pale centre and a yellow halo (Figure 17d). General necrosis may spread from the margins to engulf the spots (Figure 17e). In some instances, spots may be uncommon before oldest leaves become necrotic (Figure 17f). However, spots may subsequently appear on younger leaves, especially those from axillary branches from the lower nodes (Figure 17g).

Diagnostic tests

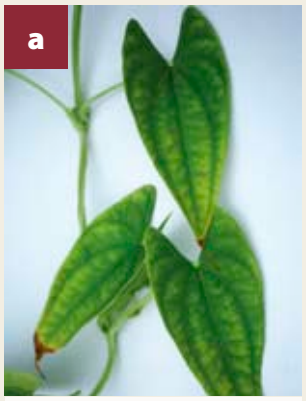
The critical concentration for B toxicity was determined to be in the range of 220–300 mg/kg, in leaf blades from the fifth and sixth nodes, in both *D. alata* and *D. rotundata*. *Dioscorea esculenta* has not been tested. Similar leaves from healthy plants generally had B concentrations between 20 and 150 mg/kg.

Hot water extraction is most frequently used to estimate the concentration of plant-available B in soil. The threshold for B toxicity in yam has not been determined. For sweetpotato, which has a greater sensitivity than yam to high B in solution culture experiments (O'Sullivan et al. 1997), the threshold is in the order of 4 mg/kg hot water-extractable B or approximately 0.15 mg/kg B in the soil saturation extract (Landon 1991). However, cultivars may vary considerably in their tolerance of excess B.

Management

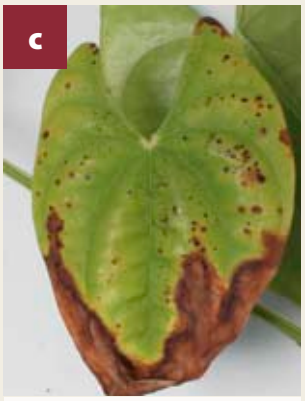
Should B toxicity be encountered in the field, liberal application of N fertiliser, especially calcium nitrate, may alleviate the problem (Bradford 1966). Additions of lime and organic matter were also reported to be effective (Olsen 1972).

Genotypic variation in tolerance of B toxicity is common in other crops, and it is likely that some varieties of yam may be selected that perform better than others on high B soils.



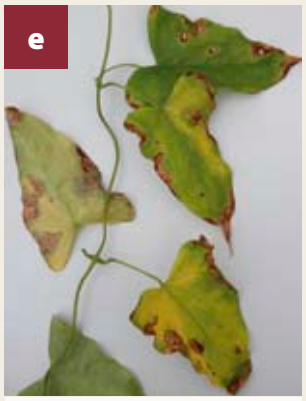
D. alata: mottled interveinal chlorosis on older leaves due to B toxicity.

D. alata: interveinal necrotic spots that are more angular and irregular in shape.

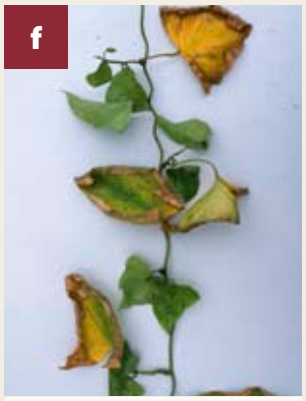


D. alata: necrotic spots in interveinal regions of an older leaf and general necrosis spreading from the tip.

D. rotundata: scattered necrotic spots on older leaves, typically having a dark edge and paler centre, and a halo of yellow tissue around them.



D. rotundata: spreading necrosis engulfs the spots—often preceded by uneven yellowing of the leaf.



D. rotundata: older leaves may senesce, with necrosis spreading from the margins, without developing necrotic spots.

D. rotundata: axillary branches growing from the lower nodes of the vine, showing necrotic spots.

B = boron

Figure 17. Symptoms of boron toxicity in yam plants.

Mineral toxicities: manganese

Manganese toxicity

Occurrence

Manganese (Mn) is often abundant in soils, but its low solubility at neutral and alkaline pH prevents excessive uptake by plants. Therefore, Mn toxicity is usually associated with acidic soils. Soils with low organic-matter content are most vulnerable, as humus binds Mn and reduces its availability.

Waterlogging may also induce or exacerbate Mn toxicity. When water excludes air from the soil, the shortage of oxygen (anaerobic condition) causes higher oxides of Mn to be reduced to plant-available Mn^{2+}. Therefore, in some instances, Mn toxicity may appear during wetter periods, with plants recovering as the soil dries out.

Manganese toxicity in plants appears to be affected by temperature—the disorder becomes more apparent in cold weather. Manganese is a component of some fungicides and may accumulate through repeated use of these fungicides, especially to crops grown on sandy soils.

Symptoms

The first and most conspicuous symptom of Mn toxicity is usually a distinct interveinal chlorosis, caused by induced iron (Fe) deficiency (Figure 18a–b). High levels of Mn reduce the plant's ability to take up sufficient Fe, both by damaging the roots and by binding with Fe in the soil, making it unavailable to plants. As for Fe deficiency, the chlorosis may progress to complete bleaching and necrotic lesions (Figure 18c). If the Mn toxicity is acute, the youngest leaves die before expanding and the shoot tip may die (Figure 18d).

Manganese accumulation in the oldest leaves causes them to senesce. This may occur when only mild symptoms of interveinal chlorosis are present. On *D. alata*, a dark stain develops, particularly on the lower leaf surface, and may be speckled or in larger patches (Figure 18e–f). The stain is lighter or absent on *D. rotundata* (Figure 18g). Sections of the main veins on the lower leaf surface may also become blackened (Figure 18f–g). This is a feature of Mn toxicity in many plant species. Usually, the blackened section is some distance away from the petiole, unlike the vein blackening seen with deficiencies of calcium (Ca) or sulfur (S). Yellowing and necrosis then spreads from the tip or interveinal zones (Figure 18h). Leaves are shed progressively from the base of the vine.

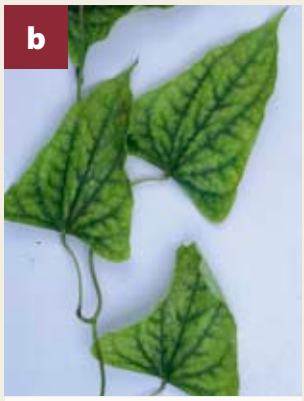
Diagnostic tests

The critical concentration for Mn toxicity in *D. alata* was determined to be in the range 5,000–7,000 mg/kg in leaf blades from the fifth and sixth nodes. Concentrations up to 40,000 mg/kg (4% of plant dry weight) were recorded in severely affected plants. *Dioscorea rotundata* had a similar critical range, but accumulated less Mn than *D. alata* at the same external Mn concentrations, possibly due to its lower transpiration rate.

Rufty et al. (1979) found that tolerance of tobacco to Mn toxicity increased with increasing temperature, despite greatly increased concentrations of Mn in the leaves of plants grown at the higher temperature. The combined effect of these two factors meant that the critical tissue concentration associated with the appearance of symptoms increased sevenfold, from 700 to 5,000 mg Mn/kg, with an increase in the day/night temperature regime from 22/18 °C to 30/26 °C. Sweetpotato crops appear to experience a similar interaction between Mn toxicity and temperature. Crops have been observed to recover from Mn toxicity as the season becomes warmer. This obviously makes interpretation of tissue Mn concentrations difficult.

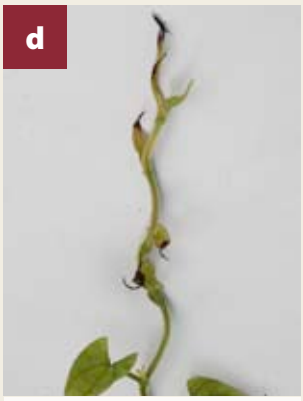
In soils, levels of total Mn (extractable by perchloric acid) of more than 2,000 mg/kg are regarded as high (Landon 1991). Measurement of 'easily extractable' Mn is more common, using chelating agents such as diethylenetriaminepentaacetic acid (DTPA) as

D. alata: interveinal chlorosis on mature leaves, caused by Fe deficiency induced by Mn toxicity.

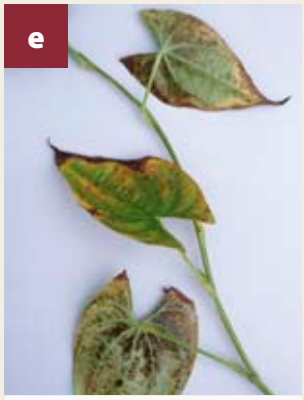


D. rotundata: interveinal chlorosis, caused by Fe deficiency induced by Mn toxicity.

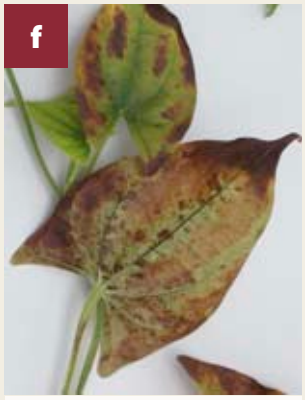
D. alata: young leaves showing bleaching of interveinal zones due to Fe deficiency.



D. alata: necrosis of a shoot tip and youngest leaves.



D. alata: dark staining, particularly on the lower surface of older leaves, preceding yellowing and necrosis.



D. alata: staining and blackening of the veins on the lower leaf surface.

D. rotundata: blackening of veins under the leaf may be accompanied by lightly stained areas on either the upper or lower surface.

D. rotundata: older leaves senescing, with general yellowing preceding necrosis.

Fe = iron; Mn = manganese

Figure 18. Symptoms of manganese toxicity in yam plants.

an extractant (Rayment and Higginson 1992). Concentrations of DTPA-extractable Mn above 45 mg/kg are considered potentially harmful to root crops such as potato and carrot (CFL 1983). In conjunction with low pH (< 5.3 as measured in water) or waterlogging, such concentrations may indicate a risk of Mn toxicity.

Management

As Mn toxicity often results from low soil pH, it can often be corrected by application of lime or dolomite to raise the pH above about 5.3 (as measured in a 1:5 solution of soil:water). If the problem is associated with waterlogging, improved drainage may be effective. Raising the height of mounds or ridges may be enough to avoid the problem. Applying mulches to increase-organic matter content is also beneficial over the longer term, as soil humus binds free Mn ions, improves drainage and reduces acidification.

Mineral toxicities: zinc

Zinc toxicity

Occurrence

Incidence of zinc (Zn) toxicity is rare and has not been reported in yam crops. Cases in other crops have been reported on acidic soils high in Zn or on soils overfertilised with Zn fertiliser. Zinc is also a component of some fungicides and may accumulate following their persistent use.

Symptoms

Two distinctive symptoms were observed on yams exposed to toxic levels of Zn. The older leaves developed silvery interveinal patches on the upper leaf surface, where the epidermis appeared to have separated from the underlying tissue (Figure 19a–c). This was most developed in *D. alata*, but also observed occasionally in *D. rotundata*. In a different variety of *D. alata*, the interveinal patches appeared as rough-textured zones with irregular light-brown markings (Figure 19d).

On young mature leaves, marginal necrosis developed—often starting at the basal lobes and spreading around the leaf margin (Figure 19e–f). Usually, it was confined to a narrow marginal band, but could extend into interveinal sectors. At higher Zn concentrations, some young leaves developed deformities, with rough, poorly expanded tissue in interveinal sectors of the leaf (Figure 19g).

Diagnostic tests

Leaf Zn concentrations up to 300 mg/kg Zn in the leaf blades of the fifth and sixth nodes were tolerated with little growth suppression. Between 300 and 500 mg/kg Zn, growth declined rapidly. However, concentrations in older leaves were much higher than those in the index leaves, with concentrations up to 1,100 mg/kg Zn in older leaves associated with leaf symptoms, but little growth suppression. Allowing for environmental influences on the age and Zn accumulation rate of leaves at the fifth and sixth node, a critical range of 280–400 mg/kg is suggested. Similar concentrations applied to both *D. alata* and *D. rotundata*. *Dioscorea esculenta* was not tested.

In soil, a diethylenetriaminepentaacetic acid (DTPA)-extractable Zn concentration above 10 mg/kg is considered potentially harmful in acid soils. 'Total Zn' concentrations in soil (perchloric acid-extractable Zn) usually fall in the range 10–300 mg/kg, with concentrations above 150 mg/kg regarded as high (Landon 1991), and likely to result in reduced plant growth.

Management

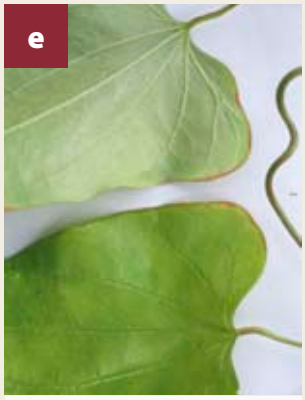
Should Zn toxicity be found to occur in field-grown yams, liming to raise the pH of the soil may alleviate the problem by reducing the concentration of plant-available Zn. Large applications of phosphorus (P) fertilisers may also have a beneficial effect.

D. alata: older leaves displaying silvery interveinal patches in response to mild Zn toxicity.

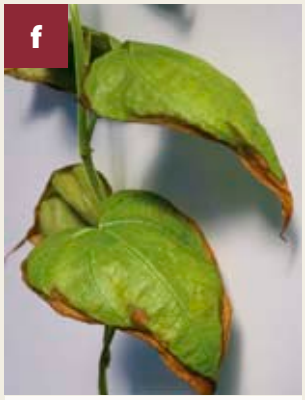
D. alata: detail of silvery patches on the upper surface of an older leaf.

D. rotundata: small silvery patches on interveinal tissue of older leaves in response to Zn toxicity.

D. alata: an older leaf showing irregular brown markings on the upper surface.



D. rotundata: tan-coloured necrosis on the margins of young mature leaves.



D. alata: young mature leaves with well-developed marginal necrosis.

D. alata: deformity of a young mature leaf, with rough textured, poorly expanded tissue in interveinal zones.

Zn = zinc

Figure 19. Symptoms of zinc toxicity in yam plants.

Mineral toxicities: copper

Copper toxicity

Occurrence

Toxic levels of copper (Cu) rarely occur naturally in soils. However, Cu may accumulate due to application of sewage sludge, pig slurries or mine slag, or more commonly through persistent use of Cu-containing fungicides or fertilisers (Tiller and Merry 1981). In most situations where yams are grown, these circumstances are unlikely.

Symptoms

Yams appeared to be relatively tolerant of high concentrations of Cu, with only mild symptoms and growth depression at 4 micromolar (μM) Cu in the culture medium. At this concentration, some fine root branches became blackened and sections of root had brown banding (Figure 20a). Dark greyish-brown lesions formed on oldest leaves (Figure 20b), and on the lower surface of the leaf, the minor veins were blackened in the vicinity of these lesions (Figure 20c). Similar symptoms were seen on both *D. alata* and *D. rotundata* (Figure 20d). The oldest leaves then died, usually turning yellow before complete necrosis (Figure 20e–f). At higher concentrations of Cu, growth was reduced and interveinal chlorosis developed on young to mature leaves due to induced iron (Fe) deficiency (Figure 20g). At 10 μM Cu, symptoms of Fe deficiency were pronounced (Figure 20h).

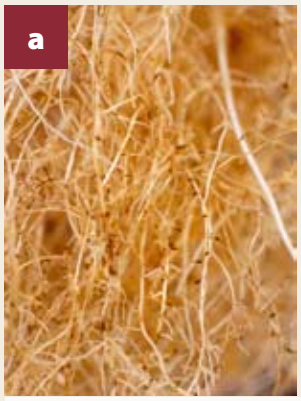
Diagnostic tests

No soil tests have been calibrated for Cu toxicity in yam. For many crops, 'total' soil Cu concentration (perchloric acid-extractable) above 100 mg/kg have been regarded as high (Landon 1991), while concentrations of diethylenetriaminepentaacetic acid (DTPA)-extractable Cu above 20 mg/kg are potentially toxic in acidic soils (CFL 1983). For citrus, using Spencer's test (Spencer 1954), soils containing more than 112 kg/ha total Cu in the top 15 cm of soil are considered at risk, particularly if the soil pH is below 6.5 (Koo et al. 1984).

Leaf analyses are generally not useful in diagnosing Cu toxicity. Copper toxicity affects primarily the plant roots; therefore, the concentration in the above-ground parts is a poor indicator of Cu toxicity stress. Alva et al. (1995) found no significant increase in foliar Cu concentrations in citrus trees as soil Cu was increased to levels that decreased growth. In yam, leaf concentrations associated with Cu toxicity in plants grown in solution culture (critical concentration 26 mg/kg) were often exceeded by concentrations in healthy field-grown plants. The same effect was observed in sweetpotato, and crops that had been sprayed with fungicide may have much higher foliar concentrations without any ill effect (O'Sullivan et al. 1997).

Management

As Cu toxicity usually results from excessive application of Cu, prevention rather than correction should be stressed. Heavy applications of P fertilisers may reduce the availability of excess Cu to the plants. Liming may be beneficial, as Cu becomes less available to plants at high pH. Maintaining the soil pH above 6.5 has been recommended for lowering Cu toxicity in citrus (Koo et al. 1984).

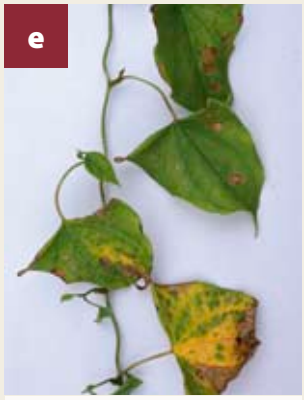


D. alata: roots showing short, blackened branches.

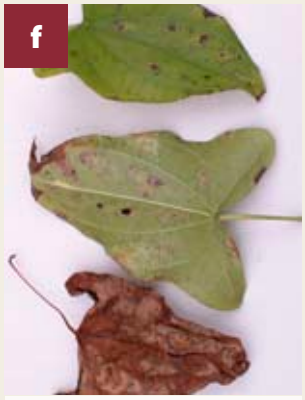
D. alata: dark-grey lesions on interveinal tissue of an older leaf.

D. alata: the lower surface of an older leaf, showing blackening of minor veins around lesions.

D. rotundata: irregular, dark-grey lesions spreading in interveinal tissue, with associated blackening of minor veins on the lower leaf surface.

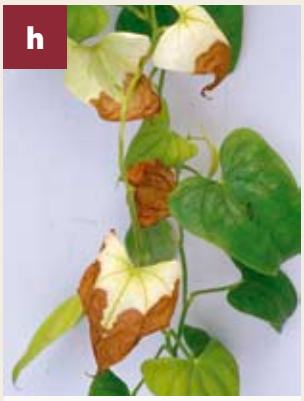


D. rotundata: oldest leaves with yellow chlorosis spreading, before the whole leaf dries up.



D. rotundata: oldest leaves showing a progression from necrotic spots to spreading necrosis and complete senescence.

D. alata: young mature leaves with mild interveinal chlorosis due to induced Fe deficiency.



D. alata: young mature leaves displaying severe symptoms of Fe deficiency, induced by root damage from Cu toxicity.

Cu = copper; Fe = iron

Figure 20. Symptoms of copper toxicity in yam plants.

Appendix
Experimental work relating yam nutritional status to tissue nutrient concentrations

The symptom descriptions and critical leaf nutrient concentrations presented in this book were mostly derived from a series of experiments conducted at the University of Queensland between 2000 and 2004. This work is summarised below, to provide technical information additional to that offered in the section on each disorder.

Methodology

Solution culture was the primary technique used to induce deficiencies and toxicities in yams. Yam germplasm was sourced locally (*Dioscorea alata* cultivars of Tongan origin sourced from the Brisbane Tongan community), and in tissue culture from the International Institute of Tropical Agriculture (IITA) in Nigeria. Six West African genotypes of *D. alata* and six genotypes of *D. rotundata* were received from IITA, and multiplied in tissue culture and the field.

Dioscorea alata was the main species studied. *Dioscorea rotundata* was included in some of the experiments, including a nutrient omission experiment comparing symptoms of deficiency for each nutrient in two *D. alata* and two *D. rotundata* genotypes. Due to the time required for multiplication of the imported germplasm, the West African genotypes were only available for experimental work from the third season. The *D. rotundata* material, despite virus-free certification, contained a number of viruses and grew poorly with a range of viral leaf symptoms, making it more difficult to obtain clear symptoms of nutritional disorders. Once the virus diagnosis was confirmed by the Natural Resources Institute in the United Kingdom, the material was destroyed for quarantine reasons. Consequently, the information on *D. rotundata* is more limited than on *Dioscorea alata*, but useful comparisons could be made from both solution culture and field plantings. *Dioscorea esculenta* was not available in Australia, nor could it be imported as neither tissue culturing nor virus indexing has been achieved for this species. To document symptoms and indicative leaf nutrient concentrations in this species, a sand-culture experiment was conducted in Papua New Guinea with the help of collaborators in the National Agricultural Research Institute. This study was published in O'Sullivan and Ernest (2007).

Preliminary work involved a nutrient omission experiment to document symptoms of a range of deficiencies and to establish nutrient profiles in leaves of varying position on the vine (O'Sullivan et al. 2001; O'Sullivan and Jenner 2006). Subsequently, separate experiments were conducted for each disorder, varying the supply of one nutrient to induce either deficiency or toxicity at a range of intensities, and establishing relationships between plant dry-matter yield and leaf nutrient concentrations for leaves sampled at varying positions on the vine. Over 5 years, 20 single nutrient-rate experiments and 2 nutrient omission experiments were conducted, involving over 1,000 plants.

Dioscorea esculenta growing in the nutrient omission sand-culture experiment at the Papua New Guinea National Agricultural Research Institute, Bubia, Papua New Guinea.

The solution culture technique was adapted from that reported in O'Sullivan and Jenner (2006). Minisetts sprouted under intermittent mist were transferred to full nutrient solution for an establishment period of 2–3 weeks, until vigorous shoot and root growth was established. The tuber piece was then removed before transferring plants into treatment solutions. Each plant was suspended over 20 L of aerated nutrient solution, using a plug of polyurethane foam to hold the base of the stem in a hole in the lid of the solution container. Solutions were prepared using high-purity deionised water and analytical reagent grade chemicals. In some instances, both water and chemicals were further purified before use. Initial solutions were formulated to provide concentrations of all nutrients in the range normally encountered in soil solution (much lower than commonly used in solution culture), but sufficient in quantity to sustain healthy growth equivalent to the addition of four mature leaves and their vine. Solutions were analysed weekly and nutrients were provided to replace those removed. When weekly growth approached the capacity of the nutrient supply, twice-weekly nutrient additions were made. Solution pH was maintained between pH 5.5 and 6.0 by weekly adjustments. From the third season, the zwitterionic buffer 4-morpholinoethanesulfonic acid (MES) was added to solutions at a concentration of 0.1 mM, to improve pH stability. Ion-exchange resins were used to generate buffered concentrations of copper and boron at very low concentrations, as well as to remove impurities from stock macronutrient salt solutions for all micronutrient work. Plants were harvested 7 weeks after applying treatments. A detailed photographic and written record was made of all symptoms during the experiment and at harvest. The leaf samples, vines, roots and tubers were dried and weighed, and leaves analysed using inductively coupled atomic emission spectrometry (ICP-AES) following acid digestion or by carbon–nitrogen–sulfur (CNS) combustion analysis for nitrogen (N) content (or both).

Sprouted minisetts of D. alata *ready for transfer to solution culture.*

Dioscorea alata *growing in the solution culture system at the University of Queensland.*

In addition to the solution culture studies, field plantings used for the maintenance and multiplication of germplasm were also sampled to compare leaf nutrient concentrations among genotypes, and at different times in the growing season. Symptom descriptions and leaf analyses from crops surveyed in four provinces of Papua New Guinea, and leaf analyses from the project's fertiliser trials in Vanuatu and Papua New Guinea, provided some verification of tissue concentrations associated with symptoms or responses to fertilisation.

In most of the charts presented, error bars show the standard deviation of individual measurements. The standard error for the estimation of the mean would be smaller by a factor of three to six, depending on the number of replicates in each case. Although depicting the standard error would imply much less uncertainty in the data, standard deviation is deliberately given, in order to record the variability that may be expected among individual samples.

Selection of index tissue for nutrient concentration analysis

Earlier reports on composition of yam leaves have varied in the time and method of sampling. Sobulo (1972b), Gaztambide and Cibes (1975), Irizarry and Rivera (1985) and Irizarry et al. (1995) analysed all leaf blades, while Sobulo (1972c), Obigbesan and Agboola (1978) and Vander Zaag et al. (1980) sampled young mature leaves. For the purpose of diagnostic sampling, obtaining a representative sample of all leaves on the plant is not practical. Leaf position is a source of considerable variability in leaf nutrient concentrations, and a well-defined index tissue is essential to make valid comparisons with reference critical concentrations.

Counting nodes from a shoot tip allows a highly reproducible sampling regime. However, yam leaves on

actively growing vines are not fully expanded for some distance from the tip, and the vine becomes difficult to trace due to entanglement.

In initial nutrient omission experiments for both *D. alata* and *D. esculenta*, leaf samples were taken from several positions on the vine, to study the variability in concentration of each nutrient with leaf position, and to provide a basis for selection of an index tissue. For *D. alata*, blades were taken from groups of four sequential nodes, from the first open leaves to the base of the vines. For *D. esculenta* (the sand-culture experiment conducted in Papua New Guinea in 2003), four samples were taken from each plant:

- the fifth and sixth node from youngest open leaf (immature leaves)
- the seventh and eighth node (young expanded leaves and the proposed index tissue)
- the middle two nodes
- fifth and sixth from the base of the vine (old leaves).

For each element, the concentration profile (leaf concentration versus the position on the vine) was compared for well-nourished plants and deficient plants. The profiles obtained are illustrated in Figure A-1 (*D. alata*) and Figure A-2 (*D. esculenta*).

In general, the mobile macronutrients (N, phosphorus [P], potassium [K], magnesium [Mg] and to a lesser extent S) showed a steep decline in concentration from the youngest to the oldest leaves, in well-nourished plants. In deficient plants, the concentration profile was usually flatter (with the exception of Mg deficiency), such that the greatest difference between control and deficient plants was found in the youngest leaves. The oldest leaves had concentrations similar to those in the well-nourished plants. This is in marked contrast to the pattern observed in most species, for example sweetpotato (O'Sullivan et al. 1996), in which mobile nutrients tended to have a relatively uniform concentration across all leaf ages in healthy plants, but to decline markedly from youngest to mature leaves in deficient plants. Low concentrations in the older leaves are indicative of the remobilisation of these nutrients to preferentially nourish the young leaves.

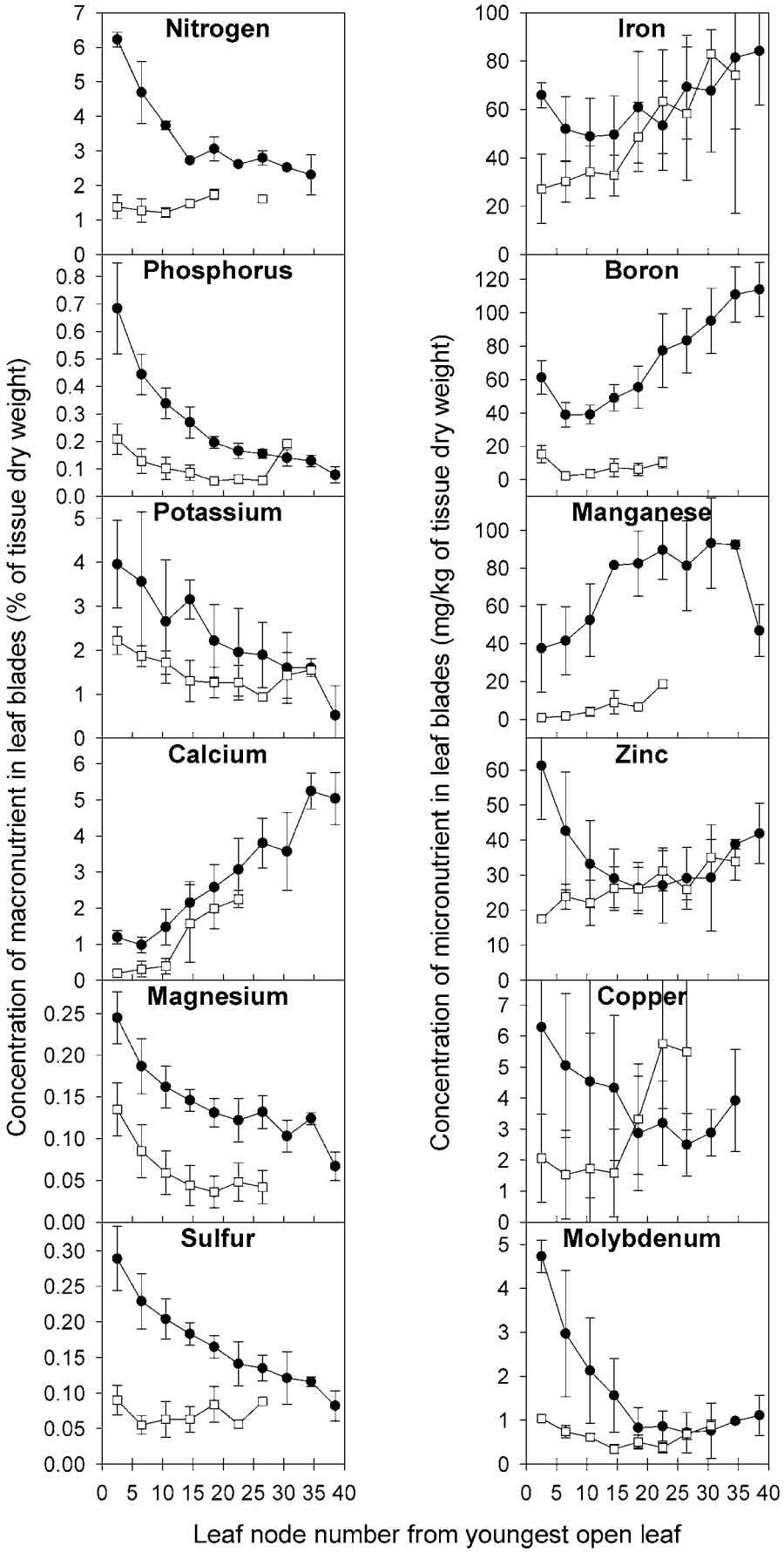
The relatively flat age profile of these nutrients in deficient yam plants supports the idea that remobilisation of nutrients is inefficient in these species. This is consistent with the observed lack of older leaf symptoms in plants deficient in these nutrients.

Concentrations of calcium (Ca), iron (Fe), boron (B) and manganese (Mn) all tended to increase with leaf age in control plants, although they may be slightly elevated in the youngest leaf sample, where incompletely expanded blades may have a concentrating effect. In contrast, concentrations of zinc (Zn), copper (Cu) and molybdenum (Mo) tended to decline with leaf age, but show some accumulation in oldest leaves. The shape of the profile in deficient plants may reflect the development of deficiency in that treatment. Zinc and Fe diverge from the healthy curve only in young leaves, corresponding to the relatively late and mild development of deficiency for these nutrients. The B concentrations were consistently low, despite the variability in producing acute B-deficiency symptoms in *D. alata*. This might suggest relative mobility of B in this species.

The high variability in Cu data prevents a confident separation of healthy and deficient concentrations. Only a small proportion of this variation can be attributed to measurement error, as standard leaf material, digested with each batch of leaf samples, consistently tested close to certified Cu concentrations. Thus, both healthy and deficient plants appeared to be highly variable in Cu concentration, which was somewhat surprising given the consistently severe development of Cu-deficiency symptoms in the *D. alata* experiment.

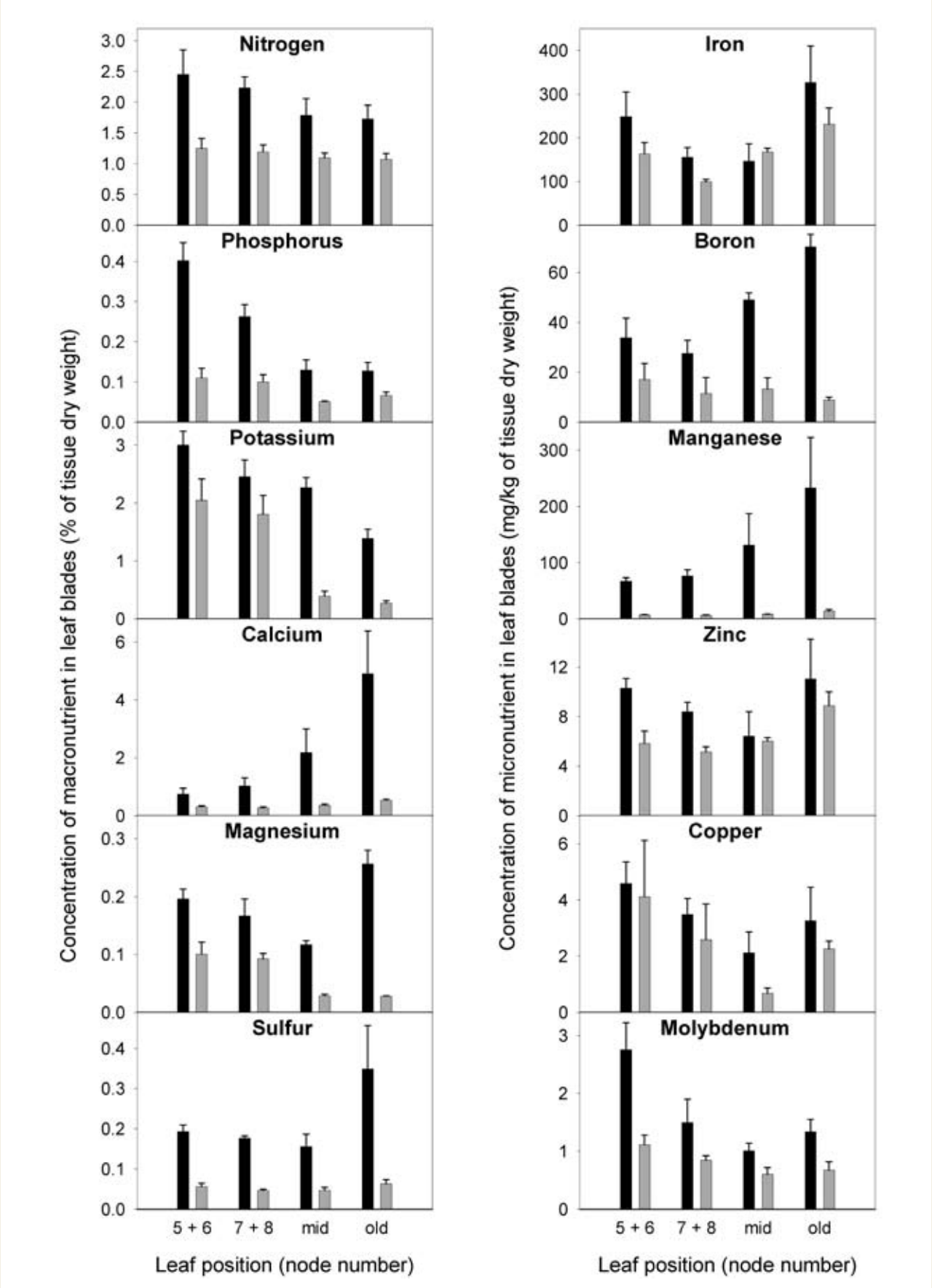
Overall, young leaves gave the best separation between healthy and deficient plants. However, the very youngest sample, containing rapidly expanding leaves, is undesirable due to rapidly changing nutrient concentrations. No leaf position offered stability in nutrient concentrations, as concentrations continued to vary with leaf position even for fully expanded leaves. From our observations of *D. alata*, leaf expansion may continue until between the sixth and tenth nodes. However, sampling from the tenth node in the field can be quite difficult, as it is generally over a metre from the vine tip and well entangled in the mass of vines typical of field-grown yams. As a compromise between maturity and accessibility, leaves of mature habit, but not fully expanded, were selected. Nutrient profiles showed that the selected leaves avoided the high variability of younger leaves.

For *D. alata* and *D. rotundata*, leaf blades at the fifth and sixth nodes were selected as an index sample, but on *D. esculenta*, which bears only one leaf at each node, leaves at this position were generally expanding rapidly and in transition to mature form. The seventh and eighth nodes provide leaves of mature habit if not full expansion, while older nodes become difficult to sample in the field due to entanglement of the vines. The immature leaves of *D. esculenta* are also densely hairy, which can hinder representative sampling of the dried tissue for analysis. We recommend the dry leaves are crushed rather than ground before analysis, as grinding allows the hairs to separate and clump.



kg = kilogram; mg = milligram

Figure A-1. Concentrations of nutrient elements in D. alata *leaf blades from youngest to oldest nodes, in plants adequately supplied with all nutrients (●) and in plants deficient in the specified nutrient (□). Error bars indicate the standard deviation of replicates.*



kg = kilogram; mg = milligram

Figure A-2. Concentration of nutrient elements in leaf blades of D. esculenta *from plants supplied with all nutrients (black) and plants deprived of the reported element (grey). Macronutrient-deficient treatments received one-tenth of the normal supply level, while micronutrients were omitted from their deficient treatment. Error bars indicate the standard error of the mean of three replicates.*

Even using a precisely defined sampling regime, the absolute age and physiological maturity of leaves at the specified position may be altered by other factors that can influence growth rate, such as temperature, light and water availability, and the position of the leaves on the canopy. The robustness of the information provided on adequate and deficient nutrient concentrations should be verified through comparison with field data from a range of production environments.

In the subsequent single-nutrient rate experiments, we continued to sample multiple leaf positions per plant, to provide further information on nutrient profiles under varying levels of nutrient stress. Results of these analyses are included in the following section.

Critical nutrient concentrations

The majority of solution-culture experiments comprised individual nutrient rate trials, in which final dry-matter yields were compared with the tissue concentrations of the test element in specified leaves. Ideally, a critical concentration for deficiency or toxicity of a nutrient is determined from the relationship between plant yield or growth and the concentration in the defined index tissue, and is designated as the concentration corresponding to 90% of maximum growth. In practice, with a limited number of plants in each experiment and high variability among plants, there is uncertainty in the fitting of the curve and in its applicability in varying growth conditions. A critical issue in determining these relationships is the definition of 100% growth. The practice used has been to take the mean of all plants in treatments that did not yield significantly less than the highest treatment mean, after removing outliers whose low growth is corroborated by a report of illness or damage, as indicated in the experiment notes. Note that, in all the following charts, error bars represent the standard deviation of the primary data, not the standard error of the mean, as it is important to acknowledge the variability in the data irrespective of sample size. Standard errors are smaller by a factor of 1.7 to 2.4, depending on the number of replicates averaged (between 3 and 6 replicates).

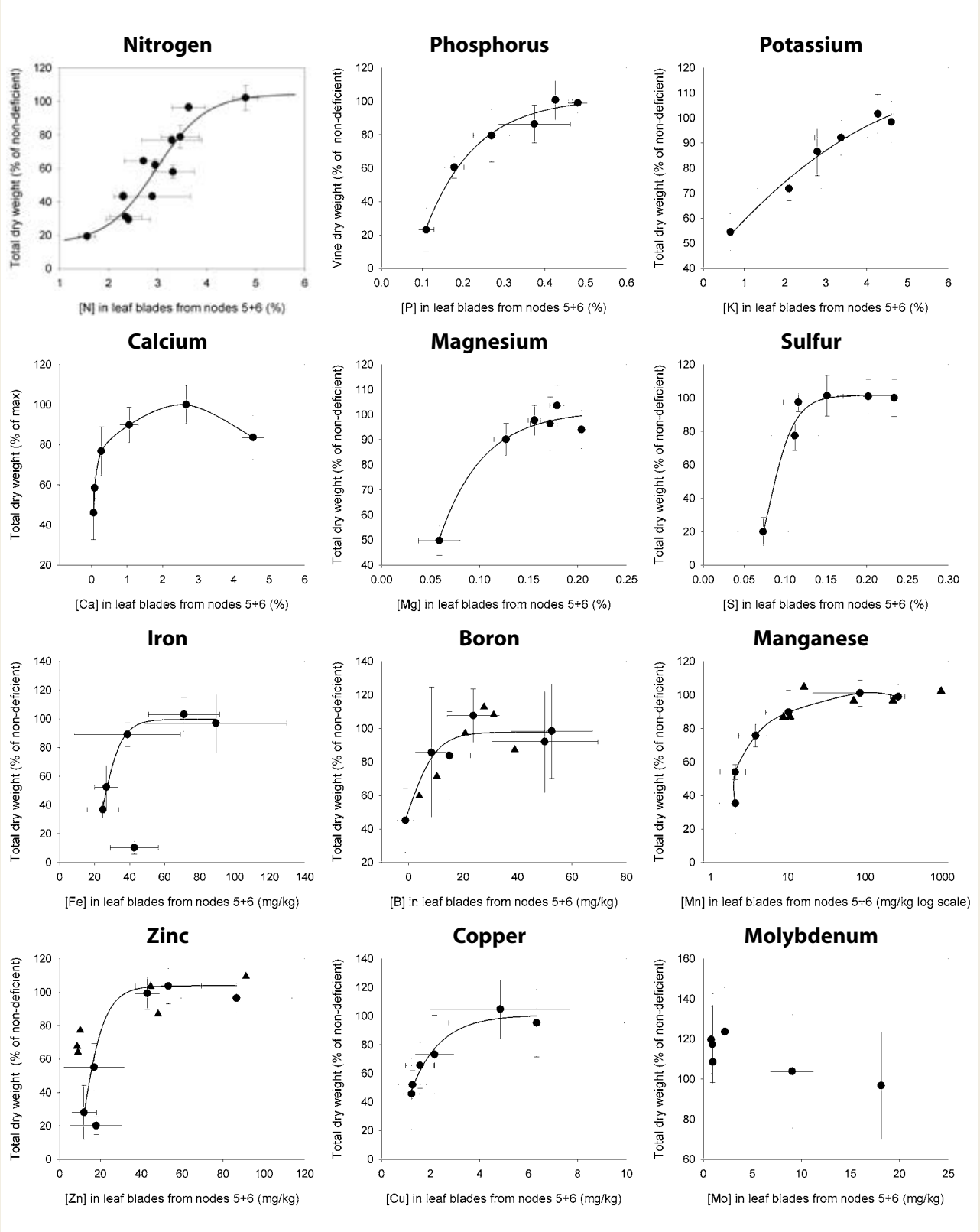
Figure A-3 summarises the *D. alata* leaf concentration and dry-matter production relationships derived for deficiency of each element, for leaf blades from the fifth and sixth nodes from the tip. Similar relationships were derived for each of the leaf samples analysed. Vine weight is used where variability in tuber development made total weight less sensitive.

In the Fe experiment, the higher Fe concentration in the lowest treatment, compared with other deficient treatments, was associated with leaf blades that were entirely dead before harvest. A curve is not fitted to the Mo data, as no growth response was obtained, despite concentrations under 0.5 mg/kg being achieved in leaves. The lowest three treatments did not differ in leaf Mo concentrations, suggesting that contamination levels were higher than dose levels for these treatments. In the B, Mn and Zn plots, treatment means for *D. rotundata* are included for comparison.

Responses to salinity and to excessive levels of B, Mn, Zn and Cu are shown in Figure A-4. It should be noted that Cu exerts its toxic effect at the root surface, and its toxicity is not accurately predicted by its concentration in leaf tissue. Higher concentrations may be recorded in field-grown plants without being indicative of toxicity. Some of the leaves from the highest Cu treatment had anomalously low Cu concentrations. These measurements were from leaves that were dead some time before the harvest date. For salinity, both sodium (Na) and chlorine (Cl) concentrations were analysed, but the relationship of dry-matter yield against Cl concentration was poorly defined. *Dioscorea alata* seems to show little exclusion of Na and this may contribute to its relatively low tolerance of salinity. In the experiments in which *D. rotundata* was included, its treatment means are also plotted. These show that *D. alata* and *D. rotundata* followed similar response curves for toxicities of B, Zn and Cu, but that the *D. rotundata* genotype used showed greater sensitivity to Mn toxicity than *D. alata*.

Similar relationships were established for each of the five leaf positions sampled (data not presented). Table A-1 gives the critical concentrations determined from these plots, and shows how sensitive the concentration may be to leaf position for a number of elements. A critical range has been suggested, which takes into consideration the steepness and variability in the relationships between the index leaf nutrient concentrations and growth (i.e. those in Figures A-3 and A-4), as well as the potential effect of variable actual leaf age, depending on growth rate in the field environment, based on the range of concentrations in the younger and older leaf samples.

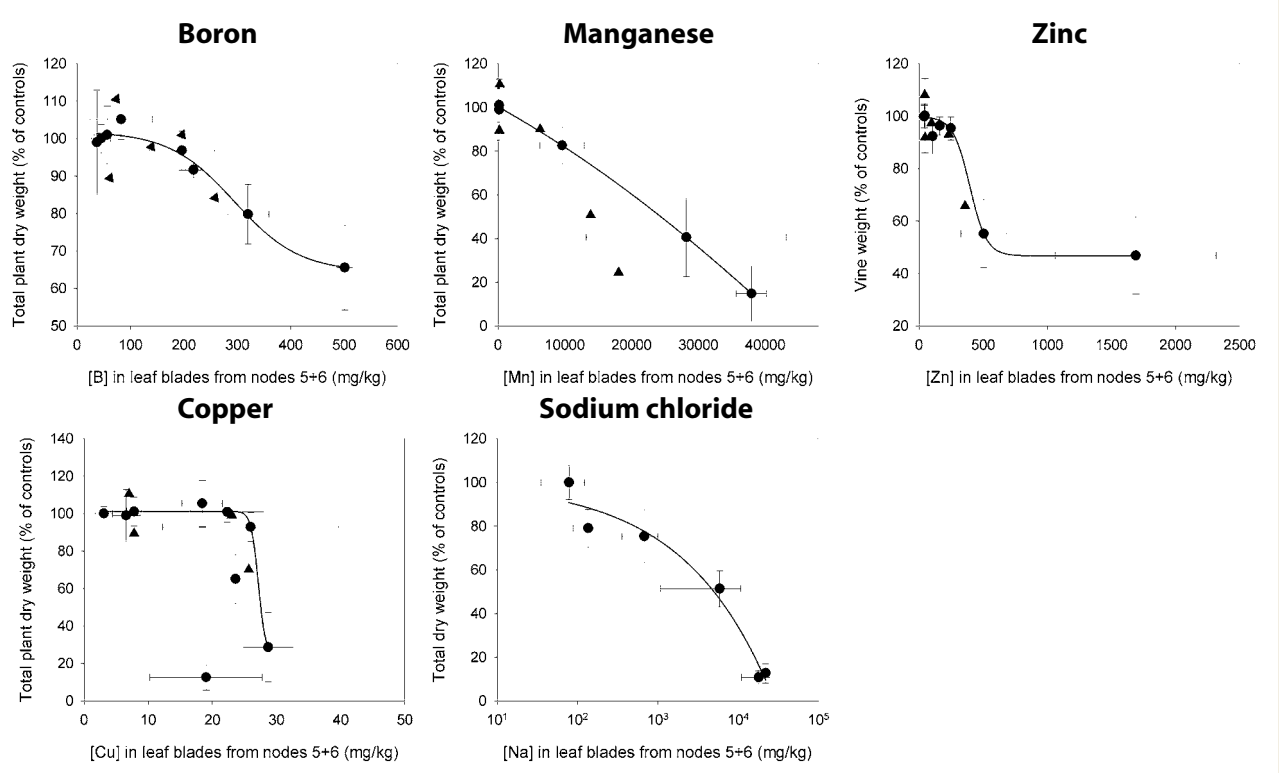
The change in leaf nutrient concentration with leaf position is shown in Figure A-5. These plots illustrate the importance of tissue selection for standardising analyses of crop nutrient status. For example, a horizontal line at the critical concentration for N cuts across all profiles from severely deficient to nonlimited. For N in particular, plants seem to respond to reduced supply by reducing growth proportionally, and maintain tissue concentrations close to the critical level. Only the highest supply level, representing luxury consumption, is clearly separated from the others.



kg = kilogram; mg = milligram

Notes: The Mn concentration is given in log scale. The data are mean and standard deviation of 4–6 replicates. For B, Mn and Zn plots, *D. rotundata* treatment means are shown (▲), suggesting both species follow a similar response.

Figure A-3. Determination of critical concentrations for deficiencies. Relationships between dry-matter production and concentration of the test element in leaf blades from the fifth and sixth youngest nodes are shown for D. alata *grown in solution culture at six supply levels of each test element.*



kg = kilogram; mg = milligram

Figure A-4. Determination of critical concentrations for toxicities. Relationships between dry-matter production and concentration of the test element in leaf blades from the fifth and sixth youngest nodes are shown for D. alata *grown in solution culture at normal and 3–5 excessive levels of each test element. The data are mean and standard deviation of 3–6 replicates. Except in the sodium chloride plot,* D. rotundata *treatment means are shown (▲), indicating that a similar critical concentration range applies to both species, although* D. rotundata *showed a steeper decline in response to excessive Mn concentrations.*

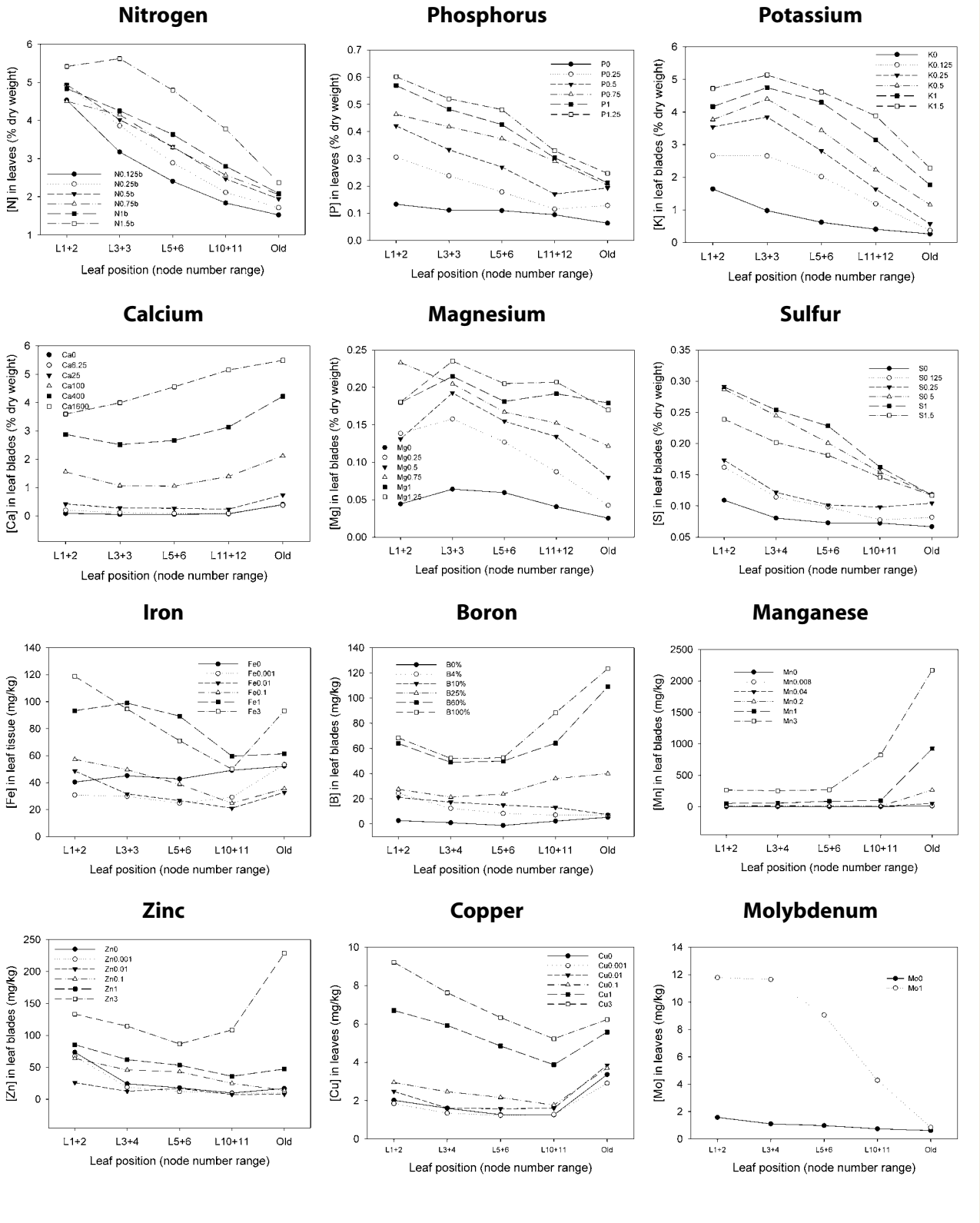
Table A-1. Critical concentration for deficiency or toxicity of each element tested in *D. alata*, estimated for each leaf sample tested

	Nodes 1+2 (youngest)	Nodes 3+4 (expanding)	Nodes 5+6 (index tissue)	Nodes 10+11 (young mature)	Nodes –10,–11 (old leaves)	Suggested critical range
Deficiencies						
Nitrogen (%)	No trend	5.0[a]	3.8	2.9	2.2	2.9–4.0
Phosphorus (%)	0.49	0.42	0.34	0.21	0.23	0.21–0.37
Potassium (%)	3.8	4.1	3.3	2.1	0.66	2.1–3.9
Calcium (%)	1.5	1.1	1.1	1.4	2.1	1.0–1.5
Magnesium (%)	0.101	0.143	0.125	0.101	0.063	0.10–0.14
Sulfur (%)	0.189	0.141	0.118	0.095	0.089	0.10–0.14
Iron (mg/kg)	74	49	38	25	36	25–45
Boron (mg/kg)	23	15	13	9.4	7.7	9–20
Manganese (mg/kg)	11	13	10	9.7	265	10–15
Zinc (mg/kg)	60[a]	35	20	18	11	15–35
Copper (mg/kg)	4.2	3.6	3.1	2.5	4.9	2.0–3.6
Molybdenum (mg/kg)	<1.0	<0.9	<0.8	<0.5	<0.4	<0.8
Toxicities						
Boron (mg/kg)	220	220	250	380	940	220–300
Manganese (mg/kg)	5,600	5,600	5,800	7,500	22,000	5,000–7,000
Zinc (mg/kg)	260	280	300	410	1,400	280–400
Copper (mg/kg)	29[a]	27[a]	26	16	10	20–30
Salt (Na conc.) (mg/kg)	270[a]	290[a]	410	390	1,020	120–450

kg= kilogram; mg = milligram; Na = sodium

[a] These values were poorly separated from the range of concentrations found in plants not showing growth reduction.

Note: Samples consisted of leaf blades, from the specified node numbers counting from the first open leaf; nodes '-10,-11' are counted from the base of the plant and represent old leaves. The sensitivity of tissue selection is indicated by the range for each element. Suggested critical ranges are for the proposed index leaves at nodes 5 and 6 but take into account the potential variation from growth-rate effects on actual leaf age, as well as variability among plants within the experiment. For deficiencies, test values above the range indicate a low probability of growth limitation, and those below the range indicate a very high probability. For toxicities, the reverse applies.



kg = kilogram; mg = milligram

[a] For Mo, only the control and 'none added' treatments were analysed across all leaf samples, due to lack of growth response.

Figure A-5. Dioscorea alata *profiles of leaf nutrient concentration changes with leaf position for each element at each supply level tested, in deficiency experiments. Data are the mean of 4–6 replicates. Legends give treatment titles indicating the multiple of 'adequate' supply delivered in each treatment, with the exception of Ca where the treatment titles refer to the external concentration in µM, and B where treatment titles are the percentage loading of B-specific resin used to generate buffered B concentrations.*

These plots also confirm the observations made from the first season's experiment (see Figure A-1), that concentrations of the mobile nutrients (N, P, K, S, and to an extent, Cu and Mo) tend to decline with leaf age in well-nourished plants, and less so in deficient plants. The reverse pattern is seen in most species, with the declining concentration in deficient plants due to remobilisation from older leaves to younger. Yams do not seem to remobilise nutrients appreciably for nourishment of the vine tip, although remobilisation into the tubers appears to be an active part of vine senescence. The reason for the steep decline with leaf position in well-nourished plants has not been determined. Measurements of lignin and polyphenols were made on leaf samples from tip to base of field-grown vines, but did not reveal an accumulation that could account for nutrient dilution. Nevertheless, the pattern is consistent in *D. alata* and *D. esculenta* (as shown in Figures A-1 and A-2).

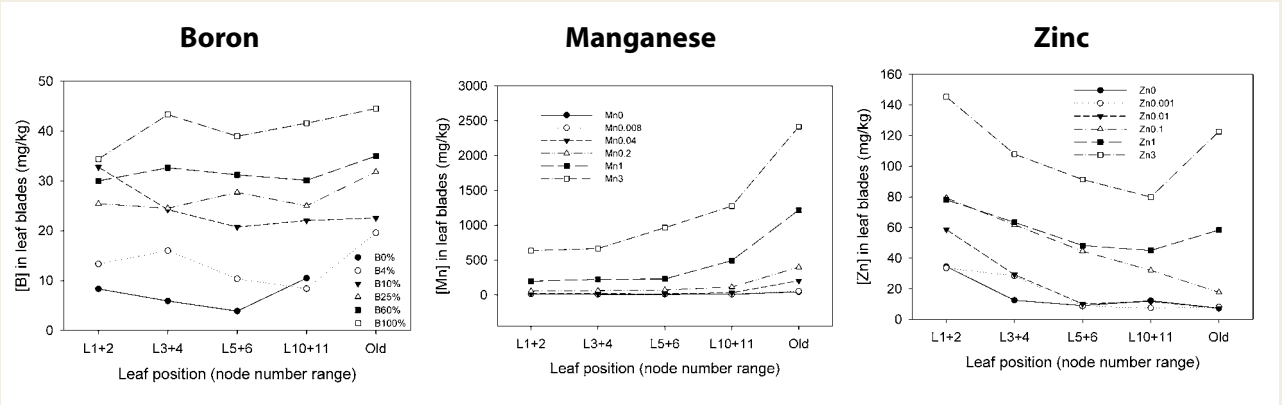
For *D. rotundata*, only three deficiency rate experiments yielded adequate data for profile plots, and these are shown in Figure A-6. The profiles do not differ markedly from those for *D. alata*.

Similar profiles were obtained from toxicity experiments and are plotted separately due to the greatly expanded range compared with data from deficiency experiments (Figure A-7). In the *D. alata* Mn data, the reduced tendency to accumulate Mn in older leaves at the highest supply levels is probably a result of these leaves dying at an early stage in the experiment. This trend was not seen for *D. rotundata*, where the older leaves did not die. Other profiles are similar between the two species. Experiments run in 2002 using both *D. alata* and *D. rotundata* did not produce severe growth reductions at the levels of B, Zn and Cu tested. Consequently, higher concentrations were tested in 2004 using *D. alata* only. Data from both are combined in the following charts. Hence the range of treatments presented for these toxicities is greater for *D. alata* than for *D. rotundata*.

Comparison of genotypes in solution culture

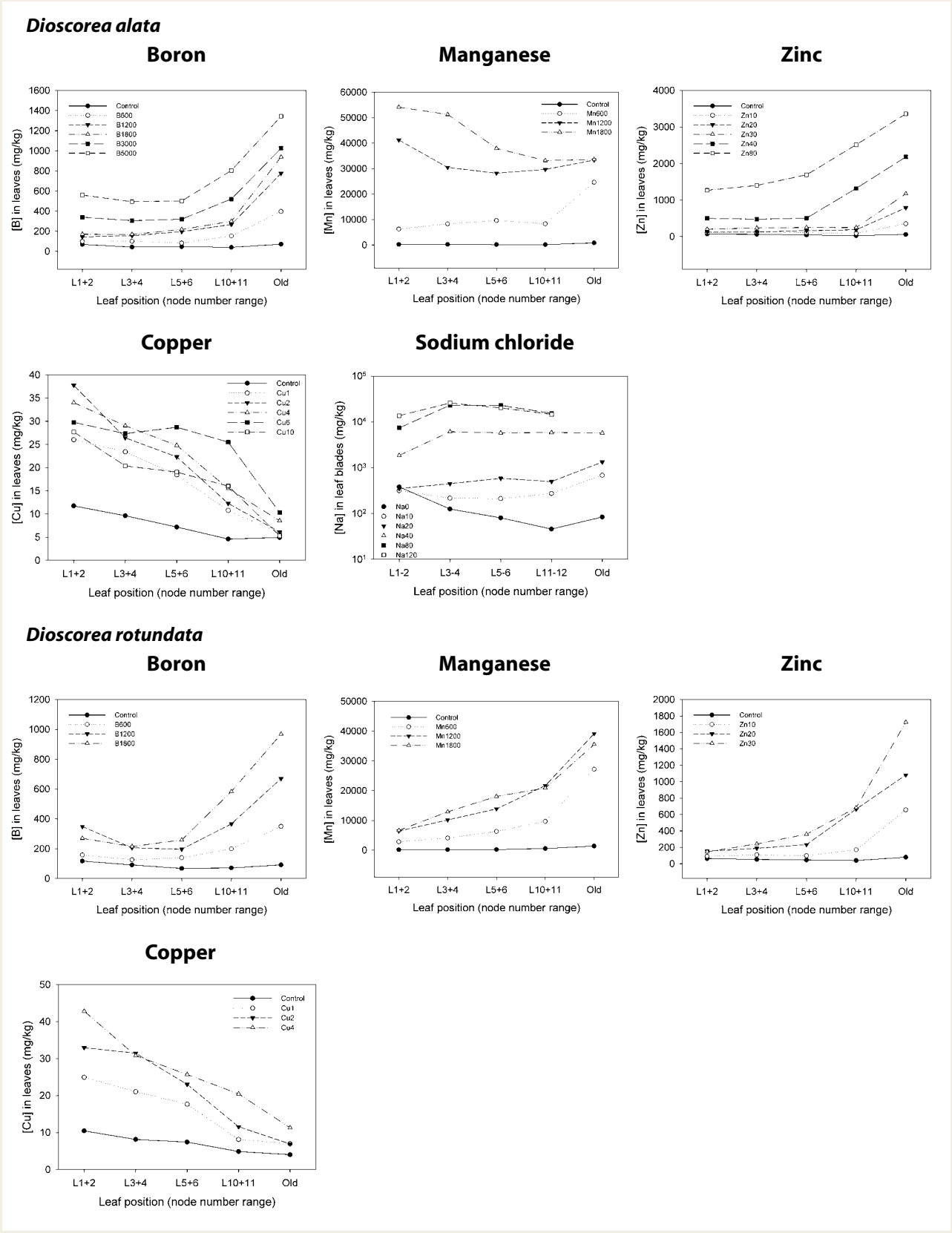
In 2002, an omission trial was conducted comparing two genotypes of *D. alata* and two genotypes of *D. rotundata*. Each pot contained one plant of each genotype, to ensure that the root environment was identical for all. The trial consisted of three replicate blocks of 14 pots. Each block contained two control 'all nutrients' treatments and an omission treatment for each of 12 elements.

The trial was conducted late in the season and variability among plants was large. Nevertheless, symptoms were induced to most disorders, providing useful genotype comparisons. No significant growth reduction was observed in 'all-Cu' or 'all-Mo' treatments (Figure A-8), despite tissue concentrations in or below the critical range, but the precision of very low concentrations of these elements is uncertain because of baseline variability in the analysis. No significant reduction in leaf concentration was obtained for Fe or B, despite an apparent growth reduction and some symptoms. The two species generally responded similarly, except *D. rotundata* appeared relatively tolerant of Ca deficiency, and symptom expression differed for a number of disorders.



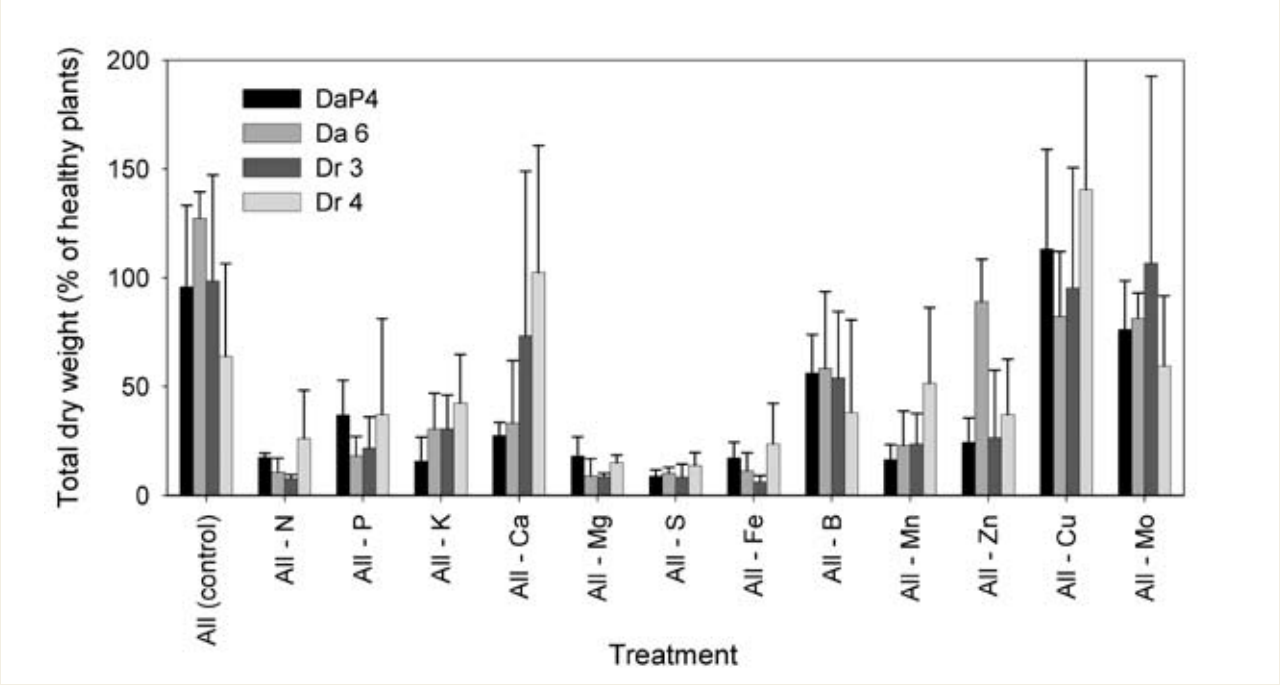
kg = kilogram; mg = milligram

Figure A-6. Dioscorea rotundata *profiles of leaf nutrient concentration changes with leaf position for each element at each supply level tested, in deficiency experiments. Data are the mean of three replicates.*



kg = kilogram; mg = milligram

Figure A-7. Profile of leaf nutrient concentration changes with leaf position for each element at each supply level tested, in toxicity experiments for D. alata *and* D. rotundata. *Values in legends give the concentration (µM) of the treatment element in the culture solution, except sodium (Na) concentration, which is in mM. Leaf Na concentration is in log scale. The NaCl trial contained six replicates of* D. alata *only, while other experiments contained three replicates of each species.*



B = boron; Ca = calcium; Cu = copper; Da = *Dioscorea alata*; Dr = *Dioscorea rotundata*; Fe = iron; K= potassium; Mg = magnesium; Mn = manganese; Mo = molybdenum; N = nitrogen; P = phosphorus; S = sulfur; Zn = zinc

Figure A-8. Relative dry-matter yield of plants in the genotype comparison trial. To define the 100% standard for each genotype, data from control 'all nutrients' treatments were combined with 'all-Cu' and 'all-Mo' treatments, which did not display significant yield effect.

Leaf nutrient analysis (Figure A-9) indicated few distinctive differences between the two species. Nitrogen analyses are not available from this experiment as samples were destroyed. It is likely that K concentrations in healthy *D. rotundata* are lower than in *D. alata*. This has been previously reported (Obigbesan and Agboola 1978) and concurs with our observations of lower K concentrations in *D. esculenta*. It is most likely related to the higher water content of *D. alata* tissues, hence a higher K requirement to maintain similar cytosolic concentrations. There appeared to be a difference in the accumulation of Mo in older leaves in *D. rotundata*. This species also showed slightly higher nondeficient concentrations of S, Mg and P. It is unclear whether this is a species generalisation, varietal variability or an effect of the virus load in the *D. rotundata* material, which yielded less than half the dry matter of the two *D. alata* genotypes in control treatments.

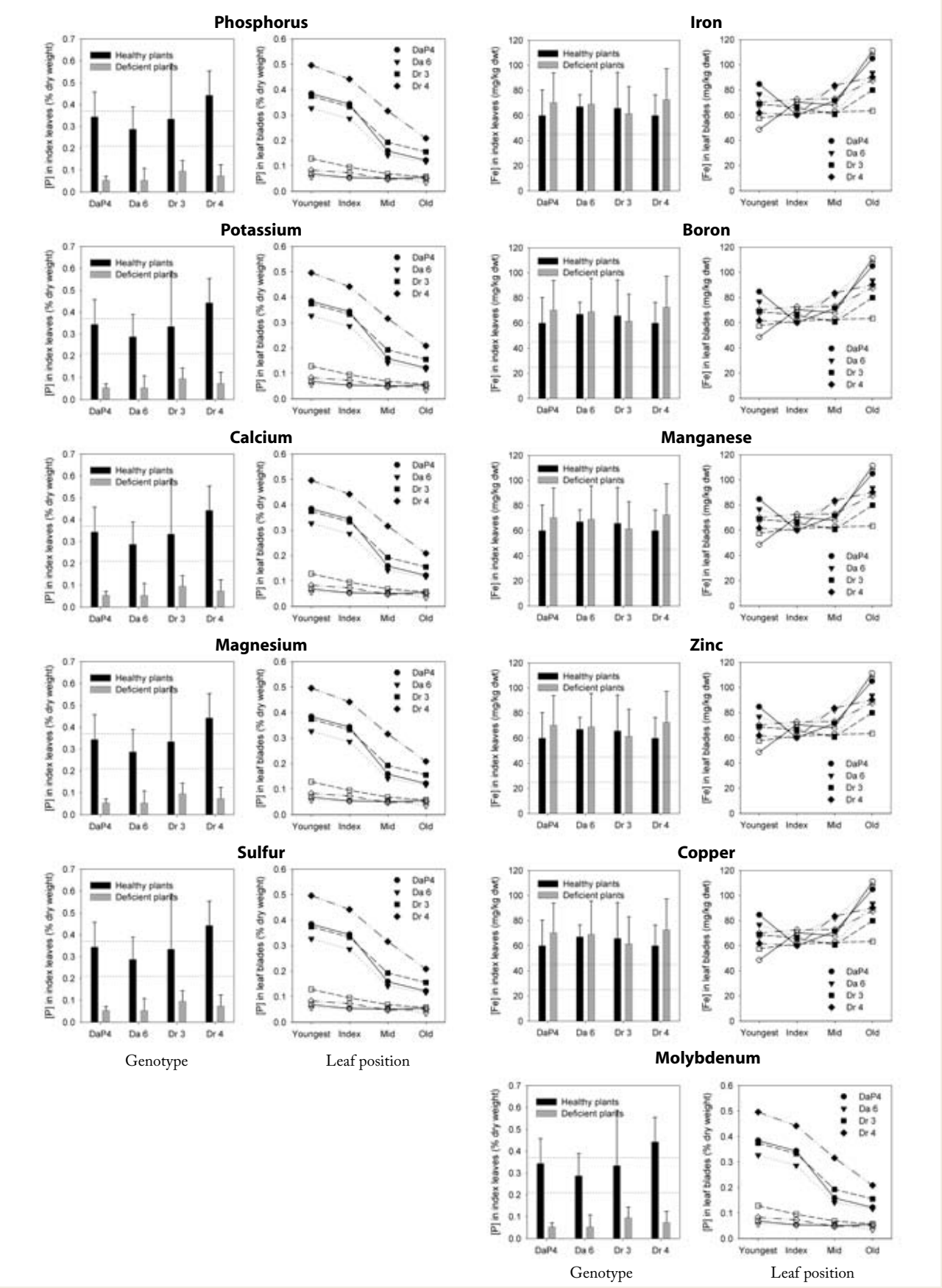
Genotypic differences and seasonal changes in field-grown plants

The germplasm held at the University of Queensland as part of the project consisted of six *D. rotundata* and six *D. alata* accessions received from IITA, and four locally-sourced *D. alata* accessions originating in the Pacific region. Table A-2 lists the accession names and the shorthand titles allocated to them (which are used in figures A-9 and A-10).

Table A-2. Names of genotypes of yam propagated at the University of Queensland, and their shorthand titles used in experimental references

Dioscorea rotundata (African)	Dr-A	*Dioscorea alata* (African)	Da-A	*Dioscorea alata* (Pacific region)	DaP
TDr 131	Dr 1	TDa 291	Da 1	Mahoa'a	DaP1
TDr 179	Dr 2	TDa 85/00247	Da 2	Pala'atea	DaP2
TDr 747	Dr 3	TDa 95/00361	Da 3	Paholo	DaP3
TDr 87/00551	Dr 4	TDa 95/00197	Da 4	Purple	DaP4
TDr 89/01248	Dr 5	TDa 95/00817	Da 5		
TDr 93-2	Dr 6	TDa 95/00846	Da 6		

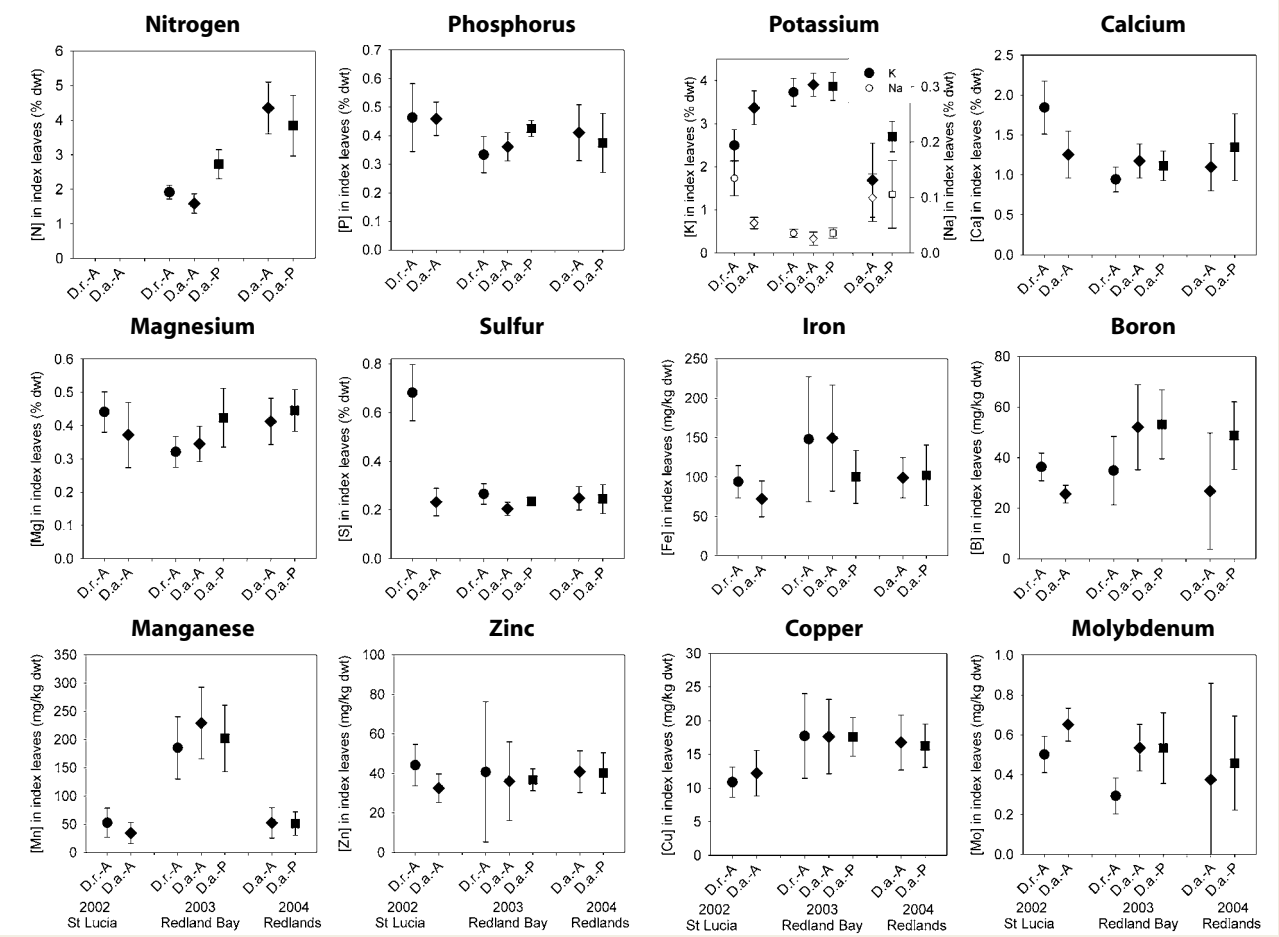
Da = *Dioscorea alata*; Dr = *Dioscorea rotundata*



Da = *Dioscorea alata*; Dr = *Dioscorea rotundata;* kg = kilogram; mg = milligram

Note: In-line plots, closed symbols are healthy plants, open symbols are deficient plants.

Figure A-9. Nutrient concentrations in index leaves of healthy and deficient plants of four genotypes (histograms; dotted lines indicate suggested critical range from Table A-1), and change in nutrient concentration with leaf position.



kg = kilogram; mg = milligram

Figure A-10. Nutrient concentrations in leaf blades from the fifth and sixth nodes (index leaves) in the various yam genotypes grown in field plantings in 2001–02 (St Lucia), 2002–03 (University of Queensland's Redland Bay Farm) and 2003–04 (Queensland Department of Primary Industries' Redlands Horticultural Research Station). Data are mean and standard deviation of six African accessions of D. rotundata *(D.r.-A, ●, sampled in 2002 and 2003 only), six African accessions of* D. alata *(D.a.-A, ♦, six accessions sampled in 2002 and 2003, one in 2004) and four Pacific accessions of* D. alata *(Da-P, ■, sampled in 2002 and 2004).*

The IITA genotypes were grown in pots for two seasons following removal from tissue culture, ensuring normal growth habit was restored. They were first planted outdoors at St Lucia (University of Queensland) in 2001–02. Index leaf samples were taken from each genotype at 5 months after planting (April 2002). Additionally, from two genotypes of each species, a leaf position series was taken, sampling blades from each pair of nodes from a tip to the twelfth node and two samples of older leaves.

In 2003, the IITA genotypes were planted out together with the locally sourced material at the University of Queensland's Redland Bay Research Farm. Leaf samples (index leaves only, sampled at 3 and 5 months after planting) were taken from the 10 *D. alata* and 6 *D. rotundata* genotypes.

In 2004, only four genotypes of *D. alata* were retained and planted in the field at the Redlands Horticultural Research Station of Queensland Department of Primary Industries, at Cleveland. These plants were sampled monthly from 2 months to 5 months, at which time the vines were entering senescence. Leaf samples were taken from each genotype from successive pairs of nodes from active tips, down to the twelfth node. Two samples were also taken of older leaves at the base of the vine mass. At 5 months, only older leaves were sampled as no active vine tips were present. Within the following month, vines died off due to low temperatures.

Genotype comparisons across the three seasons are summarised in Figure A-10. Each planting was at a different location—the St Lucia soil was a shallow, grey clay loam, and both Redland Bay and Redlands (Cleveland) were on deep red-brown krasnozems. Some site-related differences were evident, but species or race-related differences were not consistent across seasons. Potassium was lower in *D. rotundata* than in *D. alata* in 2002, but not significantly so in 2003 when K status was higher. It is noteworthy that Na

concentrations (open symbols plotted on the K chart) were consistently higher in *D. rotundata* and were relatively low in 2003 at the Redland Bay site. This may suggest that the lower K concentrations typically recorded in this species are a consequence of its tendency to take up more Na and are dependent on high Na availability.

Leaf samples were also taken from the yam germplasm collection at Bubia Research Station in Papua New Guinea in 2001. Four varieties each of *D. alata* and *D. esculenta* were sampled, and a single genotype of *D. rotundata* was available. Leaf blades were sampled at the fifth and sixth nodes, and at the ninth and tenth nodes. These analyses (Table A-3) support the conclusion that *D. alata* has higher leaf K concentrations than *D. rotundata* and *D. esculenta*. Calcium and Mo were also significantly lower in *D. esculenta* than *D. alata*. Differences in Mn and Cu were attributable to large genotype differences among the *D. esculenta* accessions. The data suggest that the critical range for deficiency of K, Ca and Mo are likely to be lower in *D. esculenta* than those determined in *D. alata*.

A number of other studies have recorded higher K concentrations in *D. alata* foliage than in *D. rotundata*, *D. cayenensis* (Obigbesan and Agboola 1978) or *D. esculenta* (Vander Zaag et al. 1980). Kabeerathumma et al. (1991) measured similar concentrations in *D. rotundata* and *D. esculenta*, but considerably higher concentrations in *D. alata*, throughout the growing season. From the data in Obigbesan and Agboola (1978), it was apparent that *D. alata* foliage also had a higher water content than the other species. This may explain the higher K concentration (on a dry-matter basis), as this would be needed to maintain similar cytosolic K concentrations in a larger cytosolic volume.

Subsequent data from the *D. esculenta* sand-culture experiment (see Figure A-2, and O'Sullivan and Ernest 2007) support lower critical ranges for K and Ca, but also suggest that critical levels of N and P may be lower in *D. esculenta*. The lower limits of concentrations in nondeficient plants were 2.2% N, 0.24% P, 2.5% K and 0.9% Ca. For other elements, the range between deficient and nondeficient plants spanned the critical range listed for *D. alata*. However, it is possible that supply of one or more of the macronutrients was not optimised in this experiment, and single nutrient rate trials would be needed to confirm the critical level.

Samplings of leaf position were considered important to verify the nutrient profiles determined in solution culture. The data above from the Papua New Guinea germ-plasm collection, comparing nodes 5+6 with 9+10, support the pattern of declining concentrations of phloem-mobile nutrients with leaf age for *D. alata* and *D. esculenta*. These patterns generally appear to apply in the yams, although our data for *D. rotundata* are inconsistent to date.

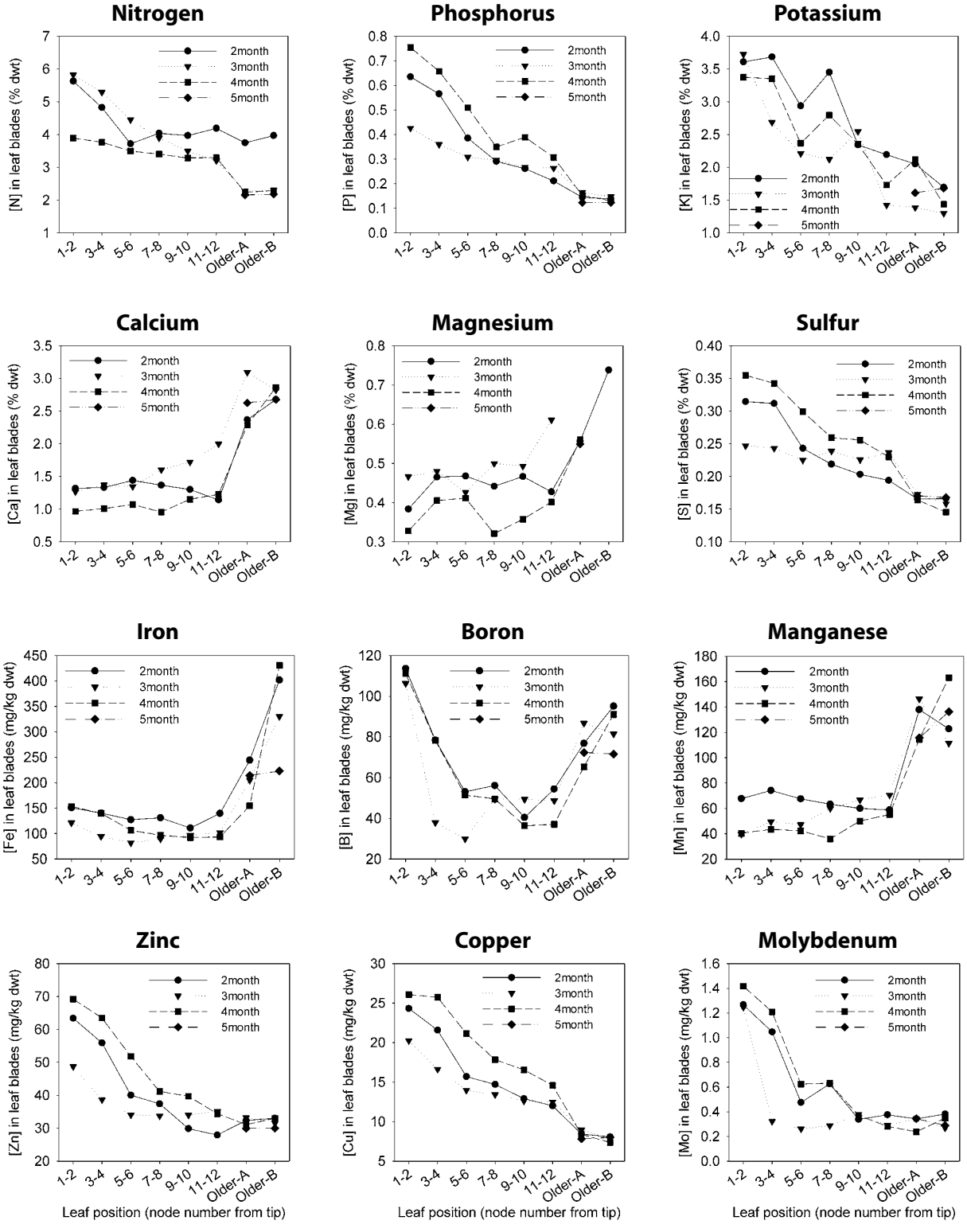
Samplings of four *D. alata* genotypes across the season in 2004 also consistently showed these trends. The leaf position profiles obtained from these monthly samplings are shown in Figure A-11, and can be compared with those from solution culture in Figure A-1. Changes from one sampling time to another do not generally show a distinct trend across the season, and may be more related to weather conditions and growth rate than physiological stage. Older leaf measurements of Mg are missing as the values were over-range. Therefore, the upward trend with leaf age (evident at 2 months) apparently persisted. Nitrogen, Ca and Mg appear to be lower in young leaves towards the end of the season, while P, S, Zn and Cu were higher. These differences were not generally seen in older leaf samples and there was no evidence of increased remobilisation from older leaves associated with tuber development in the later

Table A-3. Nutrient concentrations in leaves from yams in the National Agricultural Research Institute germplasm collection at Bubia Research Station, Papua New Guinea

Species	Node	N (%)	P (%)	K (%)	Ca (%)	Mg (%)	S (%)	Fe (mg/kg)	B (mg/kg)	Mn (mg/kg)	Zn (mg/kg)	Cu (mg/kg)	Mo (mg/kg)	Na (mg/kg)
D. alata	5+6	3.28	0.33	3.37	1.03	0.28	0.22	82.3	15.7	14.9	21.6	14.3	0.77	40.1
	9+10	2.71	0.24	2.81	0.95	0.23	0.19	87.0	17.2	12.2	22.6	11.9	0.41	22.0
D. esculenta	5+6	3.41	0.39	2.71	0.56	0.23	0.22	78.6	12.1	21.8	26.9	10.0	0.25	34.6
	9+10	2.43	0.28	2.27	0.78	0.21	0.18	78.3	12.3	23.3	22.1	8.4	0.28	28.2
D. rotundata	5+6	2.47	0.33	2.94	0.77	0.19	0.20	98.9	13.4	21.8	29.9	10.2	0.32	28.7
	9+10	2.49	0.33	2.38	1.76	0.28	0.20	124.9	10.5	34.9	27.9	6.7	0.45	40.9

B = boron; Ca = calcium; Cu = copper; Fe = iron; K = potassium; kg = kilogram; mg = milligram; Mg = magnesium; Mn = manganese; Mo = molybdenum; N = nitrogen; Na = sodium; P = phosphorus; S = sulfur; Zn = zinc

Note: Data for *D. alata* and *D. esculenta* are means from four genotypes of each species; only one genotype of *D. rotundata* was available.



kg = kilogram; mg = milligram

Figure A-11. Nutrient concentrations in D. alata *leaves grown at Redlands Research Station in 2004, sampled at 2, 3, 4 and 5 months after planting. Only older leaves were sampled at 5 months as tip growth had ceased. Data are the mean of eight measurements (two samples from each of four genotypes).*

samplings. However, only nonsenescent leaves were sampled. Indeed, little senescence of older leaves was observed at 5 months, by which time tip growth had ceased. Over the following 2 months, leaves progressively senesced and abscised from the base of the vines upward.

Irizarry et al. (1995) reported leaf, stem, root and tuber nutrient concentrations at monthly intervals for *D. alata* grown in Puerto Rico. In leaf blades, N declined from 3.6% in the early vegetative stage to 2.65% during tuber filling, but remained steady thereafter. Leaf K concentration rose and peaked at 3 months and declined steadily thereafter. Phosphorus showed a moderate decline, while Ca and Mg declined to 4 months, and increased thereafter. Irizarry and Rivera (1985) reported similar patterns in *D. rotundata*, although the extent of decline in N and K was less. Kabeerathumma et al. (1991) recorded declines in leaf N and K only after 5 months in *D. alata* and *D. esculenta*, but from 3 months in *D. rotundata*. All three species showed a steady decline in P concentration throughout the season. In each of these studies, all leaf blades from the vine were pooled for analysis. The declines observed may therefore be due, at least in part, to the increase in mean physiological age of the leaves sampled. These changes may not relate to changes in leaves of a specified position on the vine.

Concluding comments

The narrow seasonal window in tuber sprouting activity, relative weakness of sprouts from very small tuber setts, slow establishment rate and high variability among plants have all added to the complexity of efforts to characterise nutritional disorders in yam. The program was successful in determining critical ranges for 17 nutritional disorders in *D. alata*, and in providing benchmarks for adequate and deficient levels of mineral nutrients in *D. esculenta* and *D. rotundata*.

In general, the three species did not differ markedly in concentrations of nutrients in leaves, nor their dependence on leaf position. Exceptions were a probably lower critical concentration for K in *D. esculenta* and *D. rotundata*, and possibly lower critical concentrations for N, Ca and Mo, compared with those for *D. alata*.

The most remarkable outcome of this program was the lack of evidence of remobilisation of normally phloem-mobile nutrients in response to deficiency in yams. As a result, the typical symptoms expected for deficiencies of P and K did not develop or were very mild in the most growth-limited treatments, while those for N and Mg were also nondescript. Instead, deficiencies affected the youngest leaves most, particularly in the case of P deficiency.

Glossary

acidic (of a solution or soil)	Containing more free hydrogen ions than free hydroxyl ions, a characteristic that affects the behaviour of many of the chemical species contained in it. (*see* soil pH)
alkaline (of a solution or soil)	Containing fewer free hydrogen ions than free hydroxyl ions, a characteristic that affects the behaviour of many of the chemical species contained in it. (*see* soil pH)
allelopathy	The inhibition of one plant by another nearby, through the release of chemicals into the soil environment that inhibit the growth of the other plant.
anion	A soluble chemical unit (atom or molecule) that carries a net negative electrical charge.
anthocyanin	A red pigment sometimes present in plant tissues. In combination with varying levels of green and yellow photosynthetic pigments, it may produce colours from pale pink to bright orange or dark purple.
anthracnose	The common name for a foliar disease, caused by fungi of the genus *Colletotrichum*, in which necrotic lesions form and spread on the leaves and vines.
apex	The shoot or root tip.
apical meristem	The tissue in a shoot or root tip that gives rise to new leaves, stems, flowers or roots.
axil	The angle formed by the junction of the stem with a leaf petiole, from where lateral shoots arise.
axillary bud	The dormant or undeveloped shoot tip in a leaf axil.
basal lobes	Extensions of the leaf blade, extending backward from the point of attachment of the petiole.
buffering	The ability to resist change in the chemical environment, particularly with reference to the pH or nutrient concentrations of soil solution.
bulbil	An aerial tuber, forming at the axillary bud on the vine. Bulbils may be used for propagation, especially in order to avoid soil-borne pathogens.
cation	A soluble chemical unit (atom or molecule) that carries a net positive electrical charge.
cation-exchange capacity (CEC)	The capacity of a soil to loosely bind cations, determined by the surface area and charge density of particles (e.g. clay, organic matter) contained in a given weight of soil.
chlorophyll	The green pigment in plant tissue that transfers light energy into chemical reactions.
chlorosis	Loss of green pigmentation, resulting in a paler than normal colour, either light green, yellow or whitish. (adj. *chlorotic*)
cultivar	A variant within a plant species, which has arisen in domestication, either through informal or deliberate selection or breeding, and which is recognisable by defined characteristics.

denitrification	The removal of nitrogen from the soil by micro-organisms that transform it into gaseous forms.
distal	Referring to the part of a plant organ (such as a tuber or fruit) that is most distant from the point of attachment to the plant, in contrast to *proximal*, the end nearest attachment.
dolomite	A naturally occurring mixture of calcium carbonate and magnesium carbonate.
ecology	The sum of interdependent relationships between all organisms and their physical environment, in a defined space or system.
exchangeable cation	A cation that is loosely bound to a negatively charged site on the surface of a soil particle, and that may be displaced into solution by another cation taking its place at the particle surface.
fallow	Land that is being 'rested' between crops, either as bare soil or under natural or planted non-crop vegetation.
fertigation	The application of nutrients by adding them to irrigation water.
fixation	Removal of a chemical species from readily available pools in the soil by strong binding to insoluble particles.
genotype	The specific genetic composition of an organism, with reference to its entire genome or to a specific trait, and referring to all individuals carrying the same genetic make-up. For yams, which are vegetatively propagated (cloned), the terms genotype, cultivar and variety are virtually synonymous.
gypsum	Naturally occurring calcium sulfate.
index leaves or index tissue	The tissue chosen as reference material, for comparison of nutrient concentrations in a crop with those listed as indicative of deficiency, adequacy or toxicity.
intercropping	Multiple crop species grown in the same field at the same time, with each species distributed across the area according to a spacial and temporal pattern intended to minimise competition and maximise synergies between crops.
internode	The length of stem between two nodes.
interveinal	Relating to those parts of the leaf blade that lie between the veins.
lamina	The leaf blade or flat portion, distinct from the leaf stalk (*petiole*).
leaching	Removal of soluble chemical species from the soil by the flow of water.
leaf area duration	A cumulative measure of the leaf area of a crop over the total crop cycle, or over a specified phase of growth, such as the tuber-filling period.
leaf area index	The ratio of the total area of all leaves on plants in a given area, to the area of the land.
leaf blade	The broad, flat part of the leaf that provides most of the photosynthetic surface of the plant.
lesion	Localised injury (usually necrotic) of the plant tissue.
lime	Naturally occurring calcium carbonate deposited by marine organisms, including corals.
major/main veins	Thick veins on the leaf blade that branch directly from the midvein or from the point of attachment to the petiole, and radiate to the leaf margin.
midvein/midrib	The main vein bisecting the leaf blade, from the petiole to the tip.

minisett	A small piece of tuber, about 15–50 g, used for propagation to achieve rapid multiplication. They are not used for crop production because yam plants propagated from minisetts produce only small tubers.
minor veins	Secondary and tertiary branches of the major veins.
mottle	An uneven or blotchy colouration.
mycorrhizae	Soil fungi that form an intimate association with plant roots, often to mutual benefit.
necrosis	Death, affecting any section of the plant tissue, not the entire plant. (adj. *necrotic*)
node	The point on a stem where a leaf is attached.
perennial	Living for an indefinite period, more than one season or year.
petiole	The leaf stalk that supports the lamina or leaf blade. Both the petiole and the lamina make up the leaf.
photosynthesis	The process by which plants use light energy to synthesise organic material. (adj. *photosynthetic*)
proximal	Referring to the part of a plant organ (such as a tuber or fruit) that is closest to the point of attachment to the plant, in contrast to *distal*, the end most remote from attachment.
relay planted	A crop having some overlap in growing phase with the main crop.
seed rate	The weight of setts or seed tubers used per hectare of crop planted.
senescence	The processes leading up to the plant-controlled death of a plant part, such as a leaf, or the whole plant. (v. *senesce*)
sett	The tuber piece or whole tuber used as planting material for yam.
sodicity	Characteristics of soil resulting from high levels of sodium, affecting the soil structure and consequently reducing plant growth.
soil pH	A measure of the acidity or alkalinity of soil. Soil pH may be measured by mixing soil in water (e.g. 1:5 soil:water), or in a solution (e.g. 0.002 M calcium chloride). Measured in water, a pH of 6.5–7.5 denotes a neutral soil. Acidic soils have pH < 6.5, with pH < 5 being very acidic. Alkaline soils have pH > 7.5. The presence of undissolved lime or coral may raise the pH up to 8.2; a higher pH indicates the presence of sodium salts.
somatic mutation	A spontaneous change in the genetic code in a cell within the vegetative tissue of a plant, which is perpetuated in tissue derived from that cell, and in descendent whole plants propagated from that tissue.
tuber	A plant organ specialised for the storage of starch, which is derived from stem tissue, and which has the capacity to act as a vegetative (non-sexual) propagule for a subsequent generation.
vegetative propagation	Establishment of new plants from the non-sexual tissue of an existing plant (i.e. without the production of gametes, fertilisation and the development of an embryo).
ware tubers	Tubers grown for the purpose of marketing or eating that exceed the minimum marketable size. The minimum size varies according to regional standards. Distinct from seed tubers, grown for the purpose of propagation or reserved for propagation due to their small size.
wild type	Genetic form of a domesticated species that persists outside of human cultivation and is not genetically influenced by human selection.

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