1 Advances in Sweetpotato Breeding from 1992 to 2012

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Abstract

Sweetpotato, with a global annual planting area of approximately 9 million ha, is the second most important tropical root crop. It is widely adapted, being grown in more than 110 countries. Early maturing varieties grow in 3–4 months. It is hardy and has multiple uses. Both roots and foliage are edible and provide energy and nutrients in diets. Distinct quality types have different uses, with orange-fleshed sweetpotato being valued for its extremely high provitamin A content, and other types used in varied fresh and processed forms. Sweetpotato is easily bred, as true seed is easily obtained and generation cycles are short. There are five objectives of this review. The first objective is to briefly describe recent production and utilization trends by region; the second is to review knowledge about the origin and genetic nature of sweetpotato; the third is to review selected breeding objectives. The fourth objective is to review advances in understanding of breeding methods, including: (i) generation of seed through polycross nurseries and controlled cross breeding; (ii) a description of a new accelerated breeding approach; (iii) recent efforts to systematically exploit heterosis; and (iv) new approaches of genomic selection. The fifth objective is to provide information about variety releases during the past 20 years in West, East and Southern Africa, South Asia, East and South-east Asia, China and the Pacific.

Keywords: abiotic, accelerated breeding scheme, autopolyploidy, beta-carotene (β -carotene), biotic, breeding, controlled cross, genomic selection, heterosis, heterozygous, hybrid, molecular markers, orange-fleshed sweetpotato, origin, polycross, sweetpotato, traits

1.1 Introduction

Sweetpotato breeding was reviewed by Jones (1985) and Martin and Jones (1986), mainly against the background of breeding in the USA. Sweetpotato breeding was more recently reviewed by Grüneberg et al. (2009a,b) and by Lebot (2010). Carpena (2009) provides an overview of important varieties across different regions of the world. This review updates these previous reviews, highlighting recent advances in sweetpotato breeding methods. There are five objectives: (i) to briefly describe recent production and utilization trends by region; (ii) to review knowledge about the origin, centres of diversity and the genetic nature of sweetpotato; (iii) to review selected breeding objectives; (iv) to review recent advances in understanding of breeding methods; and (v) to provide information about variety releases during the past 20 years in the Americas, West, East and Southern Africa, South Asia, China, East and South-east Asia and the Pacific.

Distribution and importance

Sweetpotato was domesticated in tropical America about 6000 BC and reached Polynesia, Hawaii and New Zealand naturally or by early seafarers in pre-Columbian times. The Spanish introduced the crop to the Philippines in the 16th century, from whence it spread to other islands and the Asian mainland. By 1594, the crop was recorded in south China, where it was promoted to mitigate drought during the Qing Dynasty (ruling from 1644 to 1912). Portuguese seafarers introduced the crop into western Mediterranean Europe, Africa, India and parts of South-east Asia (O'Brien, 1972; Yen, 1976, 1982; Jia, 2013). According to the Food and Agriculture Organization of the United Nations (FAO), sweetpotato is currently cultivated in 117 countries in all tropical and subtropical regions of the world, with 104 million t of production in 2011. Asia is the world's largest sweetpotato producing region, with about 80% of annual production, followed by Africa, the Americas and Oceania with approximately 16%, 3% and 1% of annual production, respectively (FAOSTAT, 2011).

Trends in area cultivated from 1992 to 2011 by region (Fig. 1.1), notably show declines in Asia (from 6.4 to 3.6 million ha) and increases in Africa (from 1.2 to 3.2 million ha). Storage root yield trends for the same period show increases for all regions (Fig. 1.2). Yields in sub-Saharan Africa (SSA) are the lowest overall, while those of the West Pacific (China, Japan and Korea) are about four times higher (FAOSTAT, 2011)

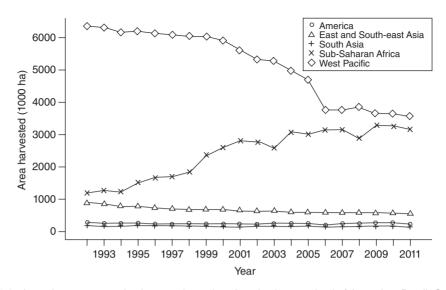


Fig. 1.1. Annual sweetpotato planting area by region. America is comprised of Argentina, Brazil, Cuba, Haiti, Peru and the USA. Sub-Saharan Africa includes East Africa with Burundi, Ethiopia, Kenya, Rwanda, Uganda and the United Republic of Tanzania; Southern Africa with Angola, Madagascar, Malawi, Mozambique and Zambia; and West Africa with Nigeria, Ghana and Mali. South Asia is comprised of Bangladesh and India. East and South-east Asia includes Indonesia, Papua New Guinea, the Philippines and Vietnam. West Pacific is comprised of China, Korea and Japan. (From FAOSTAT, 2011.)

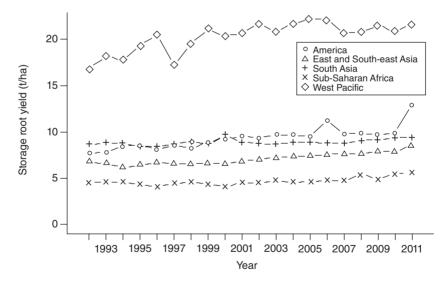


Fig. 1.2. Annual sweetpotato storage root yields by region. The composition of each region is the same as in Fig. 1.1. (From FAOSTAT, 2011.)

than global yields. Thus, there is significant potential to increase global yields through the use of improved cultural practices and varieties (Oswald *et al.*, 2009). Recent major increases in area in countries such as Nigeria and Tanzania reflect the crop's comparative advantage as populations increase and demands on production systems intensify. An overview of the storage root yields from 2002 to 2011 of the 30 countries contributing to more than 99% of worldwide annual production is given in Table 1.1. Yield increases in the West Pacific (China, Japan and Korea), the USA, SSA and South Asia (India and Bangladesh) were about 1.4%, 2.1%, 1.2% and 0.5% per year, respectively, across the past two decades. Some countries in SSA reported yield decreases (Angola, Ghana and Nigeria), whereas the annual yield increases of around 14% across the past two decades in Mali and Tanzania are probably overestimates. Four countries in SSA (Kenya, Mali,

2002

4.2

14.6

2003

3.8

16.1

2004

4.5

15.5

Rwanda and Tanzania) reported yield increases larger than 3% per year and four additional countries (Madagascar, Malawi, Mozambique and Zambia) yield increases of 1–3% per year over the past two decades. We consider that the yield estimates for Ghana and Nigeria from FAO (Table 1.1) are highly inaccurate, most likely due to overestimation of the harvested area. National scientists estimate that in both countries yields per hectare are around 8 t/ha. Moreover, the yield estimates for Uganda are likely underestimates.

Progress in yield can be achieved by breeding (replacing old varieties by new)

2008

6.5

14.0

2009

6.7

13.8

2010

6.3

14.4

2011

6.6

15.1

Table 1.1. Storage root yields (t/ha) in 30 countries which contribute greater than 99% of annual global sweetpotato production.

2005

4.6

15.5

Year

2007

5.9

14.2

2006

4.4

14.4

/ i gonina	14.0	10.1	10.0	10.0			14.0	10.0	1 7.7	
Bangladesh	9.1	9.0	9.0	8.9	9.0	9.1	9.7	9.6	9.9	9.8
Brazil	11.4	11.5	11.5	11.3	11.7	12.1	12.0	11.3	11.9	12.4
Burundi	6.7	6.5	6.7	6.5	6.7	6.7	6.6	6.7	6.9	7.0
China	21.7	20.8	21.7	22.2	22.1	20.7	20.8	21.6	20.9	21.7
Cuba	6.1	7.1	6.7	6.06	6.4	6.4	6.4	5.6	4.8	6.8
Ethiopia	10.0	10.6	9.9	8.1	7.3	8.4	8.0	8.4	9.0	9.0
Ghana	1.4	1.4	1.4	1.4	1.4	1.5	1.6	1.6	1.6	1.8
Haiti	3.0	2.8	2.7	3.0	4.7	3.0	3.0	3.6	3.3	4.6
India	8.6	8.6	8.9	8.9	8.7	8.7	8.9	9.0	9.2	9.3
Indonesia	10.0	10.1	10.3	10.4	10.5	10.7	10.8	11.2	11.3	12.3
Japan	25.4	23.7	25.0	25.8	24.2	23.8	24.8	25.3	21.8	22.8
Kenya	8.5	10.0	9.4	-	9.7	13.3	14.3	12.0	10.0	12.3
Madagascar	5.2	4.7	5.1	7.1	7.2	7.2	7.2	7.2	7.1	7.8
Malawi ^a	12.7	13.1	12.1	9.0	13.4	15.2	14.6	16.2	16.1	17.1
Mali	15.8	14.8	16.5	16.0	18.7	19.1	20.2	19.1	18.8	18.8
Mozambique	5.7	7.3	7.2	7.08	7.3	7.3	7.1	7.1	7.1	7.7
North Korea	12.6	13.7	13.1	13.2	13.1	13.5	13.6	13.5	13.8	13.6
Nigeria	3.0	3.1	3.1	3.2	3.4	2.2	3.0	2.9	2.9	2.9
Papua New Guinea	4.8	5.0	5.0	4.7	5.0	5.0	5.0	5.0	4.8	4.8
Peru	16.1	15.5	15.7	16.4	17.7	16.5	15.7	16.4	16.8	18.1
Philippines	4.5	4.5	4.5	4.8	4.8	4.9	4.9	4.9	5.0	5.0
Rwanda	6.6	5.9	5.6	6.0	5.7	5.7	5.5	6.5	7.5	8.1
South Korea	21.5	19.0	20.8	16.5	17.2	16.7	16.9	16.8	15.6	14.2
Tanzania	3.5	1.5	2.9	3.0	2.8	3.3	6.7	2.2	4.2	5.1
Uganda	4.4	4.4	4.4	4.4	4.5	4.5	4.5	4.5	4.6	4.8
USA	17.4	19.2	19.46	19.9	21.1	20.8	21.3	22.5	22.9	23.3
Vietnam	7.2	7.2	7.5	7.8	8.1	8.2	8.2	8.3	8.7	9.4
Zambia	17.0	14.7	14.9	14.9	14.5	14.6	14.6	15.4	16.9	18.4

^aFAOSTAT (2011) statistics for Malawi are confusing: potato and sweetpotato production appear to be reported under potato – for this reason we used the statistics of FEWSNET (2009), the early warning system data system, which separates the two crops.

Country

Angola

Argentina

and by cultivation techniques (e.g. weed control, crop rotation and fertilizer input). For developed countries, about 50% of vield progress across crops is usually attributed to breeding progress (Wricke and Weber, 1986). Reported yield increases by FAOSTAT do not allow the separation of total vield progress into these two categories. Genetic gain studies for sweetpotato (i.e. by comparing old and new varieties on-farm or a new breeding population with a previous population on-station) have so far not been reported – a clear gap in sweetpotato research. Such studies would be useful to calibrate genomic selection (GS) models to predict trait performance. Based on extensive onfarm observations, we hypothesize that storage root yields of 15 t/ha for sweetpotato on poor soils can be obtained through combining three factors: (i) 'good' varieties; (ii) weeding; and (iii) disease-free or 'clean' planting material.

Uses, markets and varieties

Sweetpotato is used in a variety of ways for food, feed and processed products, with the principal uses varying by region. The literature on nutritional value of cooked and fried sweetpotatoes - as well as processing sweetpotato into food products such as bread, ready-to-eat breakfast, French fries, syrup, starch and beverages - was comprehensively reviewed by Woolfe (1992), Bovel-Benjamin (2007) and Padmaja (2009). In developing countries, the crop is mainly grown for homestead food and feed use and to sell to local markets for fresh consumption. Use of both vines and roots for pig feeding is important in China, Vietnam and Papua New Guinea (Peters, 2004). Padmaja (2009) provides details on use of the crop for cattle, poultry and fish feed.

All sweetpotatoes used both as human food and as animal feed are called 'dualpurpose' sweetpotatoes. Dual-purpose sweetpotatoes should have high foliage yields, because these are mainly used for sweetpotato-based silage and high-protein supplements (fodder) for livestock (Scott, 1991; Zhang et al., 1993; León-Velarde and de Mendiburu, 2007). However, there may be a contradiction between the nutritional value for human food and the demand for extremely high digestibility by the feed industry (Zhang et al., 1993), so that consideration should be given to breeding varieties exclusively for animal feed for areas where that is its dominant use. In China, much sweetpotato is also used in starch noodle production, and use for production of distilled spirits is common in East Asia. Purple-fleshed types, high in anthocyanin, are increasingly popular in China and Japan, used fresh or in a variety of processed snacks and as a source of natural food colouring (Timberlake and Henry, 1988; Gilbert, 2005; Liu, 2008; Ma, 2010).

Awareness of the high nutritional value of sweetpotato is driving increasing consumer demand for the crop among healthconscious consumers in the USA and Europe (USDA, 2015). Orange-fleshed sweetpotato (OFSP) can be used effectively to combat vitamin A deficiency (VAD) among vulnerable populations (Low et al., 2007; Hotz et al., 2012). The leaves of sweetpotato have nutritive values comparable to common dark-green leafy vegetables (Ishida et al., 2000; Bovel-Benjamin, 2007) and leaves, including shoot tips and petioles, are an increasingly popular green vegetable in some regions of China and important in parts of Africa. Ornamental sweetpotatoes with strikingly varied foliage are commercially popular in the USA (Barnes and Sanders, 2012) and South Korea (Yeong-Sang Song, Korea, 2013, personal communication). To our knowledge, there is no significant use of sweetpotato starch in textile, paper, plywood and pharmaceuticals. The crop was traditionally a food security crop (Jia, 2013). It retains this role in many parts of the world, because it: (i) is high yielding; (ii) needs low amounts of water per unit of food and energy (see section 'Drought and other abiotic stresses'); (iii) provides relatively good yields under poor input and marginal soil conditions; and (iv) exhibits wide adaptability to climates, farming systems and uses (Diop, 1998; Hijmans et al., 2002; Jiang et al., 2004). All parts of the plant (roots, leaves and shoots) are edible. Moreover, the crop produces more edible energy per unit area and time (194 MJ/ha/day) than any other major food and it can support more people per hectare than any other crop (Norman *et al.*, 1984; Woolfe, 1992). There are efforts investigating the use of sweetpotato in bioethanol production in the USA (Estes, 2006, 2009) and China (Liu *et al.*, 2010; Wang *et al.*, 2013). On the basis of current technology, 1 t of bioethanol can be produced from approximately 8 t of fresh sweetpotatoes (Qiu *et al.*, 2010).

Two major quality classes of sweetpotato for fresh consumption are generally recognized (Martin and Jones, 1986; Kays et al., 2005). The so-called 'dessert types' are high in β-carotene, have relatively low dry matter content (< 30%) and moist texture, with a high flavour impact due to sweetness and aroma. 'Staple types' typically lack β-carotene, have relatively high dry matter content (> 30%) with drier texture, and have lower flavour impact due to lower sweetness and aroma. A third quality class was recently coined by Tumwegamire et al (2011a), namely 'OFSP dry and starchy' also called 'sabor simple' in Latin America. These are OFSP varieties, high in β -carotene, but with staple attributes such as high dry matter. Nearly all new OFSP varieties bred in SSA are 'OFSP dry and starchy' to meet adult taste preference in SSA. This new OFSP type might also be attractive for markets in South America and South Asia. Sweetpotato breeding and seed programmes are largely supported through the public sector, driven to a varying extent by policies and to a minor extent by the needs of industry. Currently significant investment in sweetpotato breeding is directed towards the development of adapted, high-yielding OFSP varieties to be used for combatting VAD among vulnerable populations in SSA. These investments are additionally supported by 'going-to-scale' disseminations of OFSP varieties in SSA. We assume that the OFSP fraction of the total sweetpotato harvested area in Uganda is still low (around 5%), whereas the OFSP in Mozambique is 22% (TIA, 2012) of total sweetpotato production, so that in the medium term Mozambique could be the first country in SSA with significantly lowered VAD prevalence due to consumption of OFSPs. The general perception of sweetpotato as a 'poor person's crop' is changing in SSA towards a 'food security and health crop'. So far, there are no comparable investments in sweetpotato breeding in South and South-east Asia, in spite of very high VAD prevalence in these regions (UN-SCN, 2004). An important factor underlying increased investment in sweetpotato breeding in SSA was the biofortification programme of HarvestPlus (Pfeiffer and McClafferty, 2007), which is linked to the AgroSalud and Biofort programmes in Latin America. However, sweetpotato is now of minor importance as a food crop in the Americas.

What is biofortification? Biofortification refers to quality breeding aiming at the enhancement of provitamin A, iron and zinc contents in major food crops so that they reach about 50% of their respective recommended daily allowances (RDAs). The micronutrients provitamin A, iron and zinc are critically deficient in our food supply (UN-SCN, 2004) and billions of people are micronutrient deficient without being hungry (so-called 'hidden hunger'). In all countries in which VAD is a serious public health problem, OFSP breeding is a cost-efficient and sustainable vehicle to alleviate VAD and to improve public health. This holds true even if only small quantities of OFSPs are eaten. OFSP, biofortified with provitamin A, is considered by HarvestPlus (Bouis and Islam, 2012; Hotz et al., 2012) to be the first biofortified crop ready to go to scale. Sweetpotatoes are not biofortified for iron and zinc, but OFSPs can contribute about 20%, 20%, 25% and 50% to the RDA of iron, zinc, calcium and magnesium, respectively, where the crop is used as a staple (e.g. Uganda; Tumwegamire *et al.*, 2011a). The target levels to reach 50% RDA, to be able to label sweetpotato as biofortified, for iron and zinc are 60 ppm and 40 ppm, respectively (Wolfgang Pfeiffer, Colombia, 2009, personal communication). Theoretically it is possible to double iron and zinc contents in sweetpotato storage roots, but this will require several breeding cycles (see sections on 'Quality' and 'Breeding Methods'). Fewer cycles may be needed if the bioavailability of iron and zinc is found to be much higher in OFSP roots than currently assumed. Leaves also contain iron and zinc (Woolfe, 1992; Ishida *et al.*, 2000; Bovel-Benjamin, 2007), whose bioavailability is also unknown. In addition, it is not clear to what extent iron levels in leaves are due to non-plant iron contamination of the samples.

For further details on uses and markets by regions, consult Loebenstein and Thottappilly (2009).

1.2 Origin of Sweetpotato, Wild Species and Centres of Genetic Diversity

Sweetpotato (*Ipomoea batatas*) is a polyploid, and is the only hexaploid species (6x = 90, x = 15) in section *Batatas* of the family *Convolvulaceae* (Table 1.2). How and where it originated have not been fully resolved. There are two hypotheses concerning the evolution of the sweetpotato ancestor. The most widely held hypothesis is that *I. batatas* evolved from interspecific hybridization between *Ipomoea trifida* and *Ipomoea triloba* (Austin, 1988). The second is that *I. batatas* developed by polyploidization in *I. trifida* (Kobayashi, 1984). Recent studies based on evaluation of chloroplast haplotypes and

nuclear DNA indicate that it was domesticated separately in Central and South America through autopolyploidization of distinct populations of *I. trifida* or a close relative (Roullier et al., 2011, 2013a). In Roullier's studies, tetraploid accessions previously classified as I. trifida, but later classified as I. batatas (Bohac et al., 1993), shared haplotypes with cultivated sweetpotato in both the northern and the southern regions of domestication. Cytological, molecular and conventional genetic studies provide evidence for some differentiation of the genomes making up the hexaploid sweetpotato, based on pairing at meiosis and tetradisomic segregation ratios (Magoon et al., 1970; Kumagai et al., 1990; Buteler et al., 1999; Kriegner, 2001).

South and Central America have long been recognized as the primary centre of genetic diversity of sweetpotato (Austin, 1978; Austin and Huamán, 1996; Zhang *et al.*, 2000). Secondary centres of diversity exist, however, on the island of New Guinea (Yen, 1974; Austin, 1988) and in East Africa (Zhang, D. *et al.*, 2004; Montenegro *et al.*, 2008). Evidence indicates that sweetpotato could have reached the New Guinea highlands around AD 1200 (Golson, 1976), but the penetration of the crop into Melanesia remains unclear. However, by the 19th century, sweetpotato was the most important staple food crop in New Guinea, and notably is

 Table 1.2.
 Species, ploidy level, origin and accession availability at the International

 Potato Center (CIP) of *Ipomoea* section *Batatas*.

Species	Polyploidy	Origin	Accessions in CIP genebank
Ipomoea batatas	4x, 6x	New World	4616
Ipomoea cordatotriloba	2x	New World	100
Ipomoea cynanchifolia	2x	New World	3
Ipomoea grandifolia	2x	New World	123
Ipomoea lacunosa	2x	New World	5
Ipomoea littoralis	2x	Australia	_
Ipomoea \times leucantha	2x	New World	13
Ipomoea ramosissima	2x	New World	32
Ipomoea tabascana	4x	New World	1
Ipomoea tenuissima	2x	New World	_
Ipomoea tiliacea	4x	New World	54
Ipomoea trifida	2x, 4x	New World	183
Ipomoea triloba	2x	New World	60
Ipomoea umbraticola	2x	New World	6

adapted to very different environments in New Guinea compared with China, Korea and Japan, where it became important nearly simultaneously. Without doubt, the sweetpotato has a secondary diversity centre in and around New Guinea (Yen, 1974; Austin, 1988). Although the genetic diversity in this secondary centre of diversity is considerable, this is probably not based on a large number of introduced clones, but due to isolated environments where the crop flowers and sets seed readily, giving rise to new varieties (Roullier et al., 2013b). This ability of sweetpotato to rapidly develop genetic diversity - even on the basis of a relatively small number of clones - has also been driven by its genetic nature as a highly heterozygous hexaploid hybrid (see section 'Sexual Reproduction, Autopolyploidy and Population Genetics'). A further secondary centre of diversity of sweetpotato has been proposed in East Africa with the discovery of dry and starchy farmer varieties of OFSP (Gichuki et al., 2003; Tumwegamire et al., 2011b).

A recent molecular marker study with both chloroplast and nuclear microsatellite markers supports the existence of two geographically restricted gene pools for I. batatas in Central and South America (Roullier et al., 2011) and the authors argued that sweetpotato could have evolved by independent domestications in Central America (including the Caribbean) and South America. Venezuela, Colombia, Ecuador and Peru are represented by 2930 I. batatas accessions in the International Potato Center (CIP) genebank (only 10% of these accessions are breeding lines or improved varieties). To date, there are not many I. batatas accessions from Central America in CIP's genebank, with 259 of 4616 accessions originating from Central America. Future germplasm collections and acquisitions should prioritize this region.

Crosses among wild species in the section *Batatas*

It is possible to re-synthesize new *Ipomoea* hexaploids (i.e. diploid *Ipomoea leucantha* ×

tetraploid Ipomoea littoralis; Nishiyami et al., 1975). Most cross combinations among species in the *Batatas* section result in interspecific hybrids (Iwanaga, 1988; Freyre et al., 1991; Orjeda et al., 1991; Cao et al., 2009). With the exception of Ipomoea nil (for grafting to induce flowering) and Ipomoea setosa (for grafting to induce flowering and to screen for viruses), wild Ipomoea species have not been used in applied sweetpotato breeding, probably because breeders so far have found sufficient genetic variation in *I. batatas* for most breeding needs by screening their own or foreign germplasm, gene-pool separation or moderate inbreeding. However, other species in the Batatas section are a potential resource for unforeseen biotic and abiotic resistance needs. The Global Trust (Dempewolf et al., 2014) programme started an initiative to use wild relatives of major food crops and plans to evaluate the *Batatas* section in heat-stress environments. This gene pool could become a source of heat-stress tolerant genes useful for more intensive sweetpotato breeding for climatic change. Moreover, wild species in the section Batatas could be a new source of additional resistances to sweetpotato weevils and sweetpotato virus disease (SPVD). The number of accessions of wild species in the Batatas section held in trust at CIP is not large (Table 1.2). However, these wild accessions are maintained as true-seed populations and each accession is formed by a large number of heterozygous genotypes. In contrast to wild Ipomoea species, I. batatas accessions are nearly exclusively maintained at CIP as in vitro clones.

Finally, we note that close wild relatives of sweetpotato are very interesting for genomic studies of sweetpotato. The sweetpotato genome is extremely large (the haploid DNA content is 1.55–2.25 pg/C nuclei or 1515–2200 Mbp; Ozias-Akins and Jarret, 1994; Kriegner, 2001) and highly heterozygous, which makes sequencing the *I. batatas* genome as well as mapping studies for sweetpotato extremely cumbersome. For this reason, many argue that the diploid *I. trifida* be used for genome sequencing to obtain information about the *I. batatas* genome, as well as diploid *I. trifida* maps to anchor the sweetpotato genome (Awais Khan, Peru, 2013, personal communication). CIP is currently incorporating an *I. trifida* mapping population, comprising about 200 genotypes, into its genebank.

1.3 Sexual Reproduction, Autopolyploidy and Population Genetics

The evolutionary forces driving sweetpotato are hexaploidy (6x), high heterozygosity, easy true-seed set by out-crossing and rapid clonal propagation. The crop is an autopolyploid highly heterozygous clone hybrid. The term clone hybrid reflects its genetic nature and presents the opportunity of applying heterosis-exploiting breeding schemes (HEBS). The genetic response of sweetpotato is often surprising - some breeders refer to it as a 'genetic monster'. Due to polyploidy with an even number of chromosome sets, more or less regular meiosis makes sexual seed production possible. Many genotypes very easily develop true seeds in nature (escapes and in farmer fields). The plant has a relatively strong sporophytic self-incompatibility system (Martin and Cabanillas, 1966; Martin, 1968) so that self-pollination usually occurs at low frequency. New genotypes are developed by recombining one highly heterozygous hexaploid hybrid with another highly heterozygous hexaploid hybrid. Incompatibility alleles result in specific cross combinations being difficult to achieve, and seeds from controlled sweetpotato crossings have especially high value (only one to three seeds are obtained from a successful pollination).

Flowering is a prerequisite for sexual reproduction, but sweetpotato genotypes differ greatly in this respect. We have observed that nature selects for prolific flowering among escaped clones (Fig. 1.3). Sweetpotato flowers can be very attractive and the plant has become an ornamental in the USA (Craig Yencho, USA, 2013, personal communication) and Korea (Yeong-Sang Song, Korea, 2013, personal communication). Some genotypes flower easily during any season, others are day-length sensitive and some have problems flowering – for example at the Xuzhou Sweetpotato



Fig. 1.3. Feral sweetpotato at San Ramon, Peru: natural selection favoured abundant flowering.

Research Center (XSPRC) in China, parental material is generally treated with short day lengths during summer. Day-length flowering can be stimulated by grafting on *I. nil* or *I. setosa* (Lam *et al.*, 1959; Wang, 1975; Jones, 1980). Readily and balanced flowering among genotypes is important to recombine genotypes in polycross and controlled cross breeding nurseries. In cases where rare genotypes with special attributes can be selfed, a rare recessive inherited trait becomes fixed in offspring comprising several clones. The frequency of self-incompatibility/compatibility in populations is material dependent.

In populations undergoing intensive breeding, the frequency of successful cross combinations, the frequency of successful crossings per genotype and the frequency of self-compatibility probably changes over time. For example, during the summer season of 2012/13 in Peru, 23 selected parents of the population Jewel (one of the first OFSP populations at CIP) were recombined in a complete diallel crossing scheme (529 cross combinations) resulting in 460 cross combinations with seed set (383 cross combinations with \geq 10 seeds) and eight parents were clearly self-compatible (with \geq 10 seeds from auto-fertilization). This contrasted with 16 selected parents of the population Zapallo (a population created in 2005) and the same crossing scheme (256 cross combinations) in the same summer season – the results were 179 cross combinations with seed set (174 cross combinations with ≥ 10 seeds) and five parents were clearly self-compatible (with \geq 10 seeds from auto-fertilization). This may indicate that sweetpotato is becoming more compatible with breeding.

The autopolyploid segregation ratios of sweetpotato are usually complex (Jones, 1967). Sweetpotato has some advantages as a model crop for breeding clonally propagated crops, especially its extremely short recombination cycles. In the case of a single dominant allele, the segregation ratios are simple (Poole, 1955) and the same is true for self-compatible clones and recessively inherited traits. Selfcompatibility in sweetpotato presents a huge opportunity to increase the number of genotypes for a desired rare and recessively inherited trait - a new unique population is formed in which the desired trait is fixed. Crossing rare clones with a recessive inherited trait to 'normal' parents most often results in failure - the recessive trait disappears as genetic load in the population. Double reduction is a phenomenon that leads to discrepancies from expected segregation ratios in autopolyploids (note: this problem does not exist in diploids). The two segregation extremes in an autopolyploid are random chromosome segregation and random chromatid segregation (Wricke and Weber, 1986). With the latter, double reduction is possible - that is, sister chromatids of a chromosome sort into the same gamete (alleles are identical and derived from the same chromosome). Chromosome segregation is more frequent for loci close to the centromere, whereas the probability of chromatid segregation increases with the distance of loci to the centromere.

Gallais (2003) describes segregation ratios in the presence of double reduction for hexaploids. Single-locus segregation ratios become more complicated due to dosage effects of dominant alleles (discrete ratios are not seen and single-locus segregation ratios become continuous). The complexity of segregation in a hexaploid makes it extremely difficult to develop sweetpotato genetic maps. Moreover, homozygous sweetpotato parents are not available to develop mapping populations. The development of homozygous genotypes by selfing is illusory for hexaploid sweetpotato. Even if plants are self-compatible it would require seven generations of selfing to reach an inbreeding coefficient of F = 0.5(for the calculations, readers are referred to p. 124 of Gallais, 2003), whereas F = 0.5 is reached in diploids after one generation of selfing. For this reason, attempts to develop double-triploids for sweetpotato are underway.

For decades, theoretical descriptions of autopolyploid genetics were limited (usually restricted to tetraploids) until the book by Gallais (2003) was published. For a hexaploid crop, more genotypes are possible and heterozygosity is much larger compared with diploid crops. Even in the simple case of one locus and biallelism, a hexaploid already allows the formation of seven different genotypes, compared with three for a diploid. With multi-allelism at a single locus the number of possible genotypes greatly increases in a hexaploid as a function of the number of alleles. Genotypes can carry a large load of alleles (i.e. five hexaploid genotypes can carry up to 30 alleles, whereas at least 15 diploid genotypes are needed to carry the same amount of alleles). Most loci across the hexaploid genome are heterozygous. In the case of biallelism, equal allele frequencies (p = q = 0.5), and random mating (and absence of double reduction) results in nearly all loci being heterozygous (Fig. 1.4). Within the allele frequency range of about q = 0.2 to q = 0.8, the frequency of heterozygosity is still > 0.75 in a hexaploid.

The heterozygosity in sweetpotato genomes has certain consequences for the ability of the crop to change and adapt in nature and breeding. This can be observed for simple inherited traits, but is perhaps much more important for complex inherited traits controlled by many loci. Several surprising observations in sweetpotato populations can be explained by multiple alleles at one locus and/or extreme heterozygosity across many loci. The first observation is that sweetpotato is capable of developing a large genetic diversity with few introductions (e.g. the diversity observed today in Papua New Guinea or East Africa). In other words, sweetpotato has a larger effective population size and is less affected by genetic drift compared with diploids. The second observation is the extreme large genetic diversity for quality traits

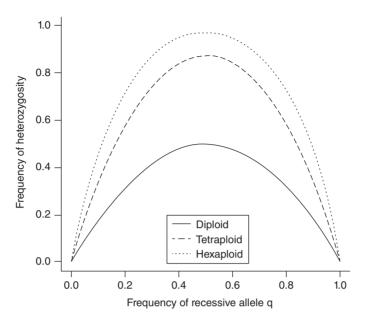


Fig. 1.4. Effect of ploidy level on the frequency of heterozygosity in a random mating biallelic population at equilibrium as a function of the frequency q of the recessive allele (p + q = 1), in the absence of double reduction. (From Gallais (2003), modified by inserting the hexaploid curve.)

(i.e. storage root shape/form, skin colour, flesh colour, stem and leaf form and colour, starch properties and micronutrient contents). On the other hand, it also has a larger 'genetic load' in the negative sense due to defective alleles compared with crops with low ploidy level. With moderate inbreeding (crossing relatives) and gene-pool separation this genetic load can be made more visible for selection. The third observation is that some attributes are very rarely found in sweetpotato germplasm and breeding populations (i.e. SPVD resistance or non-sweetness after boiling) - much worse is that they 'disappear' rapidly after recombination. Typically, less than 0.2% out of 1000 clones is resistant to SPVD in breeding populations at Namulonge in Uganda (Mwanga *et al.*, 2002a,b).

Frequency of recessive homozygosity (Fig. 1.5) and frequency of heterozygosity (Fig. 1.4) are obviously related. Recessively inherited traits are rarely expressed in a diploid open-pollinated crop in a wide range of allele frequency, but in autopolyploid crops (especially a hexaploid) the expression of a recessively inherited attribute is extremely rare, even if the recessive allele has medium frequency (q of 0.3-0.6). Only at high frequencies of the recessive allele (q > 0.7) can the desired recessive inherited attribute be observed with elevated frequencies (> 10%). This results in the paradox that a recessively inherited attribute is very rarely observed, although the recessive allele is present in the population with medium frequency. Breeding for recessive inherited attributes in sweetpotato is much more difficult than in diploids and the same is true for purging negative genetic loads in quantitatively inherited traits – it can be improved by crossing with relatives, controlled crossing by the 'best with the rest' (top clones are crossed with remaining parents) and gene-pool separation.

The extremely high frequency of heterozygosity (Fig. 1.4) in hexaploid populations indicates that the 'stimulus of heterozygosity' or heterosis might be very high in sweetpotato. During the past 5 years, a more intensive discussion has developed on HEBS for clonally propagated crops (Miles, 2007; Grüneberg *et al.*, 2009a). Actually, HEBS was proposed earlier for breeding clonaly propagated crops (Hull, 1945; Melchinger and Gumber, 1998), but the recommendations

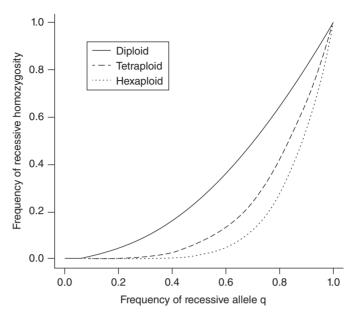


Fig. 1.5. Effect of ploidy level on the frequency of recessive homozygous genotypes in a random mating biallelic population at equilibrium as a function of the frequency q of the recessive allele (p + q = 1), in the absence of double reduction.

were buried in reports concerning heterosis in traditional hybrid crops. Arguments supporting applying HEBS in clonally propagated crops are: (i) all important clone crops are hybrids (clone hybrids); (ii) in cases where sexual reproduction is possible all clonally propagated crops are out-crossing species; and (iii) most clonally propagated crops are autopolyploids with considerably higher heterozygosity compared with the diploids in which HEBS have been applied. In theory, without large investments (simply by gene-pool separation and controlled recombination), large genetic gains might be realized. This holds true for quantitatively inherited traits (controlled enhancement of heterozygosity by inter gene-pool recombination) as well as qualitative inherited traits (controlled inbreeding by intra gene-pool recombination - see also section 'Breeding Methods').

1.4 Breeding Objectives and Genetic Variation

The multitude of potential breeding objectives in sweetpotato can be confusing. Owing to the large segregation potential and diversity and cultivation across a wide range of agroecological zones (Hijmans *et al.*, 2002) many different variety types can be developed. For clarity, we group all breeding objectives into those related to yield, quality and resistance. In reality, there is only one breeding objective – a better variety.

Variety types

Variety types are groups of varieties discriminated on the basis of their use or purpose and adaptation. Usually these are shaped on the basis of demands of agroclimatic zones and use (human consumption, animal feed, non-food industries). Often these groups are made more specific on the basis of colour, cooking quality, processing characteristics and adaptation to cropping systems as well as early or late maturity. A variety may belong to two or more groups (e.g. dual-purpose use for human food and animal feed). Breeders usually select for variety types in separate gene pools.

Formally, four variety types are distinguished in sweetpotato according to flesh colour, dry matter, total sugar and taste of storage roots. Twenty years ago, there were only two variety types: #1: the white, yellow or cream, dry, low-sweet or staple type (also called 'bonitos' or 'ricos' in the Caribbean; Baynes, 1972) and #2: the orange, moist, sweet or dessert type (Martin and Rodriguez-Sosa, 1985). A new variety type #3, 'OFSP dry and starchy' (Tumwegamire et al., 2011a), is an OFSP that in the mouth feels and tastes rather bland, like 'OFSP sabor simple' in Latin America. Nearly all OFSP variety releases in SSA are categorized as OFSP dry and starchy (Appendix 1, at the end of the chapter). Varieties of this new type are also in the pipeline for the Amazon Basin (Appendix 3). Variety type #4 is the purple-fleshed type, usually dry and low in sweetness. Additional variety types may emerge due to specific suitabilities for boiling/microwaving (e.g. the variety Quick Sweet; Katayama et al., 2006) or processing into chips, purée, juice, baby food and bakery products (Woolfe, 1992; Liu, 2008; Ma, 2010).

Informally, three more variety types are recognized (Appendix 1). The first is the 'dualpurpose' type for food and animal feed; the second is the 'good for industrial use' type – for both of these, there are no clear classification criteria. A variety classified as 'dual purpose' is usually a clone with acceptable storage root yield and abundant upper biomass production, sufficient to provide considerable fodder. A variety classified as 'good for industrial use' is most often a clone with high storage root yield and high starch content - sometimes associated with undesired form and size of storage roots. Within varieties classified as 'good for industrial use' screening is conducted for biofuel production (Estes, 2009; Liu et al., 2010; Wang et al., 2013). The third informal classification criterion is 'maturity period'. Yanfu et al. (1989) classified sweetpotato into short-duration or early-maturing (12–17 weeks after planting), medium-duration (17-21 weeks) and long-duration or late-maturing (> 21 weeks) types. In contrast to potato, this classification system is not much used in sweetpotato (Tarn *et al.*, 1992). The reason might be that Yanfu et al.'s threshold levels are not appropriate for farming systems. An improved formal maturity classification would be very useful for tropical areas where sweetpotato is used for piecemeal harvest (East Africa) and where sweetpotato needs to fit several other crops per year in a rotation system (South Asia and South-east Asia). The same holds true for subtropical areas with short rainfall seasons and temperate areas with short summers. We propose here a different classification system for maturity time: (i) 'early bulking' with < 100 days duration after planting; (ii) 'normal bulking' with 100-130 days duration; and (iii) 'late bulking' with > 130 days duration. Among new breeding materials in the pipeline at CIP in Peru, there are many clones that can be labelled as 'early bulking' (90-day sweetpotatoes are possible) and most come from hybrid populations (Federico Diaz, Peru, 2013, personal communication), indicating that earliness and hybrid vigour are associated in sweetpotato.

Storage root yield

Improvement of storage root yield is high priority in all countries where average yields are low (< 12 t/ha, see Table 1.1). However, many breeders rank yield and quality equally, because clones that do not meet consumer quality preferences are simply not permanently adopted. Without a doubt, breeders in high SPVD-pressure zones rank resistance breeding as the most important breeding objective. Susceptible varieties cannot realize their yield potential in farmers' fields where seed systems are not economically viable. Breeders in drought-prone areas rank resistance breeding to this abiotic stress as most important to realize the yield potential of new varieties and minimize the risk of adopting these varieties. Even in the USA, Martin and Jones (1986) emphasized that the yield trait was not the highest priority. With respect to the 'dessert type' in Asia and the Pacific, yield was ranked number five after: (i) eating qualities; (ii) nutritional value; (iii) appearance and uniformity; and (iv) early maturity (Lin et al., 1983).

Storage root yield can be disassembled into components at two levels. The first level comprises those components forming the biological yield or total biomass production. These are net assimilation rate per leaf area (gross photosynthesis minus respiration), leaf area, leaf area duration, water and nutrient uptake, and water and nutrient utilization. The second level comprises the allocation of biological vield into above-ground biomass and root biomass (with storage and non-storage roots). Harvest index (HI) captures this biomass allocation. Measuring the amount of non-storage roots is extremely difficult, so HI is usually calculated by storage root yield divided by above-ground biomass and storage root production. Storage root yield components consist of storage root weight and

number of storage roots. In the case of commercial storage roots, yield has two components: (i) commercial storage root weight; and (ii) number of commercial storage roots. Among all the yield components, applied breeding uses HI and commercial yield the most. This is because many yield components are either very difficult to measure or are correlated and to a certain extent complement each other.

Biological yield and HI also help inform the current storage root yield potentials of sweetpotato. This can be illustrated with an evaluation of germplasm held in trust at CIP (Tables 1.3 and 1.4 for yield traits, and later in the chapter Tables 1.7 and 1.8 for quality traits). To the best of our knowledge, this evaluation of 1174 clones from

Table 1.3. Mean (\overline{x} by least-squares mean (Ismean) estimates), minimum (min) and maximum (max) genotypic values and variance components^a estimates for sweetpotato yield traits (N = 1174 clones) evaluated in diverse environments (five environments in Peru).

Trait	x	Min	Max	$\sigma_{\rm G}^{\rm 2}$	σ_{E}^{2}	$\sigma^2_{{\rm G}\! imes {\rm E}}$	σ_{ε}^{2}
Storage root yield (t/ha)	19.0	0.0	55.5	19.8	27.2	115.9	48.3
Foliage yield (t/ha)	22.6	0.0	67.8	26.2	110.6	161.6	79.3
Biomass (t/ha)	41.5	1.8	97.5	52.8	106.5	313.1	154.1
Harvest index (%)	47.8	0 ^b	100°	65.2	207.6	230.7	93.3
Storage root dry matter (% FM ^d)	34.9	18.3	47.2	14.8	4.2	5.7	3.0

^aVariance components: σ_{G}^2 , variance component due to genotypes; σ_{E}^2 , variance component due to environments; $\sigma_{G\times E}^2$, variance component due to genotype-by-environment interaction; and σ_{e}^2 , variance component due to plot error.

blsmean estimate -10.5% set to 0.

clsmean estimate 109.2 set to 100

^dFM, fresh matter.

Table 1.4. Pearson's correlation coefficients among yield and quality traits of sweetpotato (N = 1174 clones) evaluated in diverse environments (five environments in Peru) – correlations calculated as means across phenotypic correlations for each environment and replication to obtain approximations of genetic correlations.

	Storage root yield ^a	Foliage yieldª	Biomass ^{ab}	Harvest index ^c
Foliage yield ^a	0.197			
Biomass ^{ab}	0.735	0.790		
Harvest index ^c	0.508	-0.582	-0.075	
Storage root dry matter ^a	0.168	0.095	-0.035	-0.204

^aFM, fresh matter.

^bBiomass = storage root yield + foliage yield.

^cHarvest index = (storage root yield/biomass) × 100.

different regions of the world is the largest study ever undertaken for yield and quality in sweetpotato. The study was conducted in 2006 and 2007 in Peru across varying ecogeographic conditions - four locations and five environments, respectively: La Molina, San Ramon with fertilization and without fertilization, Chiclayo with two and four irrigation treatments, and Oxapampa (no quality traits were determined at Oxapampa). At each environment, the experiment was conducted in a complete randomized block design with two plot replications. Each plot comprised two rows with five plants per row. Planting distance was 0.25 m within rows and 0.9 m between rows. An extreme range for biological yield or biomass production, respectively, was observed with a genotypic minimum of 2 t/ha up to a genotypic maximum of nearly 100 t/ha (Table 1.3). The population mean was around 40 t/ha. On average about 48% of the biological fresh matter yield was allocated to storage root fresh matter yield. Assuming an average of 20.7% dry matter in the upper biomass (Federico Diaz, unpublished, n = 6874 breeding clones) and an average of 34.9% dry matter in storage roots (Table 1.3) it can be estimated that sweetpotato allocates 58% of the biological dry matter yield (11.3 t/ha) into storage root dry matter yield (6.6 t/ha). However, sweetpotato exhibits extreme variation in HI ranging from close to zero to nearly 100%.

Obviously HI is a key yield component for storage root yield, with a huge variation in sweetpotato. There are two ways to breed for higher storage root yield: the first is to increase biological yield and the second is to increase HI. Which strategy is expected to have larger genetic gains in the short and/or long term? During the past decade, variance component estimates have been increasingly used in sweetpotato to determine if a breeding objective merits investment (Grüneberg et al., 2004, 2005; Tumwegamire, 2011; Tumwegamire et al., 2011a). Variance components are the appropriate parameters to judge investments in breeding. Although there are many heritability estimates available for sweetpotato (Martin and Jones, 1986), this parameter already depends on the test capacity (number of environments and replications), which varies among studies and experiments, respectively.

The variance component due to genotypes (σ_{c}^{2}) provides information on the genetic variability, and instability of measurements of genotypes in different environments is captured by the variance component due to genotype-by-environment interactions ($\sigma_{G\times E}^2$), whereas biological and technical errors are captured by the variance component due to the plot error (σ_{ϵ}^2) . With these three parameters, it is possible to calculate expected genetic gains and determine whether to invest in breeding. In our example (Table 1.3) comprising diverse sweetpotato germplasm in contrasting environments, the ratio of $\sigma_{G\times E}^2$ and σ_{ε}^2 relative to σ_{G}^2 for HI was estimated to be 1:3.54:1.43. Hence, for various test capacity scenarios the expected genetic gain for HI is larger than those expected for biomass (1:5.93:2.92) and storage root yield (1:5.85:2.44). On the basis of genetic correlations or approximations of genetic correlations (Table 1.4), it is possible to obtain information indirectly for selection for storage root yield by selecting for HI. The latter is more efficient than a direct selection on storage root yield. This leads to model calculations and simulation studies to optimize breeding strategies (for complex studies, refer to Longin (2007); for a simpler study, Grüneberg et al. (2004)).

CIP is working on appropriate weighting factors for HI in breeding programmes utilizing index selection. Usually the $\sigma_{G\times E}^2$ for HI is lower in studies with less diverse material and/or less diverse environments (Grüneberg et al., 2004, 2005; Tumwegamire, 2011). For example a $\sigma_{G\times E}^2$ and σ_{ε}^2 to σ_{G}^2 ratio for HI of 1:0.46:1.24 (recalculated from data of Tumwegamire et al., 2011a) indicates that during the selection process the HI has progressively lower $\sigma_{G\times E}^2$ and that HI is not the only important factor for high storage root yields. It could also be that HI stability is a key factor in selection of storage root yield stability. Overall, HI is a simple measureable trait and when selection in early breeding stages is conducted at two contrasting environments, the $\sigma_{G\times E}^2$ of HI can be captured early in the breeding process (see also section 'Breeding Methods') and it may enable the selection for storage root yield and storage root yield stability during early breeding stages. HI has,

in diverse material and contrasting environments, high associations with storage root yields (r = 0.508, Table 1.4). In other words, more than 50% of storage root yields appear to be determined by HI.

Certainly there are limits to achieving genetic gains by augmenting HI, but in the short term HI has large potential to increase storage root yields in sweetpotato. However, breeders must take into account that varieties with very high HI are not desired by farmers, because above-ground biomass is needed as planting material (also see section 'Drought and other abiotic stresses'). This leads to a question - what is the optimal HI for sweetpotato? Medium- to high-vielding varieties such as Jewel and Xushu 18 have HI of 53.1% and 66.7%, respectively, in contrasting environments (Grüneberg et al., 2005). This is perhaps too high for areas where planting material is a bottleneck. Grüneberg et al (2005) observed an HI of 42.4% for the popular African variety Tanzania, which is certainly medium to low, but not out of range for a 'good' HI. The variety CEMSA-74-228, with HI of 55.6% across 12 East African environments (Grüneberg et al., 2004), is perhaps very close to optimal. In conclusion HI especially HI stability and its association with storage root yield stability - continues to merit further investigation.

Commercial storage root weight (CSRW) and number of commercial storage roots (NCSR) are also considered valuable information by many breeders. Each plant in a sweetpotato field should have a high NCSR (four to six/plant) of medium size and good uniformity (8-23 cm in length and 5-9 cm in diameter) (Firon et al., 2009) and fields should have 35,000-45,000 plants/ha (i.e. the target in Peru sweetpotato growing areas). A limitation of our study (Table 1.3) is that CSRW and NCSR were only determined in the environment of San Ramon with fertilization; $\sigma_{G\times F}^2$ cannot be calculated for CSRW and NCSR. However, the least-squares mean (lsmean) estimates at San Ramon (Table 1.5) show that: (i) on average 78% of the storage root yield was considered commercially marketable; (ii) on average a plant had about 0.5 kg of commercial storage roots; and (iii) an average of 2.3 storage roots per plant. The maximum genotypic value was 3.3 kg of commercial storage roots per plant. The 'environment specific variance component due to genotypes' was overestimated compared with σ_G^2 by factors of 5.1, 6.6, 5.5 and 5.2 for storage root yield, foliage yield, biomass yield and HI, respectively (compare with Table 1.3), because environment specific σ_G^2 estimates are inflated by $\sigma_{G\times F}^2$.

For NCSR, corresponding broad-sense heritabilities of 0.73, 0.40 and 0.83 were reported by Martin and Jones (1986). In our germplasm study, CSRW was strongly correlated with total storage root yield (r = 0.940) and breeders should ask themselves if determining non-commercial roots is necessary. All clones with high CSRW per plant (> 2.5 kg per plant) appear to exhibit high

Table 1.5. Mean (\overline{x} by Ismean estimates), minimum (min) and maximum (max) genotypic values and variance components^a estimates for sweetpotato yield traits evaluated at San Ramon with fertilization in 2006.

Trait	N clones	\overline{x}	Min	Max	$\sigma_{\scriptscriptstyle G}^2$	σ_{ε}^2
Storage root yield (t/ha)	1160	13.7	-0.5	74.2	100.8	42.5
Commercial root yield (t/ha)	1110	10.7	-1.9	61.1	63.8	46.3
Foliage yield (t/ha)	1200	26.1	-2.1	130.4	173.5	85.1
Biomass (t/ha)	1200	37.6	0.4	135.1	290.8	132.9
Harvest index (%)	1160	34.8	-3.6	104.4	340.9	142.8
Commercial root yield per plant (kg per plant)	1110	0.51	-0.1	3.3	0.14	0.19
Number of commercial roots (number per plant)	1110	2.3	-0.4	37.2	2.75	4.68

^aVariance components: σ_c^2 , variance component due to genotypes; and σ_c^2 , variance component due to plot error.

NCSR per plant (6.1-11.5 per plant, i.e. CIP clones 441341, 440652, 441608, 440157, 490065.25 and 400375, results not presented). CSRW and NCSR appear to be similarly important key traits for sweetpotato yields as HI and should be considered in all HI and HI stability studies. Nowadays, genes that are differentially expressed in non-storage and storage roots (e.g. 22 genes were found by You et al., 2003) can be identified and these studies were recently reviewed by Firon et al. (2009). Certainly NCSR per plant is determined by fewer genes than storage root or biomass yields and it might be an interesting trait to include in studies on genomic selection (GS) for sweetpotato (see section 'Breeding Methods').

To breed for improved storage root yield, one must understand storage root initiation in sweetpotato and its interaction with the environment. Storage root initiation has been reviewed by Kays (1985), Ravi and Indira (1999) and Firon et al (2009). Storage roots only derive from adventitious roots arising from the underground stem portions of a vine cutting. Lateral roots (those roots arising from existing roots) do not form storage roots. Adventitious roots can be separated into 'thick' or 'thin' roots (Kays, 1985; Ravi and Indira, 1999). The former nearly always develop from the nodal area of the underground stem, whereas the latter arise primarily from internodal regions of the underground stem. Only thick roots can develop into storage roots (> 15 mm in diameter); however, a larger proportion of thick adventitious roots develop into pencil roots (< 15 mm in diameter). Thin adventitious roots nearly always develop into fibrous roots (< 5 mm diameter). The number of storage roots is determined early in sweetpotato, usually within less than 8 weeks after planting (Lowe and Wilson, 1975). For example, the number of storage roots in the variety Beauregard is determined within 3-6 weeks after planting (Arthur Villordon, USA, 2013, personal communication). Lignification of steles in thick adventitious roots causes irreversible storage root formation and is a result of unfavourable environmental soil conditions in early growing stages (Togari, 1950; Wilson and Lowe, 1973: Lowe and Wilson, 1975; Belehu et al., 2004). The realization of the potential to become storage roots to a large degree determines the final storage root yield (r = 0.412, Table 1.6). We hypothesize that this could be developed into early screening methods for storage root yield. Moreover, the large $\sigma_{G\times E}^2$ for storage root initiation presents opportunities to select for storage root initiation stability (e.g. in Peru we observed that the check clone Tanzania is very sensitive to abundant water supply, whereas this does not affect check clone Resisto).

Breeders do not usually pay much attention to yield physiological traits and the overall assimilation potential. However, assimilation is not a simple function of net assimilation rate per leaf area, leaf area and leaf area duration. A very important factor

Table 1.6. Pearson's correlation coefficients among yield traits^a of sweetpotato (N = 1110 clones) evaluated at San Ramon with fertilization in 2006 – correlations calculated as means across phenotypic correlations for each replication to obtain approximations of genetic correlations.

	RYLD⁵	CRYLD⁵	FYLD⁵	BIOM	HI	CRWP
CRYLD	0.940					
FYLD	0.065	0.094				
BIOM	0.638	0.627	0.805			
HI	0.681	0.595	0.513	0.004		
CRWP	0.672	0.717	0.327	0.146	0.792	
CRNP	0.423	0.412	-0.372	-0.011	0.689	0.743

^aRYLD, storage root yield; CRYLD, commercial root yield; FYLD, foliage yield; BIOM, biomass = RYLD + FYLD; HI, harvest index = (RYLD/BIOM) × 100; CRWP, commercial root weight per plant; CRNP, commercial root numbers per plant.

^bFM, fresh matter.

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for assimilation is how efficient assimilates are incorporated from the leaf source into the sinks, and among these the storage root is a very dominant sink (Kays, 1985; Ravi and Indira, 1999). The sucrose concentration is high at the source and is moved in water via the phloem to sinks where the sucrose concentration is low. With the conversion to starch by hydrolysis in the storage roots, the sucrose concentration remains low in the storage root sink. Reciprocal graft experiments between sweetpotato and I. trifida, as well as among sweetpotato genotypes with poor or strong sink capacity, show how important this factor might be in sweetpotato vield formation. Carbohydrate accumulates in the leaves of shoots grafted onto genotypes with low sink capacity (Hozyo and Park, 1971; Ko et al., 1993) and the source potential of low-yielding cultivars is increased when grafted onto genotypes with high sink capacity (Hahn, 1977; Zhong, 1991). Net photosynthetic rate drastically declines when root enlargement is restrained (Tsuno and Fujise, 1965). Note that the top five biomass-yielding clones in our study presented in Table 1.3 (biomass yield: > 90 t/ha in 199076.1, 401549, 420886, 401031 and 187016.2 (for details see lsmean values uploaded as 'sp_germ_2005-2006. pdf' on 'A sweetpotato breeding repository' available at http://sweetpotatobreeder.com)) were all clones with a strong storage sink capacity (high storage root yields of 35.6-55.5 t/ha). An active source appears to need a high sink capacity (Ravi and Indira, 1996a,b).

Certainly the sink is not the only driving force to assimilate carbohydrates. In photosynthesis (the source), it is needed to distinguish between light utilization and light uptake. Light utilization is determined by the net assimilation rate per leaf area. There are opinions that light utilization has already been well optimized during plant evolution (green plants have long existed in evolutionary history), whereas light uptake still offers opportunities. Light uptake is determined by leaf area, leaf area duration and leaf orientation to the incoming radiation. The leaf area relative to the soil surface is estimated by the leaf area index. Sweetpotato appears to exhibit a great magnitude of genetic variation for leaf area. Most sweetpotatoes rapidly cover the ground, but lack of canopy depth due to horizontal development of the canopy and poor leaf orientation, result in shading of leaves within the canopy. The optimum leaf area index of sweetpotato appears to be 3-4 (Tsuno and Fujise, 1965). Cultivars adapted to elevated altitudes in Africa are reported to be more erect and have lower leaf area indexes (Hahn and Hozvo, 1984). There is a pronounced period during the growing season in which the leaf area index of sweetpotato is larger than 3–4 (Kotama et al., 1970). Compared with rice, sweetpotato has higher crop growth rates during the first 4–6 weeks after planting and later again at 10-15 weeks after planting (Tsuno, 1971); however, between these periods rice is superior to sweetpotato and this is the period during which sweetpotatoes usually have a leaf area index greater than 3-4. Most yield physiology studies trace back to findings of Tsunoda (1959), who observed that the highest yielding varieties produced relatively thick and small leaves in response to high light intensity, which allowed good light penetration. To our knowledge such aspects have not been further investigated during the past two decades, except in a study by Kelm et al (2000) with the two clones Jewel and Tanzania. Significant options for genetic improvement probably exist, as the optimal assimilating surface of a densely planted sweetpotato monocrop should be very different from that of a single wild sweetpotato plant. Certainly clones with many branches, exhibiting long extended internodes and long vines and a horizontal leaf orientation (thereby allocating a major proportion of assimilates into the canopy) are not optimized when planted densely as a monocrop. We further examine the performance and efficiency of underground roots to supply water and nutrients for assimilation in the section 'Drought and other abiotic stresses'.

Quality

Quality demands are driven by how sweetpotato is used. Most important are the needs for direct human consumption. Second are needs associated with use as animal feed. Quality required for the food industry is determined by the product. Traits needed for sweetpotato processed into chips are different from those needed for sweetpotato processed into Chinese noodles. This discussion focuses on quality for direct human consumption in the developing world. Demands for direct human consumption (boiling, roasting and mashing into purée) vary among societies and countries. Different taste preferences depend mainly on how people have been socialized and income. In this discussion, a distinction will be made between directly noticeable quality and *not* directly noticeable quality traits.

The first group of directly noticeable quality traits is storage root shape and form, flesh colour and skin colour. These three traits have medium to high heritabilities and therefore are also used as morphological descriptors (Huamán, 1991). Drawing again on the data for 1174 clones in Peru, the variation for storage root shape and form ranges from round (resembling large-size potato tubers) to very long (nearly resembling small cassava storage roots) (Fig. 1.6a). Many breeders, growers and consumers have an ideal for how a sweetpotato storage root should look, that is uniform shape 8-23 cm in length and 5-9 cm in diameter (Firon et al., 2009). However, in most developing countries, a commercial storage root is simply defined on a weight basis, for example ≥ 100 g in the case of Malawi (Felistus Chipungu, Malawi, 2013, personal communication). The range in storage root flesh colour includes white, yellow, orange and purple (Fig. 1.6b). Yellow and orange colour in sweetpotato storage roots is determined by carotenoids. Fortunately, the proportion of β -carotene as dominant provitamin A is greater than 80% among the total carotenoid content in OFSP (Woolfe, 1992). For this reason, flesh colour alone can be used to predict β -carotene content of storage roots using colour charts (G. Burgos, R. Carpio, C. Sanches, P. Sosa, E. Porras, J. Espionza and W.J. Grüneberg, unpublished data). During the past 5 years, these colour charts have become widely used by the National Agricultural Research System (NARS) breeding programmes in SSA to estimate β -carotene contents of new selections. The purple flesh colour is determined by anthocyanins. Owing to the health-promoting effects of antioxidant anthocyanin substances such sweetpotatoes are also attractive for quality breeding. Moreover, such purple varieties can be used to obtain food colourants. which is a relatively new market for sweetpotato (Timberlake and Henry, 1988; Gilbert, 2005: Konczak, 2006). The storage root skin colour ranges from white, yellow, orange and brownish orange, red to dark purple (Fig. 1.6c). Consumers in most regions still tolerate a wide range of storage skin colour (white, brown, red and purple).

The second group of directly noticeable quality traits is mouthfeel and taste. Many believe that it is not possible to define the compound(s) which determines the 'sweetpotato taste'. Certainly, in breeding OFSPs local taste preferences are critical. Consumers like the orange-fleshed coloured clones as long as they are not associated with undesirable mouthfeel and taste. Adult consumers do not make many compromises with respect to this trait. For example, the first introduction of OFSPs into Africa where the white, dry, low-sweet and bland type was nearly exclusively consumed was hampered by the moist and sweet mouthfeel and taste of traditional OFSPs. The problem was solved by breeding for orange, dry and starchy varieties in SSA (Tumwegamire et al., 2011a,b). As a consequence, there are now over 40 variety releases and new breeding materials for orange, dry and starchy sweetpotatoes (Appendices 1 and 3). Mouthfeel and taste depend much on dry matter, starch and sugar contents of storage roots. Laurie et al. (2012) observed significant correlation of maltose content with sensory sweet and sweetpotato-like flavour, which might serve as a tool for selection in early breeding stages. However, dry matter, starch content and sugars do not exclusively control taste and flavour. Hence, storage roots must be assessed by eating for taste and flavour quality breeding. While thousands of genotypes can by screened by microwaving, taste panels need to be conducted by experienced persons.

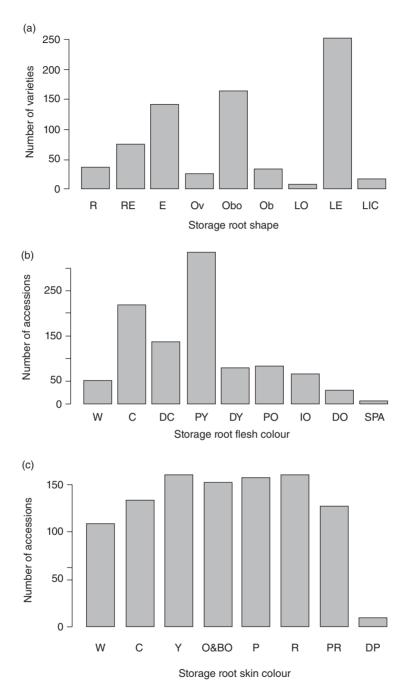


Fig. 1.6. Data bank information for storage root shape (a), flesh (b) and skin colour (c) for 1174 health status II clones held in trust at CIP and evaluated during 2006–2007 (see also Table 1.3). Root shape: R, round; RE, round elliptic; Ov, ovate; Obo, obovate inversely ovate outline; Ob, oblong; LO, long oblong; LE, long elliptic; LIC, long irregular or curved. Flesh colour: W, white; C, cream; DC, dark cream; PY, pale yellow; DY, dark yellow; PO, pale orange; IO, intermediate orange; DO, dark orange; SPA, strongly pigmented with anthocyanins. Skin colour: W, white; C, cream; Y, yellow; O&BO, orange and brownish orange; P, pink; R, red; PR, purple red; DP, dark purple. (From Huamán, 1991.)

Not directly noticeable quality traits are those associated with the nutritional value of sweetpotato and need to be determined by analytical methods. The obvious exception is β -carotene content of storage roots that turn storage roots yellow to dark orange. In the past, it was only possible to evaluate protein, starch, individual sugars, vitamins and micronutrients by complex analytical laboratory procedures. Owing to the cost and time required only a few clones were screened in a breeding programme. Such studies provided information about the range of the chemical composition in sweetpotato as described in the textbook by Woolfe (1992) or genetic variance component estimates of storage root dry matter, starch and β -carotene content on the basis of a few clones (Grüneberg et al., 2005).

Studies indicate that most nutritional traits can be efficiently changed by breeding due to the large σ_G^2 and low $\sigma_{G\times E}^2$ of these quality traits relative to σ_G^2 . However, at the end of the breeding cycle, when only a few clones remain and most have been discarded, there is not much genetic variation left to enable finding genotypes which combine desired nutritional traits with desired yields. In other words, breeders who want to change quality in the entire crop need to evaluate quality in the early breeding stages. This requires fast throughput methods

such as colour charts to predict provitamin A content. During the past 8 years it became possible to calibrate near-infrared reflectance spectroscopy (NIRS) with reference values from chemical analytic methods such as spectrophotometry for total carotenoids, high performance liquid chromatography (HPLC) for different carotenoids and inductively coupled plasma argon optical emission spectrometry (ICP-OES) for minerals (Lu et al., 2006; zum Felde et al., 2007; Lebot et al., 2011). This technology is now in use for early breeding stages at CIP headquarters and in SSA (Grüneberg et al., 2009a,b) and for germplasm evaluation (Tumwegamire et al., 2011a; Tables 1.7 and 1.8). The aim of this study was to determine maximum genotypic values, variance components, heritabilities and approximations of genetic correlations for β-carotene, iron and zinc to obtain information on how quality could efficiently be improved in sweetpotato.

What has been learned during the past decade on how efficiently yield and quality can be improved in sweetpotato? The average commercial storage root contains 34.9% dry matter with 4.3% protein, 66.0% starch, 10.3% sucrose, 143.7 ppm β -carotene, 15.6 ppm iron and 9.3 ppm zinc (Table 1.7). However, this average is quite artificial because its estimation is across very different variety types. Dry matter, starch, individual sugars

Table 1.7. Mean (\overline{x} by Ismean estimates), minimum (min) and maximum (max) genotypic values and
variance components ^b estimates for sweetpotato quality traits ($N = 1174$ clones) evaluated in diverse
environments (five environments in Peru).

Trait ^a	x	Min	Max	$\sigma_{\rm G}^2$	σ_E^2	$\sigma^2_{{\rm G}\! imes {\rm E}}$	σ_{ε}^2
Root yield (t/ha)	19.0	0.0	55.5	19.8	27.2	115.9	48.3
Root dry matter (% FM)	34.9	18.3	47.2	14.8	4.2	5.7	3.0
Protein (% DM)	4.3	2.7	8.9	0.3	6.2	0.7	0.5
Starch (% DM)	66.0	36.5	76.0	28.9	6.0	7.2	3.8
Sucrose (% DM)	10.3	2.0	33.1	12.2	0.7	5.5	3.0
Fructose (% DM)	1.7	0.0	11.1	1.6	0.0	0.6	0.3
Glucose (% DM)	2.2	0.0	16.0	3.0	0.1	1.0	0.5
β-Carotene (ppm DM)	143.7	1.8	1,220	14,751	2,262	4,640	1,817
Iron (ppm DM)	15.6	10.5	28.6	2.7	15.1	3.2	2.5
Zinc (ppm DM)	9.3	6.2	17.1	0.9	9.4	1.5	1.1

^aFM, fresh matter; DM, dry matter.

^bVariance components: σ_{G}^2 , variance component due to genotypes; $\sigma_{E'}^2$ variance component due to environments; $\sigma_{G\times E'}^2$ variance component due to genotype-by-environment interaction; and $\sigma_{E'}^2$ variance component due to plot error.

and β -carotene can be positively or negatively associated (Table 1.8). For example, varieties with very high dry matter and starch content are low in sugars and usually have no or very low β -carotene content; or varieties with very high β -carotene content are usually high in individual sugar content and low in dry matter and starch content. Obviously, quality attributes vary widely in sweetpotato (Table 1.7) with respect to dry matter (18.3-47.2% fresh weight basis (fwb)), protein (2.7–8.9% dry weight basis (dwb)), starch (36.5-76.0% dwb), sucrose (2.0-33.1% dwb), fructose (0-11.1% dwb), glucose (0-16.0% dwb) and β -carotene (1.8-1220 ppm dwb). This results in extreme differences in storage root colour, texture and taste. Differences among sweetpotato varieties with respect to storage root iron (10.5-28.6 ppm dwb) and zinc content (6.2-17.1 ppm dwb) are less pronounced than differences in dry matter, protein, starch, sucrose, fructose, glucose and β -carotene content (data for individual clones are posted on the sweetpotato knowledge portal: http://sweetpotatoknowledge.org). Many sweetpotato varieties have greatly exceeded the minimum β-carotene target level required to be labelled as 'biofortified for provitamin A', but the best varieties as of 2014, only reach 50% of the iron and zinc targets and biofortified sweetpotato for iron and/or zinc are longer term objectives. However, as mentioned previously, the label 'biofortified' depends also on intakes and bioavailability. If iron in sweetpotato has a much higher bioavailability than currently assumed, for instance, this would have tremendous impact on breeding progress towards iron biofortified sweetpotatoes.

The σ_G^2 variance components for storage root dry matter, starch, individual sugars and β -carotene are large compared to σ_{E}^{2} and $\sigma_{G\times E}^{2}$ (Table 1.7). In other words, these traits have a large genetic variation in sweetpotato and are not greatly affected by the environment and genotype-by-environment interactions. Notable negative genetic correlations exist between storage root β-carotene and dry matter content, and between storage root β -carotene and starch content, whereas positive correlations exist between storage root β -carotene and sugar content (Table 1.8). However, the magnitudes of these genetic associations are not sufficiently large to greatly slow breeding progress towards dry and starchy OFSP varieties that are rich in provitamin A. The positive genetic association between both trace minerals (iron and zinc) and β -carotene supports breeding,

Table 1.8. Pearson's correlation coefficients among yield and quality traits^a of sweetpotato (N = 1174 clones) evaluated in diverse environments (five environments in Peru) – correlations calculated as means across phenotypic correlations for each environment and replication to obtain approximations of genetic correlations.

	RYLD⁵	FYLD⁵	DM ^b	PROT⁰	STA°	SUC⁰	FRUC °	GLUC°	BC℃	FE°
FYLD	0.197									
DM	-0.168	0.096								
PROT	-0.114	-0.078	-0.071							
STA	-0.066	0.108	0.767	-0.232						
SUC	0.007	-0.068	-0.437	0.168	-0.788					
FRU	0.174	-0.060	-0.715	-0.164	-0.586	0.095				
GLU	0.170	-0.067	-0.718	-0.128	-0.608	0.117	0.982			
BC	-0.048	-0.086	-0.189	0.177	-0.425	0.462	0.059	0.072		
FE	-0.086	-0.065	-0.245	0.760	-0.458	0.362	0.004	0.054	0.264	
ZN⁰	-0.154	-0.087	-0.133	0.801	-0.310	0.291	-0.204	-0.145	0.213	0.822

^aRYLD, storage root yield; FYLD, foliage yield; DM, dry matter content of storage roots; PROT, protein content of storage roots; STA, starch content of storage roots; SUC, sucrose content of storage roots; FRUC, fructose content of storage roots; GLUC, glucose content of storage roots; BC, β-carotene content of storage roots; FE, iron content of storage roots; ZN, zinc content of storage roots.

°DM, dry matter.

but the magnitude of σ_G^2 for iron and zinc does not favour rapid genetic improvement. Finally, variance components and genetic associations favour the efficient breeding of varieties with low sugar content. Our findings are consistent with results of Woolfe (1992) and Courtney *et al.* (2008), who used US breeding material, and Tumwegamire et al. (2011a), who used East African germplasm. In summary, during the past decade, we have learned that: (i) extremely high provitamin A content can be combined with many other quality and yield attributes; (ii) breeding high iron and zinc varieties is a difficult and time-consuming process most likely achieved by several cycles of selection; and (iii) breeding for non-sweet sweetpotato varieties should be efficient and rapid.

Quality breeding is not as straighforward as theorized and we give three examples. The first is that raw non-sweet sweetpotato varieties do not necessarily stay non-sweet after boiling due to hydrolysis of starch to maltose in the cooking process by β -amylase. Without sufficient β -amylase, the normal hydrolysis of starch to maltose does not occur during cooking. This attribute is controlled by one recessive allele (Kumagai et al., 1990). Breeding for non-sweet sweetpotato varieties requires both screening for low individual sugar content and low β -amylase activity in storage roots. Owing to the recessive inheritance of the attribute 'non-sweet after cooking', this breeding effort becomes a quite difficult task in hexaploid sweetpotato. The second example is an effort to change the two starch components amylose and amylopectin in sweetpotato (Lii and Tsai, 1996; Richardson et al., 2000). The amylose content in sweetpotato starch is low (10-25%) (Noda et al., 1998). High amylose starches as well as amylose-free starches are of interest in food and other industries (Richardson et al., 2000; Ocloo et al., 2011). Amylose-free genotypes have been generated using a transgenic approach (Kimura et al., 2001), as have genotypes with increased amylose content (Shimada et al., 2006). The third example is an effort to improve the baking quality of sweetpotato – so far sweetpotato flour is only used in mixtures with wheat flour in bread making since sweetpotato has no gluten. To improve the baking quality of sweetpotato flour, a glutenin gene of wheat was introduced into sweetpotato (variety Huachano). Among the 13 transformed events obtained, three expressed glutenin in high amounts (CIP, unpublished). For details on transgenic approaches to change sweetpotato quality the reader is referred to Kreuze *et al.* (2009).

Biotic and abiotic stress

Sweetpotato is affected by about 35 bacterial and fungal diseases, more than 20 viruses or virus-like agents, 20 nematodes and 20 insect species (Martin and Jones, 1986). Recently, fungal and bacterial diseases (Clark *et al.*, 2009), viruses (Loebenstein *et al.*, 2009), nematodes (Overstreet, 2009) and insects (Sorensen, 2009) affecting sweetpotato were reviewed in the textbook by Loebenstein and Thottappilly (2009). Only five pests and diseases are known to be economically important: (i) SPVD; (ii) sweetpotato weevils; (iii) nematodes; (iv) *Alternaria*; and (v) *Fusarium*. With respect to abiotic stresses the crop is affected by drought, heat, cold and salinity.

Worldwide, the greatest biotic constraint is SPVD across all regions. SPVD often causes serious yield losses, especially in high viruspressure zones of SSA. Nearly all OFSP varieties bred outside of SSA that were introduced to East Africa failed because of SPVD. The critical component within SPVD is whitefly-transmitted Sweetpotato chlorotic stunt virus (SPCSV). This virus usually occurs in co-infection with other sweetpotato viruses in which SPCSV breaks the resistance of sweetpotato against other viruses (Ian Barker, Switzerland, 2009, personal communication). SPCSV often occurs in co-infection with aphid-transmitted Sweetpotato feathery mottle virus (SPFMV). Clear synergistic disease effects are observed by co-infection of SPCSV and SPFMV resulting in extreme yield losses (Milgram et al., 1996; Gutiérrez et al., 2003) the so-called SPVD virus complex. Viruses can be grouped into gene pools and phylogenetic groups (strains). Four strains have been reported for SPFVM: (i) East African (EA); (ii) russet crack (RC); (iii) ordinary (O); and (iv) common (C). Virus coat-protein

gene sequences have shown that EA SPFMV strains clearly form a separate cluster (Kreuze et al., 2000). Two strains have been reported for SPCSV: (i) East African (EA); and (ii) West African (WA) (Loebenstein et al., 2009). The EA strain was first identified in East Africa and is also present in Peru, while the WA strain was first identified in West Africa and is also found in the Americas and the Mediterranean, but so far not in East Africa (Hover et al., 1996; Tairo et al., 2005). There are two serotypes (SEA1 and SEA2) in the EA strain (Loebenstein et al., 2009). A resistance working against one virus strain may not necessarily work against another strain of the same virus. This complicates virus resistance breeding and can result in unexpected resistance breakdown. Moreover, recombination between strains of SPFMV can be expected (Untiveros et al., 2006). A substantial number of farmer varieties in SSA appear to have resistance to SPFMV (Carey et al., 1998; Clark et al., 2012), whereas so far no resistance to SPCSV has been reported.

All sweetpotato varieties need a certain degree of resistance to SPVD and there is considerable genetic variation for this attribute (Mwanga et al., 2002b). A high resistance level to SPVD is especially needed in high virus-pressure zones of East Africa; however, this resistance level turns up in breeding populations at very low frequencies of $\leq 0.2\%$. The resistance or immunity to SPF-MV is often not clearly pronounced, although inheritance of SPFMV resistance is supposedly recessive, but dosage effects might occur (Mwanga et al., 2002b). All clones reported resistant to SPCSV (e.g. CIP-420269; Luis Salazar, Peru, 2005, personal communication) turned out not to be resistant. Under the recent Generation Challenge Programme, a high level of resistance to SPCSV was thought to be found in at least one clone, VJ08.330 (CIP-107729.9). Fortunately, this clone is self-compatible and all offspring clones evaluated so far showed the same level of resistance to SPCSV as the parent VJ08.330 (Kelvin Huamani, Peru, 2013, personal communication). This SPCSV resistance might be recessively inherited. A major problem in SPCSV resistance screening (triple antibody sandwich (TAS)-ELISA) is false negative results. The screening should be conducted by grafting on infected material in two subsequent years; the same holds if real-time PCR is used to screen for resistance to SPCSV instead of TAS-ELISA. In the field, sweetpotato virus pressure varies widely among environments and the final decision over whether a clone is resistant to SPVD takes many years. Moreover, virus symptoms observed in field evaluation are usually due to co-infections of several viruses and a SPCSVresistant clone does not need to be necessarily free of all virus symptoms. Our experience has shown that use of nitrocellulose membrane (NCM)-ELISA testing for resistance screening is not very reliable. Assuming a recessive inheritance of SPFMV and SPCSV resistance, it appears that this inheritance is modified by quantitative variation. As mentioned previously, it is quite difficult to find recessive inherited traits in autopolyploids as long as the allele frequency q in breeding populations is < 0.7. To fix recessive resistance alleles without marker assisted selection is difficult but not impossible. It requires crossing 'the best with the rest', that is crossing confirmed SPVD-resistant clones with acceptable performance as male parents with the remaining parental material as female parents. It would be extremely helpful to find a molecular marker associated with SPCSV resistance, even if it is only a dominant marker. This would save 2-3 years of evaluation trials. Such a molecular marker would be much more attractive if it was codominant, to enable distinguishing of different heterozygous genotypes. In the absence of double reduction, a recessive genotype can only segregate out from the recessive homozygous male parent (rrrrrr) if female parents carry at least three copies of the recessive resistance allele (RRRrrr). At CIP, groups were formed comprising 'truly' SPCSV-resistant and 'truly' SPCSVsusceptible clones, aiming in a first step at molecular markers that could distinguish homozygous SPCSV-resistant from heterozygous and homozygous SPCSV-susceptible genotypes.

Another approach to achieve resistance to SPVD is transgenic. The most often used approach against viruses is the so-called pathogen-derived resistance (PDR) (Latham and Wilson, 2008). Genes or parts of genes are introduced into the plant genome encoding for virus protein. The produced virus protein activates an antiviral defence system in plants and the plant is ready for defence before the virus infects the plant. Sweetpotato has been transformed with this approach for resistance to SPFMV (Okada et al., 2001), but the resistance broke down under field conditions in East Africa (Anon., 2004). Two reasons for this resistance breakdown are proposed (Kreuze et al., 2009). The first is that the plants were not modified with a gene from the locally prevalent SPF-MV strain in East Africa. The second reason could be a co-infection under field conditions with SPCSV. At least to a certain extent transgenic approaches are facing the same problems as classical breeding.

In regions with a pronounced dry season, the greatest constraints are sweetpotato weevils (Cylas formicarius elegantulus) in all parts of the tropics, Cylas puncticollis and Cylas brunneus in Africa, and Euscepes postfasciatus in the Caribbean. The weevils have a very large host plant range within the plant family Convolvulaceae (Austin, 1991). However, co-evolution between sweetpotato and *Cylas* weevils is quite short, because Cylas evolved in the Old World, with a common ancestor in Africa, and arrived with *C. formicarius* in the Americas after the discovery of the New World (Wolfe, 1991). Production losses can reach 60-100% across different regions of the world and even slightly to moderately infested storage roots are often not palatable because of bitter tastes (due to terpenoids and phenols) produced by the plant following weevil infestation (Uritaini et al., 1975; Chalfant et al., 1990; Dinh et al., 1995; Stathers et al., 2003).

In breeding for weevil resistance it is important to understand the biology as well as genetic and environmental preferences of weevils. Adult weevils start to feed on leaves shortly after planting, but this normally causes little damage. The main damage is caused by the larvae, which tunnel inside the storage root and stem (Bohlen, 1973). The biology is well documented for *C. formicarius* and to a certain extent also for E. postfasciatus (Sorensen, 2009). As plant stems enlarge, females start making holes in stems and fleshy roots near the soil surface to deposit eggs (these holes are covered by a faecal plug). On average, C. formicarius females lay about 120 eggs; whereas E. postfasciatus females are reported to deposit on average 106 eggs/month for 4-6 months and for this they prefer to use roots within 2 cm of the soil surface. The C. formicarius larvae hatch within less than 1 week, and burrow deep into stems and fleshy roots for about 2-3 weeks. After this period the larvae return to the plant surface at the soil line to pupate. The C. formicarius pupae transform into adults within 7-10 days, and these live about 2.5-3 months at higher temperatures (up to 8 months at lower temperatures). The E. postfasciatus adults live up to 6 months (laboratory observations) and do not fly. The weevils continue to feed and breed in storage roots remaining in the soil after harvest, as well as on other host plants and stored sweetpotatoes. Weevil populations increase with higher temperature, exposed storage roots, soil cracks in the dry season and length of the growing season. Sorensen (2009) lists plant attributes affecting the weevil population: (i) time needed for harvest; (ii) storage root density, dry matter and starch content; (iii) storage root depth; (iv) vine thickness; and (v) storage root chemistry. These traits could be targets for conventional breeding efforts.

Finding weevil resistance has been an objective for more than 50 years. With reference to variety releases (Appendix 1), conventional breeding has been successful in selecting weevil-resistant varieties only to a certain extent (and often this success is disputed). However, farmers in drought-prone areas clearly distinguish varieties on the basis of weevil susceptibility. For example, in Malawi it is believed that dense storage roots developed deep below the soil surface are less susceptible than less dense, moistfleshed storage roots. There are several reports of varieties with the attribute of being less affected by weevils: TIB-2532 and TIS-70357 (Lema, 1992), Tamburin Putih (Jusuf, 2002), Porto Rico (Sorensen, 2009), New Kawogo (Stevenson et al., 2009), Brazlandia Roxa (Fuentes and Chujoy, 2009), Santo Amaro

(CIP-400011; José Bienvenido Núñez, Dominican Republic, 2008, personal communication) and CIP-PZ06.120 and CIP-105058.2 (Appendix 3); for additional varieties see Appendices 1 and 2. Moreover, a number of varieties from Papua New Guinea are supposed to be less vulnerable to sweetpotato weevil (Carpena, 2009). The reduced weevil infestation of Santo Amaro is associated with the latex in the storage root skin of this variety (José Bienvenido Núñez, Dominican Republic, 2008, personal communication). Recent findings of compounds in the latex of the Ugandan variety, New Kawogo and the effect of these compounds on weevils may be of interest for breeding investment (Stevenson et al., 2009).

Weevil resistance appears to be built up by a complex of traits. It would be useful to obtain more information about each trait supposedly related to weevil resistance and its association with overall weevil resistance. Certainly the inheritance of weevil resistance is quantitative, but heritabilities of each trait related to weevil resistance may be very different. The apparent inconsistency in weevil resistance among cultivars in different seasons and locations is not surprising, given that strong genotype-by-environment interaction has been observed for weevil damage in Malawi (Felistus Chipungu, unpublished) and it must be expected that environments differ in their suitability for weevil resistance selection. Moreover, a systematic error cannot be excluded due to feeding preferences of weevils among genotypes grown in small plots.

It remains unclear if conventional breeding for weevil resistance can result in 100% resistant varieties. For decades, considerable research has focused on breeding for resistance to *Cylas* and *Euscepes* weevils (Hahn and Leuschner, 1982) and many reports indicated that these efforts have so far shown little progress (Rolston *et al.*, 1979; Mullen *et al.*, 1985; Story *et al.*, 1996; Mao *et al.*, 2001).

Transgenic approaches were suggested to achieve weevil resistance in sweetpotato because solutions to the problem using conventional breeding were not visible. Initial work focused on transformation with proteins (i.e. trypsin and cysteine proteinase inhibitors) that decrease the digestibility of sweetpotato for insects (Cipriani et al., 1999, 2001). This strategy was abandoned due to concerns regarding nutritional impact of such compounds on the human diet. Today transgenic approaches focus on toxins from Bacillus thuringiensis (Bt). Different Bt proteins have been tested on C. puncticollis and C. brunneus (Moar et al., 2007). Several gene constructs have been developed and varieties have been successfully transformed by Agrobacterium (the toxic Bt protein is expressed in the plant) (Sefasi et al., 2013). However, it appears so far that transgenic genotypes with Bt genes do not show the required resistance levels (Rukarwa et al., 2013).

The major fungal disease of sweetpotato is Fusarium wilt caused by Fusarium oxysporum f. sp. batatas, but it is only a problem under temperate or cool subtropical climates (Armstrong and Armstrong, 1958; Jones, 1969; Collins, 1977). The disease was once important in the southern parts of the USA (Clark et al., 2009); however, it is still a problem in South Africa (Thompson et al., 2011) and Korea. The pathogen can persist in soil for many years, but appropriate crop rotations reduce disease pressure. Breeding resistant varieties has been very effective in the USA (Dukes et al., 1975; Clark et al., 2009) and China (Appendix 1). Very high heritabilities have been reported for resistance to this disease (Jones, 1969; Collins, 1977). Some strains of the tobacco pathogen, F. oxysporum f. sp. nicotianae can also cause wilt in susceptible sweetpotato and a new race of F. oxysporum f. sp. batatas was reported in California (Clark et al., 1998).

Alternaria stem and petiole blight caused by *Alternaria* spp. may be found on sweetpotato in many parts of the world, and several species of *Alternaria* can infect sweetpotato (Lenné, 1991). The disease is only a problem in the African highlands where a more aggressive blight was first reported by Bruggen (1984). Both *Alternaria bataticola* and *Alternaria alternata* have been isolated from infected plants (Anginyah *et al.*, 2001; Osiru *et al.*, 2007). Disease severity varies greatly within the African highlands from minimal levels in less humid areas up to 25–50% of the plant infected elsewhere (Anginyah *et al.*, 2001). In each reported location, cultivars differ in susceptibility. High levels of tolerance or resistance are frequently found (Sseruwu, 2012). Potential varieties in Uganda are routinely screened for Alternaria blight resistance (Mwanga *et al.*, 2003, 2009; Narayanin *et al.*, 2010).

Plant-parasitic nematodes can seriously damage sweetpotato. Many nematodes have a wide host range and nematodes can spread easily among infected sweetpotato storage roots. Among the most important genera of nematodes many feed on sweetpotato (i.e. Meloidogyne, Pratylenchus, Ditylenchus, Xiphinema, Radopholus, Rotylenchulus and *Helictotylenchus*). Only a few nematode species cause significant damage to sweetpotato (Overstreet, 2009). However, production losses of sweetpotato due to these nematodes are significant and in 1987 it was estimated that these losses were about 10% globally (Sasser and Freckman, 1987). Certainly these production losses can be much higher in areas where sweetpotato is grown frequently. One country with the great diversity of nematodes on sweetpotato is Uganda (Coyne et al., 2003). The Peruvian coast is also a hotspot area of different nematodes (Mario Tenuta, Peru, 2013, personal communication). In the French Caribbean, 13 genera of nematodes were found on sweetpotatoes and wild relatives (Massese, 1969), with Rotylenchulus reniformis being the most common. In the Philippines, 13 genera and 22 species of nematodes were associated with sweetpotato (Gapasin, 1979) and the genera Rotylenchu*lus* and *Meloidogyne* were the most common (present in 80% and 15% of the samples, respectively). In Korea *Meloidogyne* sp. were found in 30-60% of the sweetpotato fields (Dongro et al., 2006); similar results were found in Kyushu (Japan) – 94% were Meloidogyne incognita (Iwahori and Sano, 2003). The major nematodes of sweetpotato found in Papua New Guinea and the Pacific were Meloidogyne arenaria, M. incognita, Meloidogyne javanica and R. reniformis (Vilsoni and Heinlein, 1982; Bridge, 1988). In the past M. incognita was considered the most important pest nematode of sweetpotato but *R. reniformis* appears to be increasing in importance (Overstreet and McGawley, 2000;

Koenning *et al.*, 2004) at least in the USA. Generally root-knot nematodes of the genus *Meloidogyne* are the most important nematodes for sweetpotato production worldwide (*M. incognita* is extremely destructive to the root system) followed by the reniform nematodes in the genus *Rotylenchulus* (Overstreet, 2009).

Species of Meloidogyne are found throughout the tropics, subtropics and in temperate zones with a short winter. The number of species in the genus Meloidogyne is very large, but the primary species damaging sweetpotato are M. incognita and M. javanica (both have a very wide host range). For *M. incognita*, there are clear host × parasite interactions (variable virulence on genotypes; Lawrence and Clark, 1986) and these have been repeatedly used to breed new resistant varieties (Martin and Jones, 1986). Many pathotypes or races have been identified in M. incognita (Sano and Iwahori, 2005). The frequencies of *M. incognita* races can differ greatly (Sasser and Carter, 1982). It is expected that the frequency of each race is changing over time so that old and new races can break resistances in sweetpotato.

There has been recurrent success in breeding for root-knot resistance against new races of *Meloidogyne* spp. (Martin and Jones, 1986). A molecular marker linked to a dominant inherited resistance gene was identified using *M. incognita* race 3 (Ukoskit et al., 1997). However, the resistance to root-knot nematode appears to be qualitatively (by one or few major genes) as well as quantitatively controlled (Mcharo *et al.*, 2005) and/or durable (Cervantes et al., 2002). An I. trifida resistance against M. incognita may be controlled by two dominant genes (Komiyama et al., 2006). The inheritance of *M. incognita* resistance by a single dominant gene might explain why root-knot nematode resistance can be easily found in hexaploid sweetpotatoes (see Overstreet (2009) for details) and incorporated into different breeding populations.

There are ten named species of *Roty-lenchulus* but only two have been found associated with sweetpotato (Robinson *et al.*, 1997): *R. reniformis* and *Rotylenchulus borealis*. The first has a wide host range and

occurs throughout the Americas, Africa, South Asia. South-east Asia and the Pacific: and *R. borealis* has a limited host range and has been found only in Europe and Africa. Differences in population development of the reniform nematode have also been reported among sweetpotato genotypes (Clark et al., 1980) but tolerance or resistance appears to occur at lower frequencies than for root-knot nematodes. Two races of R. reniformis have been described on cotton in India (Dasgupta and Seshadri, 1971a,b). Differences in R. re*niformis* populations have been observed in the USA (McGawley and Overstreet, 1995; Agudelo et al., 2005). Other nematodes that can cause local or regional problems in sweetpotato are: (i) the lesion nematode genus, Pratylenchus (Pratylenchus coffeae in Japan and China; Yoshida, 1985; Kukimura et al., 1992; Feng et al., 2000), but for Brazil, Anguiz and Canto-Sáenz (1991) reported that sweetpotato supported very little reproduction of this nematode; and (ii) stem nematodes, Ditylenchus dipsaci and Ditylenchus destructor (in China; Lin et al., 1993; Zhang et al., 2006) causing brown ring disease which is primarily a storage problem.

Drought and other abiotic stresses

Sweetpotato originates from the humid tropics in an ecosystem experiencing high average temperatures and significant rainfall. The crop disseminated into the semi-arid tropics and warm-temperate zones (Hijmans et al., 2002). For sweetpotato in Peru, where all three agroecological zones are found within a close distance, top selections in arid costal lowlands (i.e. Adriano (CIP-105228.1), Alexander (CIP 105240.1), Arne (CIP-105086.1) and Benjamin (CIP 105085.2)) clearly differ from top selections in humid tropical lowlands (i.e. Abigail (CIP-194540.5), Isabel (CIP-189153.18) and Sumy (CIP-105523.1)). However, clones adapted across agroecological zones can be found, such as Xuzhou 18, as well as clones with striking yield advantages in low-yielding environments such as SR92.499-23 (Grüneberg et al., 2005). For the underlying physiological mechanisms associated with adaptation to low-yield environments the reader is referred to Sattelmacher et al. (1994). For sweetpotato in Africa it is recognized that it is not possible to breed for adaptation across agroecological zones and for this reason CIP recommends decentralized sweetpotato breeding (Grüneberg et al., 2009b). Genotype-byenvironment studies are very limited and to conclusively show that it is not possible to breed for adaptation across the humid and semi-arid tropics strong cross-over interactions should be observed. Within the semi-arid tropics and warm-temperate zones the crop is affected by drought, flood, heat, cold and salinity. The effects of drought, flood, shade and salinity on sweetpotato were reviewed by Ravi and Indira (1999). In this contribution we will focus on the abiotic stress of drought.

A large fraction of the sweetpotato germplasm appears to be adapted to drought and exhibits adequate harvest in critical drought vears (Anselmo et al., 1988; Ding et al., 1997; Xie et al., 1998; Hou et al., 1999; Chávez et al., 2000; Wang et al., 2003; Agili, 2012). Sweetpotato clearly needs an adequate water supply at planting and for several weeks thereafter (Indira and Kabeerathumma, 1988: Nair et al., 1996: Ravi and Indira, 1996a). In the second and third months of growth, sweetpotato can tolerate moderate drought (mid-season drought) and in the fourth or fifth month can cope well with severe drought (terminal drought). Early season drought affects storage root initiation and the number of storage roots. Under typical semi-arid growing conditions, the crop requires 500 mm of water for a 4 month period (King, 1985; Onyekwere and Nwinyi, 1989; Chukwu, 1995). Assuming a storage root yield of up to 30 t/ha (33% storage root dry matter) this corresponds to a water requirement of 500 l/kg 'sweetpotato (dry)', which is clearly less compared with soybeans (2000 l/kg), rice (1600 l/kg), sorghum (1300 l/kg) and wheat (900 kg/l) (Pimentel et al., 2004). The crop yields best when irrigated at 25% available soil moisture (Hernandez and Barry, 1966; Hammett et al., 1982) – but at high soil moisture content (flood) suffers extreme yield decreases. The critical soil moisture for storage root yield decreases is around 20% available soil moisture (Hernandez and Hernandez, 1967; Chowdhury and Ravi, 1988; Indira and Kabeerathumma, 1988; Nair *et al.*, 1996).

Adaptation to drought-prone environments is achieved by drought escape and/or drought avoidance and/or drought tolerance (Blum, 1988). A proper timing of growth cycle (completion of the most sensitive developmental stages while water is abundant) is considered to be drought escape (earliness). Avoiding water-deficit stress by reducing evapotranspiration without affecting yields or with a root system capable of extracting water from deep soil layers is considered drought avoidance (reduction of water loss and/or maintenance of water uptake). Mechanisms which result in maintaining assimilation under reduced leaf relative water content are categorized as drought tolerance. Most of the supposed drought-tolerant plants cannot tolerate true drought – they escape and/or avoid drought. It appears that sweetpotato uses all three strategies to adapt to drought. There is a large genetic variability for earliness in sweetpotato (Yanfu et al., 1989). The crop appears to have an astonishingly wide root distribution and architecture and can penetrate about 2 m deep into the soil to absorb water/nutrients from deep soil layers (Weaver and Bruner, 1927; Yoshida et al., 1970). There are striking differences in rooting depth among genotypes and these appear to be correlated with the response of sweetpotato to drought (Yen et al., 1964; Noel Pallais, unpublished). Deep rooting is an attribute difficult to investigate and it can only be hypothesized that sweetpotato is as different underground as above ground. Certainly associations of canopy characteristics, water use efficiency and storage root yields under waterdeficit stress merit investigation. Droughtadapted germplasm may have distinct leaf morphology (narrow leaves) compared with regular types (broader leaves) (Francisco Vilaró, unpublished observations). Droughtadapted germplasm often has narrow leaves, erect to semi-erect growth types and reduced foliar area which could result in reduced loss of water. The two varieties Jewel (broader leaves) and Tanzania (narrow leaves) clearly differ in canopy attributes

and water use efficiency (Kelm et al., 2000). Tanzania is considered a clone well adapted to drought-prone areas and is used by CIP as a check across regions. Under water stress conditions the plant leaf water potential or leaf relative water content decreases (Sung, 1985a,b; Indira and Kabeerathumma, 1988; Chowdhury and Naskar, 1993; Ravi and Indira, 1995). Leaves permanently wilt when their water potential decreases to -1.3 MPa, and between -1.6 and -2.0 MPa the leaves senesce (Sung, 1985b; Ravi and Indira, 1995). However, at different growing stages (even early stages) the crop can recover from wilting and there are striking differences in this attribute among genotypes (Robert Laurie, South Africa, 2013, personal communication). The relative content of free amino acids, soluble sugars, ATP and chlorophyll a/b ratio appear to correlate with drought tolerance (Zhang, M.S. et al., 2004, 2005) indicating an association of these compounds with drought tolerance and overall sweetpotato drought adaptation.

Van Heerden and Laurie (2008) investigated four sweetpotato varieties (Resisto, Excel, W-119 and A15) under long-term restricted water supply and found two contrasting responses to drought. Although restricted water supply decreased leaf relative water content similarly in Resisto and A15, the negative effects on stomatal conductance disappeared with time in A15 (indicating high drought acclimation in A15). The suppression of aboveground biomass accumulation during restricted water supply was considerably lower in A15 than in Resisto – photosynthesis on a leaf area basis in A15 was not inhibited. whereas CO₂ assimilation in Resisto was inhibited and A15 yielded much better than Resisto under conditions of restricted water supply. Other clones with similar responses to restricted water supply as A15 might be Chissicuana-2, Nhacutse-5, ADMARC, Xiadlaxakau, Nwanaqtsjo, 199062.1 and TIS-2534 (Maria Andrade, Mozambique, 2013, personal communication). Most drought-tolerance related parameters are very cumbersome to determine, even for a few clones. However, a fast throughput method, in vitro screening using polyethylene glycol salt, was found to be efficient and simple enough to select for drought tolerance in sweetpotato (Agili, 2012). Agili (2012) demonstrated that salt tolerance is associated with drought tolerance in sweetpotato. Chávez et al. (2000) selected varieties with tolerance to drought, salinity, and boron for the arid Pacific coast of Peru and northern Chile. Sweetpotato is considered to be semi-tolerant to salinity (tolerant to an electrical conductivity (EC) of 4.0 dS/m in irrigation water or an EC of soil saturated extract at 6-11.0 dS/m with vield reductions of 50%; Bernstein, 1974) and also semi-tolerant to boron (saturation extract of 2 mg/l; Wilcox, 1960). However, such studies have so far only considered a small fraction of sweetpotato germplasm (i.e. anecdotal clones were observed which survived EC ≤ 25.0 dS/m after some rain on salt-prone soils in northern Peru; Roberto Quiroz, Peru, 2013, personal communication).

A further attribute required by farmers in drought-prone areas is 'vine survival' (Yanggen and Nagujja, 2005; Lebot, 2010). For example, the variety Resisto was disappearing on farms after drought years in Mozambique due to inadequate vine survival under drought stress. Genotypes with strong and thick vines (often lignified) and medium to high upper biomass production provide sufficient planting material, which has a long storability and withstands short dry spells after planting. Vine survival became a key attribute for new variety releases in Mozambique (Maria Andrade, Mozambique, 2010, personal communication). However, yield under waterlimited conditions is determined by yield potential and/or drought avoidance and/or drought tolerance - yield potential is defined as the maximum yield realized under non-stress conditions (Blum, 2005). Especially for sweetpotato it appears that many genotypes are simply not affected in the 'statistical sense' by drought because they have low yield potential (low storage root yield under non-stress conditions). Within this fraction of clones we observed two types of clones: the first not responding to water, but the second responding to non-stress water supply by increasing biomass production allocated nearly completely to foliage production (a typical clone with such a response to water is Tanzania). In breeding for areas with irregular rainfalls it may have been underestimated that drought-adapted clones need to adequately respond to rain (biomass production increases in association with HI stability such as for clones Chissicuana-2, ADMARC, Xiadlaxakau, Taca and TIS-2534: Maria Andrade, Mozambique, 2013, personal communication). The statement 'what is good under high-yielding environments is also good under stress environments' is nearly accepted as an axiom in breeding (Blum, 2005). However, how can a crop become adapted in evolution to stress if it is not grown under stress? We think that for sweetpotato and early breeding stages (see accelerated breeding scheme in section 'Breeding Methods') there is merit in investigating populations in a first selection step under stress (discarding all genotypes below the lowest acceptable value) followed by a second selection step under non-stress conditions. This can also be conducted as simultaneous selection under stress and no stress conditions so that very elegant index selection procedures (Pesek and Baker, 1969) could be applied for desired gains under abiotic stress conditions.

1.5 Breeding Methods

The breeding methods for a crop are not set in concrete. Depending on the pollination and propagation biology various options exist on how to breed a crop (Schnell, 1982). What is the pollination biology of sweetpotato? It is an open-pollinated crop propagated by cloning. For population improvement, sweetpotato should be treated as an open-pollinated crop and for variety development as a clonally propagated crop.

The general principle of breeding clonally propagated crops is to break normal clonal propagation by generating true seeds, which results in a new population and genetic variation. All subsequent propagation steps are asexual by clonal propagation in which selection is carried out (Grüneberg *et al.*, 2009a). This selection aims at a set of individuals superior to previous sets. Finally, superior clones are used to generate true seeds. This process leads to recurrent cycles of recombination and selection and results in a combination of good attributes in genotypes which appeared in different genotypes before selection. However, in the medium and long term, recurrent selection also results in generation of new genotypes with trait performance outside of the distribution range of previous populations. For the extreme forces of this process the reader is referred to the fundamental long-term breeding experiments using maize as a model crop (Dudley, 1977).

The efficiency of a breeding method is determined by the genetic gain and the time needed to achieve the genetic gain. Across several recurrent selection cycles, high genetic gains across traits can only be achieved by structuring plant breeding into two components: (i) variety development; and (ii) population improvement. Gallais (2003) proposed a new way of thinking in breeding autopolyploid crops (in addition to new information about their population genetics), a comprehensive breeding scheme comprising variety development and population improvement. Variety development aims at the selection of the best or very few best clones (maximum response to selection and complete or nearly complete exploitation of the genetic variation). Population improve**ment** aims at the selection of the 'best' parents to generate new genetic variation around an improved population mean (in practice the population mean across all traits for which the breeder desires improvement). Variety development and selection for the 'best' clone for the current needs of clients is relatively straightforward and what is the 'best' is usually best known locally on the ground. However, population improvement or identifying the best parents to create a new and better population for future selections is a challenge in sweetpotato, as it is for all other clonally propagated crops. Population improvement is indeed complex and should be carried out by an interconnection of breeders for an agrogeographic zone. It often requires more resources and capacities than small- to medium-sized breeding programmes can usually afford. Note that commercial breeding companies, especially smaller ones,

also form alliances or crossing unions for strategic population improvement. For a better understanding, details and illustrations of the importance of population improvement, consult Gallais (2003) part III: 'Population improvement and varietal development'.

In 2009, sweetpotato breeding in Africa had the opportunity through the Sweetpotato Action for Security and Health in Africa (SASHA) project, funded by the Bill & Melinda Gates Foundation (BMGF), and Alliance for a Green Revolution in Africa (AGRA) projects, funded by the Rockefeller Foundation and BMGF, to organize sweetpotato breeding programmes on the basis of comprehensive breeding (for details, see Grüneberg et al., 2009b). Sweetpotato breeding platforms were established with emphasis on population improvement providing NARS breeding programmes with improved true-seed populations (SASHA), whereas NARS breeding programmes emphasize variety development using these improved true-seed populations to select new varieties as well as better parents for their own breeding programmes (AGRA). In this way, it was possible for CIP to implement its concept of decentralized breeding in which each NARS partner maintains its independence and autonomy.

This breeding network for sweetpotato comprises four breeding platforms (at the National Crops Resources Research Institute (NaCRRI) in Uganda, the Mozambique Institute of Agricultural Research (IIAM), the Council for Scientific and Industrial Research, Crops Research Institute (CSIR-CRI) in Ghana and CIP in Peru) and 12 NARS breeding programmes (at NaCRRI, IIAM, CSIR-CRI, the Agricultural Research Council (ARC) in South Africa, the Kenya Agricultural Research Institute (KARI), the Agricultural Research Institute (ARI) in Tanzania, the Zambia Agriculture Research Institute (ZARI), the Department for Agricultural Research Services (DARS) in Malawi, the Rwanda Agriculture Board (RAB), the National Root Crops Research Institute (NRCRI) in Nigeria, the Ethiopian Institute of Agricultural Research (EIAR) and the Environment and Agricultural Research Institute (INERA) in Burkina Faso). CIP and NARS breeding programmes together aim at four strategic objectives with respect to efficiency of sweetpotato breeding methods: (i) more recombination and parents; (ii) accelerated breeding and improved allocation of breeding resources; (iii) more controlled cross breeding in addition to stepwise reduction of polycross breeding; and (iv) in the future, most likely heterosis-exploiting breeding schemes and molecular tools for sweetpotato breeding. However, by 2003, NARS in SSA had started alliances and exchanged seeds obtained in crossing blocks for strategic OFSP population improvement in the frame of the HarvestPlus programme, which were taken up and extended by SASHA in 2009. This first step towards decentralized OFSP breeding might serve today as a blueprint for South and South-east Asia.

We do not want to give the impression that sweetpotato breeding requires huge investments. Exactly the opposite is true, as can be seen from the history of sweetpotato breeding (Martin and Jones, 1986). All successful sweetpotato breeding programmes initiated in the past century such as those at Louisiana State University (LSU), North Carolina State University (NCSU), the XSPRC and NaCRRI had one characteristic in common that they intensified recombination and conducted gene-pool separation (recombination of parents adapted to local needs). The intensification of recombination is nearly an axiom for success in sweetpotato breeding. In crop evolution of sweetpotato, farmers did and still use and test sweetpotatoes derived from true seeds (e.g. by gathering planting material in the fields for the next growing season).

To use and/or care for true-seed-derived plants is regarded as one of the driving factors of the formation of sweetpotato variation in the diversity centres, such as in and around Papua New Guinea (Yen, 1974; Schneider, 1995; Fajardo *et al.*, 2002). How efficient this process is can be seen from the fact that before DARS in Malawi had no crossing blocks the breeder Felistus Chipungu collected true seeds from clones in selections from local and introduced germplasm trials and in this way selected several new varieties: Nyamoyo, Sungani, Anaakwanire, Mathuthu, Kaphulira, Chipika and Kadyaubwerere (the first two are cream fleshed and the others are OFSP). This procedure is a 'precursor' of a polycross seed nursery. In the second half of the last century, a major sweetpotato breeding advance was to establish polycrosses for clones adapted to local needs (i.e. at LSU, NCSU and NaCRRI). Polycross recombination became the standard recombination technique (Martin and Jones, 1986), except in China where due to climatic conditions quite early controlled crosses were conducted (Daifu Ma, China, 2004, personal communication). The NCSU breeding programme became the blueprint of many NARS breeding programmes in SSA.

For theoretical reasons, controlled cross breeding should be superior to polycross breeding. From the practical point of view, polycrosses must not be necessarily inferior to controlled crosses. The reason is that controlled cross breeding requires more resources (especially skilled technicians) so that usually much more true seed can be generated in polycross than controlled cross breeding, which results in higher selection intensities. The SASHA breeding network continues strong support for polycross breeding, but encourages all breeders to do more controlled cross breeding. At the current stage it is a major mistake in sweetpotato breeding to conduct no recombination or to conduct recombination with a small set of parents (< 15). It appears that the major bottleneck in sweetpotato breeding is not creating large variability for selection but improvement of the population mean from one recurrent selection cycle to the next. Thus, the number of parents and the choice of parents is the most difficult task in sweetpotato breeding.

There are two strategies to raise more good crosses/families in sweetpotato population improvement: (i) increase the respective number of parents and cross combinations; and (ii) change from polycross to controlled cross breeding. A third strategy using offspring information to select for better parents is being tested at CIP in Peru. Most programmes work with 20–30 parents in polycross seed nurseries, and thus the programme of NCSU and the recommendations of Martin and Jones (1986) are used as examples. During the past 10 years the breeding platform in Uganda, which serves East and Central African NARS,

increased the number of parents in polycross breeding from 25 to 150. This large number of parents was divided into two gene pools on the basis of simple sequence repeat (SSR) markers (David, 2012). CIP's breeding programme in Peru completely changed from polycrosses to controlled cross breeding in 2004, and two populations were formed: Jewel and Zapallo. This programme used about 200 parents per population recombined by crossing the 'best with the rest' (crossing five to eight top clones as male parents with the remaining clones as female parents) and completed in 2009 two recurrent selection cycles for each population (note not all cross combinations result in seed set). All NARS breeding programmes in Africa funded by AGRA established polycrosses and allocated at least some crossing capacity into controlled crosses. We assume that across all these sweetpotato breeding programmes the respective number of parents and cross combinations used have increased by a factor of about 15 compared with before 2003. The rationale underlying this change is solidly based on the findings of selection theory. There are two theoretical approaches to optimize number and size of crosses (Wricke and Weber, 1986): (i) 'risk minimization of raising no good crosses' (mathematical proof by Liapounoff inequality in Kendal and Stuart, 1958); and (ii) prediction of responses to selection on the basis of variance components estimations among and within families (Weber, 1979; Wricke and Weber, 1986). Both approaches result in the following recommendation: as long as there is no prior knowledge of the value of the cross (no offspring information) the number of crosses needs to be maximized and the size of a cross needs to be minimized. In other words, breeders should make as many cross combinations as possible when they do not have prior knowledge of the value of a cross. This is exactly what we did in breeding in Africa for Africa under SASHA. In the case of prior knowledge concerning a cross (e.g. offspring information due to test crosses), the breeder discards all parents from population improvement which are not good 'family makers'. This third strategy to raise more good families in population improvement could be the most efficient one and is being tested at CIP in Peru, Uganda and Mozambique (see 'Heterosis-exploiting breeding scheme (HEBS)' below).

In addition to raising more good crosses, a key factor in breeding is the time needed from the cross to variety release and the time required for one recurrent selection cycle in population improvement (selection of a new set of parents). The breeder Gerhard Röbbelen wiselv said to his students: 'There is only one breeding objective: a better variety and to come with this at least one year before the competitor.' Traditional breeding schemes for clonally propagated crops take too long; consult Grüneberg et al. (2009a) for illustrations of a traditional breeding scheme. Donors are very reluctant to invest when it takes a decade to materialize concrete outputs and to reach clients (i.e. varieties in farmers' fields). In SASHA- and AGRA-funded breeding programmes only 2 years are used for later breeding stages before entering the variety release process. The recommended allocation of the test capacity is to enter about 150-300 clones into later breeding stages and to test these in two to three environments in a first stage, and to select 20-30 clones and test these in five to six environments in a second stage using no more than two plot replications. The rationale underlying this resource allocation in later breeding stages are the findings of intensive research of the resource allocation problem by selection theory (e.g. Cochran, 1951; Hanson and Brim, 1963; Finney, 1966; Utz, 1969, 1984; Mi *et al.*, 2014) including with parameters obtained from sweetpotato (Grüneberg et al., 2004). A three-stage selection is only about 5-10% superior to a two-stage selection (at the optimum resources allocation) if $\sigma_{G\times Y}^2$ is large, which appears not to be the case in sweetpotato, at least in East Africa (Grüneberg et al., 2004). Moreover, we consider variety release testing as the third and additional selection stage. It should be noted that the optimum around the maximum response to selection is flat (for yield or an index which includes yield as a component) so that the breeder is not moving out of the flat area as long as he/ she allocates around one-third of the test capacity to the number of tested genotypes

at the first selection stage and selects 'aggressively' (8-15% of clones). The value of a variety is not only determined by yield. We have had good experiences in later breeding stages with aggregating several traits using the Elston index (Elston, 1963); for examples with sweetpotato see Grüneberg et al. (2004). The weakness of the index which is also an advantage - is that it does not attach weight to traits, but this can be relatively easily achieved (i.e. by including yield components such as HI or number of commercial storage roots into the index). However, in later breeding stages appropriate multi-trait selection procedures do not appear to be a major problem - in contrast with selection in early breeding stages and selection of new parents where multi-trait selection is very important. What remains interesting in research on selection in later breeding stages is the suitability of selection sites, for example by slope of regression lines and/or location-specific heritabilities (Mechelke, 1986), which may vary tremendously in sweetpotato breeding programmes.

Accelerated breeding scheme (ABS): The ABS targets the early stages of breeding clonally propagated crops to increase breeding efficiency. Where $\sigma_{G\times Y}^2$ is not very important, temporal variation of test environments can be replaced by spatial variation of test environments (Patterson, 1997). Thus, more locations can compensate for reduction in test years. ABS uses the simple fact that in breeding clonally propagated crops each true-seed plant is already a potential variety. An additional advantage of sweetpotato is the very short crop duration (3–5 months) and high propagation coefficient (up to 90 cuttings per plant within 3-4 months). Directly after the multiplication step of trueseed-derived plants the genotypes are tested in small 1 m row plots (three plants) in two to three environments without plot replications. All that is measured in early breeding stages in subsequent years is measured in 1 year at several environments. Different traits can be measured simultaneously and aggregated into an index or sequentially in the environments (so-called independent culling). About 150-300 clones are selected and the breeder enters these clones directly into the later breeding stages. ABS was proposed by Grüneberg *et al.* (2009a) and it is also discussed by Lebot (2010). The human and financial resources required are manageable if controlled cross breeding is applied with about 10–20 genotypes per family. However, in the case of polycross breeding with a generation of 50,000–100,000 seeds, ABS requires selection among single seed plants in the multiplication step to enter with 5000–10,000 clones into ABS.

ABS originated in 2005 by breeders under pressure by donors and by farmers calling for more adapted OFSP varieties to deliver new OFSP varieties within a few years. On the basis of the variance component estimates in later breeding stages (Grüneberg *et al.*, 2004) it was assumed that $\sigma_{G_{XY}}^2$ was also not of much importance in early breeding stages. Instead of planting A clones (1 m row plots) in only one environment, three environments were used. The results of this A clone evaluation with several environments or ABS (Table 1.9) supported an ABS as theory predicted. The ratios $\sigma_G^2/\sigma_{G\times E}^2$ were 1:2.05, 1:1.47, 1:0.45, 1:0.28, 1:1.03 and 1:0.95 for storage root yield, foliage yield and dry matter, total carotenoid, iron and zinc contents of storage roots, respectively. It was decided to select 200 clones on the basis of the Pesek-Baker index (Pesek and Baker, 1969) using the square root of σ_G^2 as the desired genetic gain and to enter these directly into later breeding stages. Similar results were obtained with the population Jewel during 2007 and the population Zapallo in 2006 and 2008 (results not presented). In April 2010 it was possible to launch four varieties together with INIA in Peru: Adriano (CIP-105228.1), Alexander (CIP 105240.1), Arne (CIP-105086.1) and Benjamin (CIP 105085.2). All these clones traced back to the population Zapallo 2006, which was crossed in 2005 and entered the field for the first time in 2006.

Using ABS in Mozambique enabled the release of 15 varieties in 2011: Amelia, Tio, Joe, Irene, Bela, Delvia, Cecilia, Ininda, Lourdes, Esther, Melinda, Erica, Jane, Namanga and Sumaia. Since 2009 several NARS breeding programmes in Africa have taken up ABS. Rapid uptake was no doubt driven by the donor, AGRA, as their 3 year grant required breeders to have advanced breeding

Traits⁵	σ_{G}^{2}	$\sigma_{\scriptscriptstyle E}^2$	$\sigma^2_{G imes E}$	N clones	N Loc	h²			
Storage root yield (t²/ha)	47.7	23.2	98.0	4,175	3	0.59			
Foliage yield (t²/ha)	237.0	52.1	349.0	4,167	2	0.58			
Dry matter content of roots (% FM)	13.94	8.18	6.22	2,709	2	0.82			
Carotene content of roots (ppm DM)	33,651	3,453	9,539	2,709	2	0.88			
Iron content of roots (ppm DM)	7.41	5.79	7.61	2,709	2	0.66			
Zinc content of roots (ppm DM)	3.10	4.63	2.92	2,709	2	0.68			

Table 1.9. Variance components^a and operative heritability for observed traits in early breeding stages of the population 'Jewel 2005' planted at three locations (Loc) in Peru (San Ramon, La Molina and Cañete) without replications in 1 m row plots.

^aVariance components: σ_{G}^{2} , genotypes; σ_{E}^{2} , environments; $\sigma_{G\times E}^{2}$, genotype-by-environment interactions; h^{2} , operational broad-sense heritability.

^bFM, fresh matter; DM, dry matter.

clones by the end of the funding period to be eligible for further funding. All East African countries that received AGRA support for sweetpotato breeding are using ABS: Kenya, Rwanda, Tanzania and Uganda. However, more experiments are still needed to strengthen this new breeding scheme approach for sweetpotato and other clonally propagated crops.

Three types of studies are used to investigate the efficiency of ABS. The first is to estimate the variance components (σ_c^2 and $\sigma_{G\times L}^2$) and corresponding heritabilities when ABS is applied in early breeding stages: $h^2 = \sigma_G^2$ / $(\sigma_G^2 + \sigma_{G \times L}^2 / L)$, where h^2 denotes operative broad-sense heritability and L the number of locations and environments (see Table 1.9). Since it is an efficiency study at least with respect to yield traits, data should be recorded for all clones (discarding clones by visual selection results in bad estimates of σ_G^2 and $\sigma_{G\times I}^2$). The second type of study on ABS efficiency is to estimate variance components $(\sigma_G^2 \text{ and } \sigma_{G\times I}^2)$ and corresponding heritabilities when ABS is applied with check clone(s) and plant the selected fraction of clones again with the same check(s) for one further breeding stage to estimate the observed response to selection relative to checks ($R_{_{\rm obs}}$ = the mean across the selected fraction relative to check(s) in year 2 minus the mean across all clones in ABS relative to check(s) in year 1). The third type of study on ABS efficiency is to estimate the

variance components (σ_{G}^{2} , $\sigma_{G \times L}^{2}$, $\sigma_{G \times Y}^{2}$, $\sigma_{G \times L \times Y}^{2}$ and σ_{ε}^{2}) and corresponding heritabilities when ABS is applied in early breeding stages with plot replications (at least two plots per location) and replant all clones in year 2 without selection at the same locations and same plot replication numbers. The first two types of studies can be managed alongside ongoing efforts in applied breeding even when data are recorded for all clones and no visual selection is applied (breeders usually do not like to measure what obviously does not merit efforts, but for efficiency studies this needs to be made). The third type of efficiency study requires considerable resources in addition to ongoing efforts – all breeders are very reluctant to replant material once discarded and often consider such work a waste of time and funds. However, the third type of study separates all variance components of genotype-by-environment interactions ($\sigma_{G\times L}^2, \sigma_{G\times Y}^2$ and $\sigma_{G \times L \times Y}^2$ from σ_G^2 and allows estimation of R_{obs} and prediction of response to selection for different breeding scenarios by model calculations. Moreover, estimates for plot error in early breeding stages are obtained, which differ from those in later breeding stages. For the time being only one thirdtype study is ongoing within the SASHA project, and soon we expect to have information concerning $\sigma_{G\times Y}^2$ and plot error in ABS.

What makes this new breeding scheme approach efficient in sweetpotato is still

speculative. We assume it is associated with early capturing of the σ_G^2 and $\sigma_{G\times E}^2$ of yieldrelated traits, especially HI and HI stability in contrasting environments. ABS is certainly very efficient for the quality traits dry matter, starch, sugars and carotene content of storage roots. Currently, CIP scientists are working on appropriate weighting factors for yield-related traits in ABS in the context of index selection. Finally, we note that by ABS very short breeding cycles can be achieved in population improvement - selected clones enter later breeding stages, but are also used as parental material for the next cycle of recombination and selection – and by working with two populations the technical workload can be balanced with respect to crossing and field capacity each year - when one population is recombined the other is in the field and vice versa. An additional advantage of ABS is that farmer participatory selection approaches (Gibson et al., 2008), which are critical for assessing client needs, can be very elegantly implemented in the ABS by conducting at one of the two to three environments the selection in cooperation with farmers. Consult Grüneberg et al (2009a) for further details.

Heterosis-exploiting breeding schemes (HEBS): The phenomenon of heterosis is well known in breeding as the increase in yield or other traits in hybrid offspring, which are significantly superior to those of the parents. In the case of sweetpotato, the frequency of heterozygosity indicates that the 'stimulus' of heterozygosity' or heterosis might be very large (Fig. 1.4). It is hypothesized that the performance of quantitative traits in autopolyploid crops, such as sweetpotato, are largely determined by heterosis (Gallais, 2003). HEBS for clonally propagated crops have been proposed by Hull (1945), Melchinger and Gumber (1998), Miles (2007) and Grüneberg et al (2009a). There are several possible reasons why HEBS have so far found no place in applied clonal breeding. The major reason is that it is difficult to estimate heterosis in clonally propagated crops, because the total magnitude of heterosis is defined by the difference between the mean of two homozygous parents and their offspring (H = F1)-(P1 + P2)/2; where F1 denotes the offspring and P1 and P2 the homozygous parents). It is illusory to develop homozygous genotypes for sweetpotato and nearly all other clonally propagated crops. Nevertheless, it is possible to determine a fraction of the full amount of heterosis in clonally propagated crops, which is the 'heterosis increment' or 'heterotic gain' by crossing two heterozygous parents and use the mid-parent-mid-offspring heterosis increment as a parameter to obtain information about the exploitable amount of heterosis. The 'heterosis increment' or 'heterotic gain' has often been used to determine the magnitude of exploitable heterosis in traditional hybrid crops when homozygous inbred lines were not available or simply too weak to be used as parents (Moll et al., 1965; Becker, 2011). The heterosis increment can also be determined by comparing intra gene-pool cross combinations (A and B) with inter gene-pool cross combinations (A × B hybrid population) – this corresponds to the classical heterosis experiment in maize by Moll *et al.* (1965).

There is no reason why the phenomenon of heterosis cannot be investigated in clonally propagated crops. For storage root yield we present an experimental cross population evaluated together with their parents and provide estimates of heterosis increments in sweetpotato (Table 1.10). The population was generated with 16 clones crossed in a factorial design using four varieties as male parents and 12 breeding clones as female parents. The field experiment was carried out at San Ramon (planting date: 15 April 2007; harvest date: 1 October 2007) and at La Molina in Peru (planting date: 15 December 2007; harvest date: 30 June 2008). Each cross combination was represented by 15-20 offspring clones. Each clone was planted in 1.5 m row plots with six plants and two plot replications per location. For many offspring the storage root yield family means were larger than the mid-parent means. Parents clearly differed in their combining ability. Heterosis increments of up to 58.7% (Wagabolige × SR02.174) were observed, and for highyielding parental combinations we also found storage root yield offspring means larger than mid-parent means (i.e. Zapallo × SR02.174). To our knowledge this is the first detailed

			Male parent						
Female parent		INIA100 (25.2)		Zapallo <u>(22.0)</u>		Wagabolige (10.9)		Tanzania <u>(23.3)</u>	
SR02.132	<u>(33.5)</u>	26.8	(-8.5%)	21.5	(-22.5%)	17.3	(-21.9%)	28.4	(-0.1%)
SR01.024	<u>(11.7)</u>	19.5	(5.6%)	20.8	(23.3%)	16.8	(48.9%)	22.5	(28.5%)
SR01.022	<u>(12.7)</u>	16.6	(–12.4%)	19.1	(9.9%)	14.2	(20.6%)	22.7	(26.0%)
LM02.082	<u>(18.4)</u>	19.4	(–11.2%)	23.9	(18.3%)	16.6	(13.4%)	23.3	(11.5%)
SR02.174	<u>(22.7)</u>	27.4	(14.7%)	28.8	(28.9%)	26.6	(58.7%)	28.2	(22.6%)
SR02.177	<u>(41.3)</u>	23.2	(–30.3%)	22.9	(–27.8%)	17.3	(-33.7%)	25.2	(–22.0%)
LM02.032	<u>(23.1)</u>	20.3	(–16.1%)	19.2	(–15.1%)	15.6	(-8.0%)	21.5	(-7.4%)
LM02.035	(13.7)	18.2	(-6.4%)	18.9	(5.8%)	15.1	(23.2%)	17.9	(-3.0%)
SR90.021	(4.6)	14.6	(-1.8%)	11.5	(-13.9%)	11.1	(43.5%)	13.1	(-6.6%)
SR01.029	(8.6)	15.0	(-11.3%)	13.8	(-10.1%)	10.9	(12.1%)	14.6	(-8.5%)
SR01.005	(11.5)	15.1	(-17.7%)	12.9	(-23.0%)	8.0	(-28.7%)	12.7	(-27.0%)
SR01.002	(32.1)	24.5	(–14.5%)	19.1	(-29.6%)	18.3	(-15.1%)	20.3	(-26.7%)

Table 1.10. Storage root yield (t/ha) of four male and 12 female sweetpotato parents (underlined), their offspring means and heterosis increments of offspring on basis of mid-parent–mid-offspring estimates^a (italics) evaluated at two locations, San Ramon and La Molina, in Peru.

^aMid-parent to mid-offspring correlation r = 0.705, Pearson's correlation coefficient, N = 48.

study of heterosis in sweetpotato and clonally propagated crops. Breeders should certainly be interested in doing more crosses of the type Zapallo × SR02.174.

To systematically increase the frequency of heterotic cross combinations, the breeder needs to work with separate gene pools and more precise mutually heterotic gene pools. CIP tested applied breeding populations, Jewel (PJ) and 'Zapallo' (PZ), in Peru to determine if they were mutually heterotic. PJ and PZ have different genetic backgrounds (origin of parental material) and have been developed independently since 2005 (no PJ clone is used as a parent in PZ and vice versa). Selected parents were tested by SSR markers and results indicated that PJ and PZ formed clearly segregated clusters and gene pools. In total, 6898 offspring clones were developed that traced back to 231 offspring derived from PJ × PZ crosses (49 PJ05 and 31 PZ06 clones). The hybrid population (PJ \times PZ) exhibited on average a mid-parentmid-offspring heterosis increment of 14% for storage root yield (dwb). We observed storage root yield (dwb) heterosis increments in > 70% of all offspring, about 25% of all offspring exhibited a heterosis increment of $\geq 26\%$, and two offspring had heterosis increments of close to 80% (Federico Diaz, Peru, unpublished). CIP considered this as a 'go decision' to start heterosis studies in the breeding platforms of Uganda and Mozambique. Moreover, CIP is continuing with the heterosis study in Peru after discarding parents found to be poor 'family makers' and/or which developed SPVD problems over time. After one reciprocal recurrent selection cycle we expect a yield jump in storage root yield (dwb) of about 30% in the next hybrid population. Such a HEBS cannot only increase the efficiency of population improvement for yield-related traits, but can also increase the efficiency of breeding for recessive inherited traits (such as resistance to SPVD and/or non-sweet sweetpotatoes) by moderate inbreeding through intra genepool recombination. However, the adoption of HEBS will clearly depend on whether breeders clearly see an advantage for their own breeding programmes.

Molecular tools for sweetpotato: Molecular tools have greatly improved our understanding about origin and centres of diversity of sweetpotato, but to date in sweetpotato applied breeding, molecular tools have not been used much. An exception is SSR markers for gene-pool subdivision, especially among parental material for breeding. Up to now expressed sequence tag (EST) sequencing has resulted in identification of about 1600 gene-based SSR markers for sweetpotato (Schaftleitner et al., 2010). Few SSR primers have been published for applied characterization of breeding material (Tumwegamire *et al.*, 2011b), but there are > 200SSR primers available for sweetpotato and about 75 SSR primers are routinely used at CIP for gene-pool subdivision and marker association studies. This set of SSRs were used to confirm gene-pool subdivision of parental material at CIP in Peru (Federico Diaz, Peru, unpublished), to characterize parental material in the Uganda breeding platform (David, 2012) and to search for potential heterotic gene pools among accessions from China, Korea and Japan held in trust at CIP (Maria David, unpublished).

With respect to experimental breeding material, several studies have used random amplified polymorphic DNA (RAPD), amplified fragment length polymorphism (AFLP) and SSR markers for genetic mapping or marker-trait associations. There are two AFLPbased sweetpotato linkage maps available for Beauregard × Tanzania crosses (Cervantes, 2006; Cervantes et al., 2008; Solis and Grüneberg, 2008) and a set of about 250 Beauregard × Tanzania clones are being processed to be available for international distribution by CIP's genebank. Marker associations have been reported for several yield, quality and resistant traits (Table 1.11), but so far none of these molecular markers have been validated and investigated for their efficiency in applied breeding material. Finally, we want to note that in early 2015, a new 4 year project called 'Genomic Tools for Sweetpotato Improvement (GTSPI)' will begin. This project will primarily focus on sequencing the *I. trifida* genome, developing high-throughput molecular marker systems such as genotyping by sequencing (GBS), developing statistical tools to process the huge amount of raw GBS data and testing genomic selection (GS) for sweetpotato. GS proposes the prediction of the performance of genotypes based on genomic data using the genomic estimated breeding values (GEBVs) approach. GS is a further extension of association mapping, but in contrast to the initial idea of association mapping by comparing different alleles of candidate genes, the basis of GS will be to associate a large number of single nucleotide polymorphisms (SNPs) and finally all sequence differences with differences in quantitative trait performance. With respect to applied breeding, GS is abandoning the idea of dividing quantitative variation into values of single quantitative trait loci (OTLs) followed by identifying candidate genes within OTLs. It is a statistical approach somewhat similar to Fisher's approach of considering quantitative variation as a result of small contributions of an infinite number of genes. This means it does not need information about genes contributing to quantitative trait performance. Theoretically, all historical information on phenotypic performance of genotypes can be used to generate GS prediction models, provided that DNA of these individuals is still available. It appears that among all the arguments in favour of GS one is missing, and that is the advantage that GS has the potential to predict many traits simultaneously. Nevertheless, the efficiency of GS has to be tested in applied breeding populations similar to that outlined above for ABS.

1.6 Released or Launched Varieties and New Breeding Material

This short but critical section provides a very condensed overview on released and launched sweetpotato varieties in the world and we focus on SSA. During 1994–2003 a total of 56 sweetpotato varieties were released in SSA (12 countries). Fifteen of these releases were OFSP. During this period, eight OFSP variety releases were made in Mozambique, but nearly exclusively with introduced varieties. During 2004-2013 a total of 89 sweetpotato varieties were released in these 12 countries in SSA and 62 of these variety releases were OFSP (Fig. 1.7). For variety releases in other regions in the world, consult Appendix 1. Predominantly grown varieties across regions and breeding material in the pipeline are listed in Appendices 2 and 3, respectively. The lists are updated on the web (http://sweetpotatobreeder.com) and on the Sweetpotato Knowledge Portal (www. sweetpotatoknowledge.org).

Trait	Population	Marker	Reference
Sweetpotato virus disease (SPVD) resistance	Tanzania × Wagabolige mapping population	Two markers, E41M33.a and E38M36.u located on linkage groups 22 and 35, respectively, were highly significant ($P < 0.0001$) for resistance to sweetpotato chlorotic stunt virus (SPCSV), and marker S13.1130 located on linkage group 6 was highly significant ($P < 0.0001$) for resistance to sweetpotato feathery mottle virus (SPFMV). The markers explained 72% (SPCSV) and 71% (SPFMV) of variation	Mwanga (2001)
SPVD resistance	47 diverse clones in a training group (15 susceptible and 15 resistant) and a validation group (14 susceptible and three resistant)	Four amplified fragment length polymorphism (AFLP) markers resulted in 100% correct classification: E33M49.202 (cag202), E33M59.168 (cta168), E33M59.110 (cta110) and E33M59.334 (cta334)	Miano <i>et al.</i> (2008)
Root-knot nematode resistance	71 progenies of the F1 single-cross population produced from parent Regal (resistant) and and Vardaman (susceptible)	One random amplified polymorphic DNA (RAPD) marker was selected: OP15 ₁₅₀₀ ; estimated recombination fraction of (0.2421 \pm 0.057) between the marker and the root-knot- nematode-resistance gene	Ukoskit <i>et al.</i> (1997)
Southern root-knot nematode resistance	48 half-sibs developed at Louisiana State University (LSU) and 54 full-sibs developed by International Potato Center (CIP) in East Africa	Five and four AFLP markers with strong associations to resistance selected in LSU and CIP populations, respectively. The markers E33M61.218 (ctg218), E33M61.227 (ctg227), E33M59.098 (cta098), E33M49.267 (cag267), E33M61.232 (ctg232) – LSU population, and E33M61.228 (ctg228), E33M49.118 (cag118), E33M49.108 (cag108) and E33M59.148 (cta148) – CIP population, resulted in 88.78% and 88.04% classification efficiency, respectively	Mcharo <i>et al.</i> (2005)
Root-knot nematode resistance	Beauregard × Tanzania mapping population of North Carolina State University (NCSU) 240 individuals	Seven significant quantitative trait loci (QTLs) in Tanzania and two in Beauregard: E32M4920, E42M6022, E46M3201, E35M4414, E32M3722, E38M4512 and E36M3811 in Tanzania and E40M6008 and E42M3525 in Beauregard; each explained 20% of the observed variation	Cervantes (2006)

 Table 1.11. Overview of molecular markers and trait association studies in sweetpotato.

Continued

Trait	Population	Marker	Reference
Storage root dry-matter content (SRDM)	Beauregard × Tanzania mapping population of NCSU 240 individuals	Eight AFLP markers in Beauregard: four regions had positive effect on SRDM associated with E35M4511 (LG B05.26, $P = 0.0247$), E32M3202 (LG B07.40, $P = 0.0098$), E40M4010 (LG B11.61, $P = 0.0138$) and E36M5408 (LG B89, $P = 0.049$); four loci with negative effect – E42M3421 (LG B01.03, $P = 0.0056$), E43M5403 (LG B1.62, $P = 0.0007$), E36M5103 (LG B11.62, $P = 0.0005$) and E34M4906 (LG B12.70, P = 0.0006). In Tanzania four markers with a positive effect – E35M3603 (LG T01.05, $P = 0.0064$), E36M3808 (LG T05.25, $P = 0.0224$), E31M3208 (LG T06.32, $P = 0.0021$) and E46M6011 (LG T07.37, P = 0.0486); and one with negative effect – E43M3524 (LG T02.07, P = 0.025)	Cervantes (2006)
SRDM	Beauregard × Tanzania mapping population of CIP 135 individuals	E40M32_309.5 (8% variation, negative effect); E41M42_449 (8.4% variation, positive effect); E39M60_204 (9.2% and 8.3% variation, positive effect); E33M60_66 (7.6% negative effect); E31M37_71 and E40M34_191 (7.7% positive effect)	Solis and Grüneberg (2008)
β-Carotene content	Beauregard × Tanzania mapping population of NCSU 240 individuals	In Beauregard, four loci linked to E43M5403 (LG B04.23), E38M3725 (LG B08.48), E36M5103 (LG B11.62) and E44M4902 (LG B12.69) were significant. In Tanzania, four loci located near E45M3611 (LG T13.74), E40M3105 (LG T13.76), E46M3901 (LG T78) and E36M4015 (LG T82) were significant	Cervantes (2006)
Total carotenoid content	Beauregard × Tanzania mapping population of CIP 135 individuals	E31M36_446 (9.7% negative), E45M37_127 (7.5% negative), E41M42_449 (7.5% negative), E42M35_70 (7.8% negative), E31M37_345 (7.5% negative), E44M36_184.5 (10.5% negative), E43M49_119 (8.8% positive)	Solis and Grüneberg (2008)
β-Carotene content	Two contrasting groups (38 clones with high and 17 clones with low β-carotene)	Nine AFLPs achieved 100% correct classification: E33M62.240 (ctt240), E33M62.347 (ctt347), E33M49.224 (cag224), E33M59.067 (cta067), E33M61.186 (ctg186), E33M61.149 (ctg149), E33M62.092 (ctt092), E33M.099 (ctg099) and E33M62.167 (ctt167)	Mcharo and LaBonte (2010)

	Table	1.11.	Continued.
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Continued

Trait	Population	Marker	Reference
Starch content	Beauregard × Tanzania mapping population of CIP 135 individuals	E41M42_449 (11.7% positive), E31M36_446 (9.6% positive), E34M51_194 (8.5% positive), E32M54_328 (7.2% positive), E40M34_191 (8.3% positive)	Solis and Grüneberg (2008)
Sucrose content	Beauregard × Tanzania mapping population of CIP 135 individuals	E40M34_191 (0.3% positive) E31M36_446 (7.3% negative), E45M60_234 and E34M51_194 (6.7% negative), E32M54_328 (9% negative), E40M34_191 (6.7% negative)	Solis and Grüneberg (2008)
Maltose content	Beauregard × Tanzania mapping population of CIP 135 individuals	E33M54_292 (7.7% negative), E40M34_303 and E42M40_138 (13.4% positive), E42M45_148 (8.7% positive), E42M35_74 (9.7% positive)	Solis and Grüneberg (2008)
Storage root yield (SRYLD)	Beauregard × Tanzania mapping population of NCSU 240 individuals	In Beauregard, four markers (E33M4213, E35M3317, E33M6104 and E41M5911) located on linkage groups B02.10, B03.14, B09.53 and B11.65, respectively, with positive effect on SRYLD. Three other regions near markers E36M3610, E36M3414 and E42M3606 on linkage groups B05.29, B07.37 and B09.54, respectively, with negative effect on SRYLD (explained approx. 12% of total variation of SRYLD). In Tanzania, four regions showed positive effect: E37M3109, E41M3217, E34M3501 and E40M3309, on linkage groups T02.10, T06.35, T07.40 and T07.41, respectively (explained approx. 10% of total variation of SRYLD). Seven markers showed negative effect: E41M3215, E42M5002, E43M5018, E37M4301, E44M4513, E32M3722 and E38M3718, on linkage groups T01.05, T02.08, T02.12, T03.18, T06.32, T07.39 and T72, respectively (explained approx. 20% of	Cervantes (2006)
SRYLD	Beauregard × Tanzania mapping population of CIP 135 individuals	variation of SRYLD) E43M60_337 and E32M54_137 (13.6% variation, positive effect); E32M54_88 (11.4% variation, negative effect)	Solis and Grüneberg (2008)

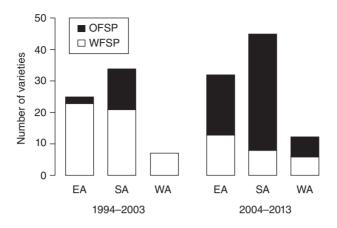


Fig. 1.7. Number of sweetpotato variety releases in SSA during 1994–2013 by subregion and flesh colour. EA, East Africa (Kenya, Rwanda, Tanzania and Uganda); SA, Southern Africa (Madagascar, Malawi, Mozambique, Republic of South Africa and Zambia); WA, West Africa (Burkina Faso, Ghana and Nigeria); OFSP, orange-fleshed sweetpotato; WFSP, white-fleshed or yellow-fleshed sweetpotato.

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Appendix 1: Released/Launched Sweetpotato Varieties

This appendix provides details about released/ launched sweetpotato varieties over the past two decades by 15 classification variables, namely: (i) country; (ii) year of release/launch; (iii) variety type; (iv) storage root flesh colour; (v) taste type; (vi) adaptation range; (vii) CIP-code; (viii) maturity time; (ix) resistance to SPVD; (x) resistance to weevil; (xi) resistance to *Fusarium*; (xii) resistance to *Alternaria*; (xiii) resistance to nematodes; (xvi) abiotic stress resistance; and (xv) comments about special uses, resistances, names or development.

Abbreviations used for classification variables for released/launched varieties

1. Country: BD, Bangladesh; BF, Burkina Faso; BR, Brazil; BU, Burundi; CN, People's Republic of China; CU, Cuba; GH, Ghana; IN, India; JP, Japan; KE, Kenya; KR, Republic of Korea; MG, Madagascar; MW, Malawi; MZ, Mozambique; NG, Nigeria; PE, Peru; PG, Papua New Guinea; PH, Republic of the Philippines; RSA, Republic of South Africa; RW, Rwanda; TL, East Timor; TW, Taiwan; TZ, Tanzania, UG, Uganda; US-NC, USA North Carolina; US-LS, USA Louisiana; ZA, Republic of South Africa; ZM, Zambia.

2. Year of release/launch: 1992–2013.

3. Variety type: BL, breeding line; FV, farmer variety; MV, modern variety; or if not available '.' for missing value.

4. Storage root flesh colour: C, cream; DO, deep orange; DPU, deep purple; DY, deep yellow; IO, intermediate orange; LO, light orange; LPU, light purple; O, orange; OY, orange yellow; PO, pale orange; PU, purple; PY, pale yellow; W, white; Y, yellow.

5. Taste type: DS, dry and starchy; HD, high dry matter; HS, high starch; HTS, high total sugars; LD, low dry matter; LTS, low total sugars; MD, medium dry matter; MDS, moderately dry and starchy; MMS, moderately moist and sweet; MSS, medium starch and sweet; MST, moist and sweet taste; MTS, medium total sugar; SD&MS, semi-dry and medium sweet; SD&SS, slight dry and semi-sweet; SS, sweet and starchy, ST, starchy taste.

6. Adaptation: CFGS, Coastal–Forest (CF) transition and Guinea Savannah (GS) of West Africa; DST, dry subtropics; HLA, highland adaptation; HRA, high rainfall areas; HST, humid subtropical; HTL, hot tropical low-lands; SGS, short grassland savannah; SSZ, Sudano-Sahelian-Zone; STDL, subtropical dry land; TDL, temperate dry land; TGS, tall grassland savannah; TRDL&RF, tropical dry land and rice field; MUMZA, mid- and upper midland zone adaptation; WA, wide adaptation; WAD, wide adaptation to dry lands.

7. CIP-code: number or if not available '.' for missing value.

8. Maturity time: EM, early maturing in months (mths); MM, medium maturing in months (mths); LM, late maturing in months (mths).

9. Resistance to SPVD: MRVD, moderate resistance to SPVD; RVD, resistant to SPVD; SVD, susceptible to SPVD; TVD, tolerant to SPVD; or if not available '.' for missing value.

10. Resistance to weevil: MRW, moderate resistance to weevils; RW, resistant to weevils; SW, susceptible to weevils; or if not available '.' for missing value.

11. Resistance to Fusarium wilt (Fusarium oxysporum): RF, resistant to Fusarium wilt; SF, susceptible to Fusarium wilt; TF, tolerant to Fusarium wilt; or if not available '.' for missing value.

12. Resistance to *Alternaria*: MRAB, moderately resistant to Alternaria blight; RAB, resistant to Alternaria blight; SAB, susceptible to Alternaria blight; TAB, tolerant to *Alternaria bataticola* stem blight; or if not available '.' for missing value.

13. Resistance to nematodes: RN, resistant to nematodes; SN, susceptible to nematodes; or if not available '.' for missing value.

14. Abiotic stress resistance: DT, drought tolerant; TMD, tolerates mild dry spells; TS, tolerant to salinity; or if not available '.' for missing value.

15. Comments about special uses, names, resistances or parental material: DC&T, direct consumption and table use; DPU, dual-purpose use as a food and feed; EBA, excellent to boil as 'ampesi'; EFB, excellent for baby-foods and FDP fortification of dairy products; EFC, excellent for fried chips; EFF, excellent for French fries; EFS, excellent form and size for fresh market; EFU, excellent for fufu; FGT&MDMF, fairly good taste and moderate dry mouthfeel boiled roots; HF, heavy foliage; IT, industrial type; IU, industrial use (starch); LA, low adoption; OP, open pollination; RFB, moderate resistance to the sweetpotato flea beetle (Chaetocnema confinis); RSSR, resistant to Streptomyces soil rot (Streptomyces ipomoeae); WADLZ, wide adaptation to dry land zones; or if not available '.' for missing value.

Table A1. Name of released/launched sweetpotato varieties from 1992 to 2013.

Americas

Peru: **Costanero** [PE 1992 MV LO MS TDL CIP-187016.2 TS.(P: DLP339 x PC_SALT87)], **Yarada** [PE 1992 MV C MS TDL CIP-187018.1 TS. .(P: DLP341 x PC_SALT87)], **Nacional** [PE 1992 MV W MST&HS TDL CIP-187003.1 TS IU (P: RCBIT-57 x PC_SALT87)], **Tacna** P[PE 1992 MV C MST TDL CIP-187019.1 TS .(P: CRBIN-15 x PC_SALT87)], **Caplina** [PE 1992 MV C MST&HS TDL CIP-187016.1 TS .(P: DLP339 x PC_SALT87)], **Atacama** [PE 1992 MV C MST TDL CIP-187020.1 TS .(P: RCBIN-17 x PC_SALT87)], **INIA-100** [PE 2001 MV DO MS TDL CIP-192033.50 SN . .(P: NCSU 240 x PC92_5NACIONAL)], **Milagrosa** [PE 2000 FV LO HS

TDL&WAD DPU], **Mejorada** [PE 2005 MV LO HS TDL&WAD DPU], **Adriano** [PE 2010 MV W HS TDL CIP-105228.1 IU(P: SR02.039, CIP-102062.2 x TANZANIA, CIP-440166)]; **Alexander** [PE 2010 MV Y HS TDL CIP-105240.1 IU (P: SR02.132, CIP-102022.3 x TANZANIA, CIP-440166)], **Arne** [PE 2010 MV O MST TDL CIP-105086.1 . RSVD (P: SR02.178, CIP-102028.3 x INA-100, CIP-102033.5)], **Benjamin** [PE 2010 MV DO MS TDL CIP-105085.2 . SVD EFS (P: SR02.177, CIP-102025.3 x INIA-100, CIP-102033.5)].

USA: Beauregard [US-LS 1986 MV O MS TDL&HTL CIP-440132 . SVD . RF . SN . RSSR&OP], Carolina Ruby [US-NC 1992 MV DO LD&MS HST RF . SN . RSSR&RFB& OP], Carolina Rose [UA-NC 1992 MV DO LD&MS HST RF . . . OP], Covington [UA-NC 2005 MV DO LD&MS HST RF . RN . RSSR&RFB&OP], Hatteras [UA-NC 2008 MV DO LD&MS HST RF . RN . RSSR&RFB&OP], Murasaki-29 [US-LS 2008 W MV HD TDL . . . RW RF . RN . RSSR&OP], NCPUR06-020 [US-NC 2012 MV PU DS&HD HST RF . SN . IT], Bonita [US-LS 2011 MV W MD TDL&HTL RF. RN . RSSR].

West Africa

Burkina Faso: **Caromex** [BF 2005 MV LO MDS SSZ CIP-440136 . MRVD (from USA)], **199062.1** [BF 2005 MV LO MS SSZ CIP-199062.1. MRVD (from PE)].

Ghana: CRI-Faara [GH 1998 MV W HD<S CFGS IITA-TIS-3017 MM(4mths) EFC&HF&DPU], CRI-Okumkom [GH 1998 MV W MD&MTS CFGS IITA-TIS-8266 MM(4mths) MRVD MRW EFC], CRI-Sauti [GH 1998 FV Y HD <S CFGS . MM(4mths) TVD TMD EFC&(also named Tanzania or Kenva from MW)]. CRI-Santom-Pona [GH 1998 MV PY HD<S CFGS IITA-TIS-84/0320 MM(4mths) EFC], CRI-Apomuden [GH 2005 MV O LD&HTS CFGS CIP-440254 EM(3-4mths) EBF&FDP&(also named amala Sundari from IN)], CRI-Hi-starch IGH 2005 MV C HD<S CFGS . MM(4mths) MRVD MRW EFC&EFU&IU&(probably Satsumahikari JP via CIP)], CRI-Oqyefo [GH 2005 FV W HD<S CFGS CIP-440163 MM(4mths) MRVD MRW . . . TMD EFC&EFUIU&HF&DPU&(also named Mugande from UG)], CRI-Otoo [GH 2005 FV PY HD&MTS CFGS CIP-440034 MM(4mths) MRVD MRW EFF&HF&DPU&(also named Mogamba from BU)]. CRI-Bohye [GH 2012 MV PO HD&MTS CFGS CIP-199062.1 MM(4mths) MRVD MRW EFC&EFU&EFF&IU]. CRI-Dadanyuie [GH 2012 MV W HD&MTS CFGS CIP-440170 MM(4–5mths) MRVD MRW EFC&EFFIU. KEMB-37/from KEI. CRI-Ligri [GH 2012 MV PY HD&MTS CFGS CIP-400004 MM(4–5mths) MRVD MRW EFC&EFF&IU&(also named CEMSA-74-228 from CU)], CRI-Patron [GH 2012 FV DY HD&MTS CFGS CIP-440034 MM(4-5mths) MRVD MRW EFC&HF&DPU&IU&(also named Mohc fromBU)].

Nigeria: NIGIB-01-1 [NG 1992 MV W HD CFGS&WA IITA-TIS-87/0087 . . TW], NIGIB-01-2 [NG 1992 MV W HD CFGS IITA-TIS-8164 DPU&(used fried & boiled)], NIGIB-01-3 [NG 1993 MV W HD CFGS IITA-TIS-2532.OP.1.13 used fried & boiled], UMUSPO/1 [NG 2012 MV LO HD&SD&MS CFGS CIP-199004.2 MM(4mths) MRVD MRW OP], UMUSPO/3 [NG 2012 MV DO MD&SD&SS GS . MM(4mths) MSVD SW (unknown clone via CIP perhaps CIP-440293)].

East Africa

Tanzania: **Mavuno** [TZ 2002 FV C DS Lake_Zone . . SSPVD . . SAB . . .], **Jitihada** [TZ 2002 FV C MDS . . EM SVD . . SAB . . LA], **Simama** [TZ 2002 FV Y DS WA . . RVD . . RAB . . .], **Ukerewe** [TZ 2002 FV Y WA . . RVD . . RAB . . .], **Sinia-B** [TZ 2002 FV C DS Lake_Zone .. SVD], **Vumilia** [TZ 2002 . Y DS . . . RVD .. RAB . . LA], **Mataya** [TZ 2010 MV Y DS . . . RVD . . RAB . . LA], **Kiegea** [TZ 2010 MV O DS . . . SVD . . SAB LA], **Ejumula** [TZ . FV O DS TGS CIP-443750 . SVD . . . MRAB, . . (landrace from Uganda)], **SPK-004** [TZ 2014 FV LO DS Lake_Zone CIP-441768 . MRVD . . MRAB . . (introduced from KE also named **Kakamega**]], **Polysta** [TZ 2014 FV C DS WA . . MRVD . . . MRAB . . (also named **Polista**)], **NASPOT-1** [TZ 2014 MV Y DS Lake_Zone CIP-191133.1 . MRVD (introduced from UG where it is SAB)].

Rwanda: **Mugande** [RW 1992 MV W DS WA . . RVD . .RAB . . .], **Kwezikumwe** [RW 1993 MV Y DS WA . . RVD . . RAB . . .], **Cacearpedo** [RW 2008 MV O MDS WA . . SVD . . RAB . . .], **SPK-004** [RW 2006 FV LO . CIP-441768 . RVD . .SAB . . (introduced from KE also named **Kakamega**)], **92-062** [RW 2004 MV O MDS WA . . SVD . . SAB . . (also named **Gihangamuhungu**)], **Ukerewe** [RW 2013 . Y DS WA . MM RVD . . RAB . . .], **2000-038** [RW 2008 . Y . . EM RVD . . RAB . . (LA in East & South RW)], **2000-040** [RW 2008 . O . . EM RVD . . RAB (LA in East & South RW)], **2000-024** [RW 2008 . Y DS . . RVD . . RAB . . (LA in East & South RW)], **RW11-17** [RW 2013 . W DS WA . MM (also named **Maryoha**)]; **RW11-1860** [RW . . W DS WA (also named **Giramata**)], **RW11-4923** [RW 2013 MV W DS WA . MM], **RW11-2419** [RW 2013 MV W DS WA . MM (also named **Izihirwe**)], **RW11-2560** [RW 2013 MV DO MDS . . MM RVD RW (also named **Terimbere**)], **RW11-2910** [RW 2013 MV O MDS . . MM RVD RW (also named **Ndamirabana**)]; **RW97-062** [RW 2013 MV DO MDS . . EM (also named **Gihungumuhungu**]].

Uganda: Bwaniule [UG 1995 FV W DS TGS CIP-440168 MM RVD MRW , RAB , DT DC&T]. New-Kawogo [UG 1995 FV W DS TSGS CIP-441743 LM RVD MRW . SAB . DT DC&T], Sowola [UG 1995 MV C DS TGS CIP-441744 EM MRVD SW . RAB . . DC&TI. Tanzania [UG 1995 FV PY DS SGS CIP-440166 MM MRVD SW . MRAB RN . DC&T], Wagabolige [UG 1995 FV W TGS CIP-440168 . RVD MRW SAB RN . .], Tororo-3 [UG 1995 FV W FV TGS . . MRVD MRW DC&T], NASPOT-1 [UG 1999 MV PY DS WA CIP-191133.1 MM MRVD SW . SAB . . DC&T], NASPOT-2 [UG 1999 MV C MDS TGS CIP-191133.2 MM RVD SW . SAB . . DC&T], NASPOT-3 [UG 1999 MV C DS TGS CIP-191133.3 LM RVD MRW RAB . . DC&T], NASPOT-4 [UG 1999 MV PY DS TGS CIP-191133.4 LM RVD MRW SAB . . DC&T], NASPOT-5 [UG 1999 MV O DS TGS CIP-191133.5 MM MRVD MRW RAB . . DC&T], NASPOT-6 [UG 1999 MV W DS TGS CIP-191133.6 MM MRVD MRW . RAB . . DC&T], Kakamega [UG 2004 FV O DS TGS CIP-441768 MM MRVD SW . MRAB . . DC&T (introduced from KE also named SPK-004)], Ejumula [UG 2004 FV O DS TGS CIP-443750 . SVD SW . MRAB . . DC&T], NASPOT-7 [UG 2007 MV O DS TGS CIP-100200.1 MM MRVD SW MRAB . . DC&T], NASPOT-8 [UG 2007 MV O DS TGS CIP-100200.2 MM MRVD SW . MRAB . . DC&T], NASPOT-9-0 [UG 2007 MV O DS TGS CIP-100200.3 MM RVD SW . RAB . . DC&T(also named Vita)], NASPOT-10-O [UG 2007 MV O DS TGS CIP-100200.4 MM RVD SW , RAB . . DC&T(also named Kabode)], Dimbuka-Bukulula [UG 2007 FV C MDS TSGS CIP-443752 EM SVD SW. MRAB . . DC&T], NASPOT-11 [UG 2010 MV C DS TSGS CIP-100201 MM RVD SW . RAB . . . (also named Tomulabula)], NASPOT-12-O [UG 2014 MV O MDS TGS . EM MRVD SW . MRAB . . DPU], NASPOT-13-O [UG 2014 MV IO MDS TSGS . MM MRVD . . MRAB . . DC&T].

Southern Africa

Madagascar: Rotra [MG 1998 MV Y . MUMZA 188004 DPU], Mahafaly [MG 1997 MV C MD MUMZA CIP-440063 MM DPU&(also called TIS-2544)], Naveto [MG 1998 MV C MD MUMZA CIP-440131 MM DPU], Mahasoa [MG 1997 MV C MD MUMZA CIP-440034 MM DPU], Riba [MG 2000 MV O LD MUMZA CIP-420027 EM DPU], Rangita [MG 2000 MV O LD MUMZA CIP-420009 EM DPU], Mavo [MG 2002 MV PY HD MUMZA CIP-400011 MM DPU], Ravo [MG 2002 MV C HD MUMZA CIP-440004 MM DPU], Mahavoky [MG 2003 MV C HD MUMZA CIP-440163 MM DPU], Mafotra [MG 2004 MV C HD MUMZA CIP-440170 MM DPU], Mendrika [MG 2007 MV O MD MUMZA CIP-199004 EM DPU&EFC], Bôra [MG 2008 MV O MD MUMZA CIP-199062.2 EM DPU&EFC], P162 [MG 2011 MV O HD . . MM DPU&(also called Zambezi)], P163 [MG 2011 MV O HD . . MM DPU&(also called Ukerewe)], P167 [MG 2011 FV O HD . CIP-443750 MM DPU&(also called Ejumula)].

Malawi: Tainon [MW 1999 . PO MS (suitable for HRA) . . SVD SW (from Asian Vegetable Research and Development Center (AVRDC), also named Tainon-57)], Mugamba [MW 1999, C SS WA., RVD TW (from CIP Nairobi, also named Mogamba)], Semusa [MW 1999 . C SS WA CIP-440034 . TVD SW. TAB. . (from CIP-Nairobi, from Cuba, also called Cemsa-74-228)], Salera [MW 2002 . W SS WA . . TVD MRW]. Zondeni [MW 2008 FV O MDS&HD (adapted high to mid-altitudes) CIP-443750 . TVD MRW (longer postharvest shelf life, MDMF, called Gloria in MZ and Ejumula in UG)], Sakananthaka [MW 2008 . C SS WA LU96/303 . TVD TW], Sungani [MW 2011 MV C SS WA BV07/009 . TVD TW (P: LU96/374 x OP)], Nyamoyo [MW 2011 MV C HS WA BV07/008 . TVD TW . . . (P: Mogamba x OP)], Mathuthu [MW 2011 MV IO MDS&HD (suitable for HRA) LU06/146 . TVD TW (sweet&MDMF, P: Mugamba x OP], Kaphulira [MW 2011 MV IO DS&HD WA LU06/428 EM TVD MRW (suitable for piece meal harvesting, sweet&DMF, P: Mugamba x OP)], Kadyaubwerere [MW 2011 MV O MDS&HD WA LU06/252 . TVD MRW (longer postharvest shelf life, sweet&MDMF, P: Mafutha x OP)], Chipika [MW 2011 MV PO SS WA LU06/527 SAB .. (suitable for the Shire Valley in medium to high temperatures, P: SPN/O x OP)], Anaakwanire [MW 2011 MV O MMS&HD HRA&(adapted in well rain fed areas) BV07/028 LM TVD MRW (recommended for children under five, sweet&MDMF, P: Ejumula x OP)].

Mozambique: 199062.1 IMZ 2000 MV IO MMS&HD WA CIP-199062.1 . . MRW (sweet&MDMF, P: SPV78.001.3 x OP, from Peru)], Caromex [MZ 2000 MV DO MD&LD WA CIP-440136 (very sweet, MDMF. P: NC-228 x NC- 234, from USA)]. CN-1448-49 [MZ 2000, IO LD WD CIP-440181, ... SW (verv sweet, MDMF, from TW)], Japon Tremesino Selecto [MZ 2000 MV LO MS&LD WA(in MZ) CIP-420009 . . SW (sweet&MDMF, P: JaponTresmesino x OP, from Peru)], Kandee [MZ 2000 MV O MS&MD WA CIP-440140. . MRW (MDMF, P: (Yellow Yam x Nancy Hall) x Porto Rico, from USA)]. LO-323 [MZ 2000, IO MS&LD WA CIP-440185 . . MRW (sweet&MDMF, from USA)], Resisto [MZ 2000 MV DO MS&MD WA CIP-440001 . . SW ... SD (very sweet & soft mouthfeel boiled roots, P: W72 x OP, from USA)], Tainung-64 [MZ 2000. O MS&LD . CIP-440189 SD (sweet&MDMF, from TW)]. Cordner [MZ 2006 . DO MD WA(in MZ) . . . MRW (very sweet&MDMF, introduced from Zimbabwe, country of origin: USA)], Persistente/MGCL01 [MZ 2006 FV DO MDS&HD (adapted to central MZ) . . . RW (very sweet&MDMF)], Amelia [MZ 2011 MV O MDS&HD (adapted to Southern-Central MZ) CIP-106768.1.. RW (FGT&MDMF. P: Mafutha-1 x OP)]. Bela [MZ 2011 MV O MDS&MD WA(in MZ) CIP-106763.5 . . RW (FGT&MDMF, P: W-119 x OP)], Cecilia [MZ 2011 MV PO MDS&MD (adapted Southern-Central MZ) CIP-106766.1 . . RW (FGT&MDMF, P: UW119 x OP)]. Delvia [MZ 2011 MV OY MDS&HD WA CIP-106771.1.. RW (FGT&MDMF. P: 105369-4 x OP)], Gloria [MZ 2011 FV O MDS&HD (adapted Central MZ) CIP-443750 . . TW (FGT& intermediate texture of boiled roots, from UG, also called Ejumula)], Erica [MZ 2011 MV PO MDS&MD (adapted to Southern-Central MZ) CIP-106763.2 . . MRW (FGT&MDMF, P: UW119 x OP)], Esther [MZ 2011 MV IO MDS&HD . CIP-106770.1 . . RW (FGT&MDMF, P: MUSG-0603 x OP)], Gaba-Gaba [MZ 2006 . DO MS&LD WA CIP-440215 . . SW (very sweet&MDMF, from TW, also called Tainung-65)], Ininda [MZ 2011 MV O MDS&HD WA CIP-106765.1.. RW (FGT&MDMF. P: Tacna-2 x OP)]. Irene [MZ 2011 MV O MDS&HD WA CIP-106764.1 . . RW (FGT&DMF, P: Kakamega-7 x OP)], Jane [MZ 2011 MV IO MDS&HD (adapted to Central-Northern MZ) CIP-106767.1 . . RW (FGT&MDMF, P: LO323 x OP)], Lourdes [MZ 2011 MV IO MDS&MD WA(in MZ) CIP-106763.6 . . RW (moderately good taste & somewhat dry mouthfeel, P: UW119 x OP)], Melinda [MZ 2011 MV LO MMS&LD (adapted to Southern & Central MZ) CIP-106763.1 . . RW (good taste & MDMF, P: UW119 x OP)], Namanga [MZ 2011 MV IO MDS&MD WA CIP-106763.3 . . RW (FGT&MDMF, P: UW119 x OP)], Sumaia [MZ 2011 MV DO MDS&MD (adapted Southern-Central MZ) CIP-106763.4 . . RW (FGT&MDMF, P: UW119 x OP)], Tio Joe [MZ 2011 MV DO MS&MD WA CIP-106769.1 . . RW (MDMF, P: MUSG-0616 x OP)]. Republic of South Africa: Ndou [ZA 2003 . C SD&MS TDL&DST 1995-13-2 EM SVD SW TF MRAB . . .]. Monate [ZA 2003 . C SD&MS TDL&DST 1989-17-1 EM SVD SW TF MRAB . . .], LetIhabula [ZA 2003 . C LD&SS TDL&DST 1985-6-3 EM SVD . SF TAB . . (high yield & guality)], Amasi [ZA 2004 . CO SD&MS TDL&DST 1985-6-3 . SVD . SF TAB . . (prone to sprouting)], Phala [ZA 2003 . C SD&MS TDL&DST 1984-2-201 . SVD . TF TAB . TMD (uniform short oblong)], Mamphenyane [ZA 2003 . C SD&MS TDL&DST 1984-10-340 . SVD . . TAB . . (thin vines)], Mokone [ZA 2003 . C SD&MS TDL&DST 1987-16-1 . SVD . TF MRAB . . (latex)], Serolane [ZA 2007 . YO D&MS TDL&DST 1998-12-3 . SVD . TF SAB . . (long roots)], Khano [ZA 2007 MV DO LD<S WA&TDL&DST 1999-6-1 . SVD . TF MRAB . . (soft skin, moist & not-sweet, P: Phala x OP)], Impilo [ZA 2008 MV LO LD TDL&DST 1998-21-1

(not widely adapted, sweet&MDMF, P: Amasi x OP)], **Purple Sunset** [ZA 2009 . . SD&SS TDL&DST 2001-5-2 . SVD . TF SAB . . (attractive roots, pre-packing)], **Isondlo** [ZA 2007 . O SD&SS TDL&DST 2000-10-7 . SVD . TF SAB . . (good keeping ability, uniform)], **Bophelo** [ZA 2011 . O SD&SS TDL&DST 2001-21-1 . SVD . TF TAB . . (uniform ovate)], **W119** [ZA . . O . WA(in RSA) CIP-440004 . RVD RW MF MAB . . (MDMF, promoted but not released, from USA)], **Mvuvhelo** [ZA 2014 . C MDS TDL&DST 1999-9-4 . SVD SW TF MRAB . . (round shape)].

Zambia: Luapula [ZM 1993 . W DS WA&HRA], Zambezi [ZM 1993 MV DO MS&MD . . . SVD SW . MRAB . SD (MDMF, P: TIS2537 x OP)], Chingovwa [ZM 1993 . C HD (widely grown on commercial base) (used as vegetable, well grown in KE, MW & MZ)], Lukulu [ZM 2003 . C MD WA . . . RVD], Lukusashi [ZM 2003 . LO MS&MD WA (medium sized roots)], Lunga [ZM 2003 . W . WA . . . MRW (high yields, prolific vine producer)], Mulungushi [ZM 2003 MV Y . HD WA], Kalungwishi [ZM 2003 . LO MRW (medium sized roots)].

South Asia

Bangladesh: **Tripti** [BD 1985 . Y MMS STDL BARI-SP-1 MM (from PH)], **Kamla Sundari** [BD 1985 . O MS STDL BARI-SP-2 MM (from ADRDC)], **Daulapuri** [BD 1988 FV W MS&HS STDL BARI-SP-3 MM (local cultivar)], **BARI-SP-4** [BD 1994 MV PO MS&HS STDL . EM&MM (TCRC hybrid)], **BARI-SP-5** [BD 1994 MV PY MS&HS STDL . EM&MM (TCRC hybrid)], **BARI-SP-6** [BD 2004 . Y MS&HS STDL CIP-440258 EM&MM (also named **Lalkothi**, from IN)], **BARI-SP-7** [BD 2004 . Y MS&HS STDL CIP-440258 EM&MM (also called **Kalmegh**, from IN)], **BARI-SP-8** [BD 2008 . Y MS&HS STDL CIP-440025 EM&MM (high yielding)], **BARI-SP-9** (BD 2008 . Y MS&HS STDL CIP-44074.2 EM&MM (high yielding)], **BARI-SP-10** (BD 2013 MV Y MS&HS STDL . EM&MM (TCRC hybrid, through OP)].

India: Rajendra Shakarkand-47 [IN 1993 MV W SS . . MM(4mths) . MRW (tolerant to Cercospora leaf spot and frost)], Kian [IN 1994 MV MM(4mths) . MRW], SreeBhadra [IN 1996 MV W MS STDL S-1010 (high yielding, seed population from IITA CHDSS-S-1010 EM-3)], SreeRethna [IN 1996 MV O SS STDL X-108-2 EM(3mths) (progeny of S-187 x SreeVardhani)], Gouri [IN 1998 MV O MS STDL 85-15 MM(4mths) . SW (progeny of H-219 x H-42)], Sankar [IN 1998 MV PY SS STDL 85-70 MM(4mths) (progeny of H-219 x S-73)], COCIP-1 [IN 1999 . Y . . . EM(3mths) . MRW (progeny of IB 90-10-20)], Rajendra Sakarkhand [IN 2001 MV EM(2.5mths) . MRW (tolerant to Cercospora leaf spot, low temp. and flood)], Konkan Aswini [IN 2000 MV EM(3.5mths) (high yielding)], Narendra Shakarkand [IN 2001 MV PY HDSS . . MM(4mths) . MRW], SreeArun [IN 2002 MV W MSS STDL RS-III-3 EM(3mths)], SreeVarun [IN 2002 MV W MSS STDL CIP-490056 EM(3mths)], Kalinga [IN 2004 MV W HDSS STDL 90/704 MM(3.5mths) (high yielding)], SreeKanaka [IN 2004 MV O MS H80/168 EM(3mths) . SW . . . (progeny of S-187 x H-633)], Goutam [IN 2005 MV W SS STDL Pol-21-1 MM(3.5mths) . MRW], Sourin [IN 2005 MV PY HDSD&SS STDL Pol-4-9 . . MRW], Kishan [IN 2005 MV PY HDSS STDL Pol-13-4 MM(4mths) . MRW], IndiraNaveen [IN 2006 MV C HDSS . . EM(3mths) . MRW (OP seeds of Sree Vardhini)], IndiraNandhini [IN 2006 MV C SS . . MM(4mths) . MRW], IndiraMadhur [IN 2006 MV O SS . . MM(4mths) . MRW], KamalaSundari [IN 2008 MV DO MDMST . . MM(4mths) . MRW (resistant to storage root rot, tolerant to leaf curl virus)].

West Pacific

Xingxiang [CN 2007 MV OY DS TDL . EM (DC&T, EFS & taste)]. Xushu-27 [CN 2010 MV W DS TDL SN DT IU], Xushu-28 [CN 2011 MV W DS TDL . EM DT DPU&(good taste)], Xuzishu-3 [CN 2011 MV PU HS TDL . EM RN . (anthocyanin extraction use)], Yanshu-25 [CN 2012 MV O MST TDL FR . RN . (DC&T, EFS & taste)], Yuzishu-7 [CN 2012 MV PU MST TDL RN . DC&T]. Republic of Korea: Yulmi [KR 1990 MV PY], Shinyulmi [KR 1991 MV PY DC&T], processing)], Yeonmi [KR 1997 MV PY DC&T], Shinhwangmi [KR 1998 MV O (DC&T & processing)], Jami [KR 1998 MV PU (processing)], Jinhonhmi [KR 1998 MV Y IU&(DC&T & starch extraction)], Shinchonmi [KR 1999 MV Y DC&T], Borami [KR 2000 MV LPU (DC&T & processing)], Shingeonmi [KR 2001 MV PY IU&(DC&T & starch extraction)], Shinjami [KR 2001 MV PU (processing)], Gogeonmi [KR 2002 MV PY (DC&T & processing)], Hayanmi [KR 2002 MV W (edible use)], Juhwangmi [KR 2002 MV DO (DC&T & processing)]. Helssimi [KR 2003 MV PY IU&(DC&T & starch extraction)]. processing)], Yeonhwangmi [KR 2005 MV DY DC&T], Matnami [KR 2006 MV Y (edible use)]. Morning-purple [KR 2007 MV Y (ornamental)], Morning-white [KR 2007 MV Y (ornamental)], Daeyumi [KR 2008 MV DY IU&(bioethanol)], Yeonjami [KR 2008 MV LPU IU&(DC&T & starch extraction)], Geonpungmi [KR 2008 MV Y DC&T], Jeonmi [KR 2009 MV PY IU&(bioethanol & starch extraction)]. Dahomi [KR 2012 MV PO DC&T].

East and South-east Asia

Indonesia: Muara Takus [ID 1995 . PO MD TRDL&RF BIS-192-Op (resistant to scab)], Cangkuang [ID 1998. PY MD TRDL&RF SRIS2260PSr75...... (medium resistant to Cercospora)], Sewu [ID 1998 . O LD TRDL&RF I1186-Daya-Op-Sr-8 (medium resistant to scab & Cercospora)], Kidal [ID 2001 . O MD . Inaswang-OP95-6], Sari [ID 2001 O MD WA MIS104-1-Op (resistance to scab)], Boko [ID 2001 . PY MD TRDL MIS-146-1 (resistance to scab)], Cilembu [ID 2003 FV O MST TRDL&RF (honey taste, good for baking)], Jago [ID 2001 . W HD&HS (adaptable to poor soil fertility) CIP-B0053-9-Op DT (good taste, recommended for flour and starch processing, adaptable to humid tropic areas with poor soil fertility)], Sukuh [ID 2001 . W . HD&DS TRDL CIP-AB94001.8 DT (good taste, recommended for flour and starch processing, adaptable to poor soil fertility)], Shiroyutaka [ID 2003 . W HD TRDL&RF Kyukei-708-13-X-S684-6 . . MRW (resistant to scab, register proposal by PT Totota Bio Indonesia)], Papua Salossa [ID 2006 . DY MD (tropical highland of Papua - up to 1000 m above sea level (asl)) MSU99051-1 . . MRW (medium resistance to scab)], Papua Pattipi [ID 2006 . PY MD (tropical highland of Papua - up to 1000 masl) CIP- BB97089-12-Op . . MRW (moderate resistant to scab)], Sawentar [ID 2006 . C HD (tropical highland of Papua - up to 1000 masl) CIP-BB97256-9-Op . . MRW (medium resistance to scab)], Beta-1 [ID 2009 . DO MST TRDL&RF MSU01015-07-Op . . MRW (medium resistance to scab)], Beta-2 [ID 2009 MV O MST TRDL&RF ... MRW (medium resistance to scab, Progeny of Kidal x CIP-BB97281-16)], Antin-1 [ID 2013 . . MD TDLRF . . . MRW . . . DT (medium resistance to scab)].

East Timor: Hohrae-1 (TL 2007 . PY HD TRDL&(suited to upland) CIP-B0053-9-Op (also named Jago in ID)], Hohrae-2 [TL 2007. Y HD TRDL&(suited to upland)], Hohrae-3 [TL 2007 . O MD TRDL&(suited to upland) CIP-BB97020.1-Op].

Oceania

Appendix 2: Predominantly Grown Sweetpotato Varieties

This appendix provides details about predominantly grown sweetpotato varieties by 14 classification variables, namely: (i) country; (ii) variety type; (iii) storage root flesh colour; (iv) taste type; (v) adaptation range; (vi) CIP-code; (vii) maturity time; (viii) resistance to SPVD; (ix) resistance to weevil; (x) resistance to *Fusarium*; (xi) resistance to *Alternaria*; (xii) resistance to nematodes; (xiii) abiotic stress resistance; and (xiv) comments about special uses, resistances, names or development.

Abbreviations used for classification variables for predominantly grown varieties

1. Country: BD, Bangladesh; BF, Burkina Faso; BR, Brazil; BU, Burundi; CN, People's Republic of China; CU, Cuba; GH, Ghana; IN, India; JP, Japan; KE, Kenya; KR, Republic of Korea; MG, Madagascar; MW, Malawi; MZ, Mozambique; NG, Nigeria; PE, Peru; PG, Papua New Guinea; PH, Republic of the Philippines; RSA, Republic of South Africa; RW, Rwanda; SB, Solomon Islands; TL, East Timor; TW, Taiwan; TZ, Tanzania; UG, Uganda; US-NC, USA North Carolina; US-LS, USA Louisiana; ZA, Republic of South Africa; ZM, Zambia.

2. Variety type: BL, breeding line; FV, farmer variety; MV, modern variety; or if not available '.' for missing value.

3. Storage root flesh colour: C, cream; DO, deep orange; DY, deep yellow; IO, intermediate orange; LO, light orange; O, orange; OY, orange yellow; PO, pale orange; PU, purple; PY, pale yellow; W, white; Y, yellow.

4. Taste type: DS, dry and starchy; HD, high dry matter; HS, high starch; LD, low dry matter; LTS, low total sugars; MD, medium dry matter; MDS, moderately dry and starchy; MMS, moderately moist and sweet; MST, moist and sweet taste; MTS, medium total sugar; SD&MS, semi-dry and medium sweet; SD&SS, slight dry and semi-sweet; SS, sweet and starchy; ST, starchy taste.

5. Adaptation: CFGS, Coastal-Forest transition and Guinea Savannah of West Africa; DST, dry subtropics; HLA, high land adaptation; HRA, high rainfall areas; HTL, hot tropical lowlands; SGS, short grassland savannah: SSZ. Sudano-Sahelian-Zone; STDL, subtropical dry land, TDL, temperate dry land; TGS, tall grassland savannah; TRDL&RF, tropical dry land and rice field; MUMZA, mid- and upper midland zone adaptation; WA, wide adaptation; WAD, wide adaptation to dry lands.

6. CIP-code: number or if not available '.' for missing value.

7. Maturity time: EM, early maturing in months (mths); MM, medium maturing in months (mths); LM, long maturing in months (mths).

8. Resistance to SPVD: MRVD, moderate resistance to SPVD; RVD, resistant to SPVD; SVD, susceptible to SPVD; TVD, tolerant to SPVD; or if not available '.' for missing value.

9. Resistance to weevil: MRW, moderate resistance to weevils; RW, resistant to weevils; or if not available '.' for missing value.

10. Resistance to Fusarium wilt (*Fusarium oxysporum*): RF, resistant to Fusarium wilt; SF, susceptible to Fusarium wilt; TF, tolerant to Fusarium wilt; or if not available '.' for missing value.

11. Resistance to *Alternaria*: MRAB, moderately resistance to *Alternaria* blight; RAB, resistant to Alternaria blight; SAB, susceptible to Alternaria blight; TAB, tolerant to *Alternaria bataticola* stem blight; or if not available '.' for missing value.

12. Resistance to nematodes: RN, resistant to nematodes; SN, susceptible to nematodes; or if not available '.' for missing value.

13. Abiotic stress resistance: RD, tolerant to drought; TMD, tolerates mild dry spells; TS, tolerant to salinity; or if not available '.' for missing value.

14. Comments about special uses, names, resistances or parental material: DC&T, direct consumption and table use; DPU, dual-purpose use as a food and feed; EBA, excellent to boil as 'ampesi'; EFB, excellent for baby-foods and FDP fortification of dairy products; EFC, excellent for fried chips; EFF, excellent for French fries; EFS, excellent

form and size for fresh market; EFU, excellent for *fufu*; FGT&MDMF, fairly good taste and moderate dry mouthfeel boiled roots; HF, heavy foliage; IT, industrial type; IU, industrial use (starch); LA, low adoption; OP, open pollination; RFB, moderate resistance to the sweetpotato flea beetle (*Chaetocnema confinis*); RSSR, resistant to Streptomyces soil rot (*Streptomyces ipomoeae*); or if not available '.' for missing value.

Table A2. Currently predominantly grown farmer varieties or modern varieties - updated on 21st May 2014.

Americas

Huambachero [PE FV LO ST TDL CIP-42265 . MRVD DPU], Jonathan [PE FV O MDS TDL&WDL CIP-420014 . MRVD], Milagrosa [PE MV LO ST TDL DPU], INIA-100 [PE MV DO MST TDL CIP-192033.50 SN . .], Mejorada [PE MV LO ST TDL&WAD DPU], Benjamin [PE MV DO MS TDL CIP-105086.1 . SVD EFS].

Covington [USA-NC MV DO LD&MS HST . . . RF . RN . RSSR&RFB&OP], Beauregard [US-LS MV O MS TDL&HTL CIP-440132 . SVD . RF . SN . RSSR&OP], Bonita [US-LS MV W MD TDL&HTL RF. RN . RSSR].

West Africa

Safaré [BF FV W DS SSZ BF-18 (very uniform shape)], Gambagre [BF FV Y DS SSZ BF-77 (very uniform shape)], Tiébelé [BF FV W DS SSZ BF-13 (very uniform shape)], Djakani [BF FV Y DS SSZ BF-75 (very uniform shape)].

Blue-Blue [GH FV Y HD<S CF (fried & boiled, low perishability, also named **Mon Ami**, Tib 2/looks like Ex-Igbariam from NG)]; **Eworleworme** [GH FV W], **Kufuor** [GH FV O ... EM(3mths) (Bawku, Upper East)].

Ex-Igbariam [NG FV Y HD<S WA ... MRW (fried & boiled, low perishability)], **Butter Milk** [NG FV Y HD<S CFGS ... MRW DPU&(fried & boiled, low perishability)].

East Africa

Bungoma [KE MV Y DS MUMZA . LM MVD . RAB . . .], Nyatonge [KE FV Y DS MUMZA . . MRVD . MRAB . . .], Marooko [KE FV C MS MUMZA . LM MRVD . MRAB . . .], Jayalo [KE FV W . MUMZA MM MRVD . MRAB . . .], Bikra-Maria [KE FV . MDS MUMZA . LM MRVD . MRAB . . .].

Mugande [RW MV W DS WA . LM RVD . RAB . . .], Kwezikumwe [RW MV . DS WA . EA RVD . RAB . . .], Gihingamukungu [RW MV O DS . EM SVD . SAB . . (also named 97-062)], Cacearpedo [RW MV O MDS WA . . SVD . RAB . . .], Gihinja [RW FV W DS (adapted to mid-altitude in RW)].

Juhudi [TZ MV C MDS . . EM RVD .RAB . . (also named Jitihada)], Polista [TZ FV W DS Lake_Zone . LM RVD . RAB . . (also named Polysta)], Ukerewe [TZ MV C_with_O DS . . MM SVD . . RSAB . . .].

Araka [UG FV W DS SGS . EM . . .MRAB . . .], **Dimbuka-Bukulula** [UG FV, W DS TSGS CIP-443752 EM SVD . MRAB . . .], **Magabali** [UG FV C DS HAA . MM . . MRAB . . .], **Tanzania** [UG FV PY DS SGS CIP-440166 EM . .MRAB . . (also named **Mwezigumu** or **Soroti** or **Mbale**)], **New-Kawogo** [UG FV W DS TSGS CIP-441743 . RVD MRW SAB . . .].

Southern Africa

Kenya [MW FV W SS WA . . . SW (poor storage shelf life, also called **Tanzania**, **SPN/O** in TZ, and **Chingovwa** in MZ & ZM)], **Zondeni** [MW FV O SS WA. . TSPVD MRW (longer postharvest shelf life, also named **Gloria** in MZ and **Ejumula** in UG)], **Semusa** [MW MV , S, WA. . TVD SW TAB . . (one of the highest yielding varieties, from CU, also named **Cemsa-74-228**)], **Mugamba** [MW . C SS WA . . RVD MRW (from CIP-Nairobi, also named **Mogamba**)].

Irene [MZ MV O MDS&HD WA CIP-106764.1 . . RW (good establishment and vigour , FGT&DMF)], Delvia [MZ MV OY MDS&HD WA CIP-106771.1 . . RW (FGT&MDMF)], Sumaia [MZ MV DO MDS&MD (adapted Southern-Central MZ) CIP-106763.4 . . RW (FGT&MDMF)], Resisto [MZ MV DO MS&MD WA CIP-440001 . . SW . . . SD (very sweet & soft mouthfeel boiled roots)], Jonathan [MZ FV O MDS WA CIP-420014 . MRVD (good establishment, good taste)], Namanga [MZ MV IO MDS&MD WA CIP-106763.3 . . RW (FGT&MDMF)], Chingova [MZ FV C MD WA . . . RW (good establishment and vigour, also called Kenya, SPN/O, Admarc and Tanzania)].

Ndou [ZA MV C SD&MS TDL&DST&(WA in ZA) 1995-13-2.....], Monate [ZA MV C SD&MS TDL& DST 1989-17-1.....], Impilo [ZA MV LO SD&SS TDL&DST 1998-21-1... TF TAB.. (uniform round elliptic)], Bophelo [ZA MV O SD&SS TDL&DST 2001-21-1.... TAB.. (uniform ovate)], Dagga [ZA MV YO SDTDL&DST CIP-199062.1.... TAB. TD (tolerant to insects, from PE].

Chingovwa [ZM FV C HD WA (commercial use, also used as vegetable, also named Kenya and Tanzania)], Lukulu [ZM MV C MD WA . RVD], Mulungushi [ZM MV Y HD WA], Red [ZM FV W HD WA].

South Asia

Sundori [BD FV W MS&HS STDL . MM (red skin, also called Lal-Alu)], Mati-Alu [BD FV W MS&HS STDL . MM (white skin, also called Sada-Alu)], Jamalpur [BD FV W MS&HS STDL . EM (white skin)].

Kanjan-Gad [IN FV C SS WA . MM(4) (high yielding, long tubers)], SreeBhadra [IN MV W MS STDL S-1010 (high yielding, seed population from IITA CHDSS-S-1010 EM-3)].

West Pacific

East and South-east Asia

Beta-2 [ID . . . WD&(adapted to fertile soils) (good plant type, mostly planted by SP farmers in East Java since 2009, widely planted in Lombok and Barru in South Sulawesi)], **Kidal** [ID (planted by SP farmers in Kuningan West Java for the last 2 years, tuber quality as good as Beniazuma)], **Sawentar** [ID (planted by SP farmers in Kuningan West Java for the last 2 years, tuber quality as good as Beniazuma)], **Sawentar** [ID (planted by SP farmers in Kuningan West Java for the last 2 years, tuber quality as good as Kidal)], **Helaleke** [ID FV W MD&MDS . W0116 LM (the most highly consumed in Papua – 84%)], **Musan** [ID FV W MD&SD&MS . W0568 LM (for pig feed – 90%, very large size of storage roots)], **Wortel** [ID FV O MST . W0017 LM (for children's food)], **Papua Salossa** [ID MV . . HLA MSU99051-1 (is growing widely in areas where was 'Dilanda Kelaparan', which was drought susceptible)], **Cilembu** [ID FV O MMS&SD&MS (called honey sweetpotato, susceptible to scab, good for baking, very popular in West Java)], **Manohara** [ID FV Y MDS WA (for paste and export to Korea and Japan)], **AC-Putih** [ID FV Y MSD (for meeting the request of local company)], **Beniazuma** [ID MV Y (processing for paste and export to JP, from JP)]; **Ayamurasaki** [ID MV PU MMS (for local market, from JP)], **Ir.Melati** [ID FV W HD (high demand for local market in Malang)], **Pak-Ong** [ID FV O LD (high demand for making tomato sauce)].

Oceania

DOY-2 [PG FV W MMS CFGS DPU&HF], SILIBO [PG FV C MS TDL&DST&CFGS DPU&HF], L-43 [PG FV O&PY MD<S CFGS TLD MM], KAISLOK [PG FV C MMS CFGS DPU&DPU], K-9 [PG FV C HD&(sweet) CFGS CIP-441101 MM DPU&HF].

Appendix 3: Breeding Material in the Pipeline for Release

This appendix provides details about breeding material in the pipeline for variety release by 13 classification variables, namely: (i) country; (ii) storage root flesh colour; (iii) taste type; (iv) adaptation range; (v) CIP-code; (vi) maturity time; (vii) resistance to SPVD; (viii) resistance to weevil; (ix) resistance to *Fusarium*; (x) resistance to *Alternaria*; (xi) resistance to nematodes; (xii) abiotic stress resistance; and (xiii) comments about special uses, names, resistances or parental material.

Abbreviations used for classification variables for breeding material in the pipeline for release

1. Country: BD, Bangladesh; BF, Burkina Faso; BU, Burundi; CN, People's Republic of China; CU, Cuba; GH, Ghana; ID, Indonesia; IN, India; JP, Japan; KE, Kenya; KR, Republic of Korea; MW, Malawi; MZ, Mozambique; NG, Nigeria; PE, Peru; PG, Papua New Guinea; PH, Republic of the Philippines; RSA, Republic of South Africa; RW, Rwanda; TL, East Timor; TZ, Tanzania, UG, Uganda; US-NC, USA North Carolina; US-LS, USA Louisiana; ZM, Zambia.

2. Storage root flesh colour: C, cream; DO, deep orange; DY, deep yellow; IO, intermediate orange; LO, light orange; O, orange; OY, orange yellow; PO, pale orange; PY, pale yellow; W, white; Y, yellow.

3. Taste type: DS, dry and starchy; HD, high dry matter; HS, high starch; LD, low dry matter; LTS, low total sugars; MD, medium dry matter; MDS, moderately dry and

starchy; MMS, moderately moist and sweet; MST, moist and sweet taste; MTS, medium total sugar; SD&MS, semi-dry and medium sweet; SD&SS, slight dry and semi-sweet; SS, sweet and starchy, ST, starchy taste.

4. Adaptation: CFGS, Coastal–Forest transition and Guinea Savannah of West Africa; DST, dry subtropics; HLA, highland adaptation; HRA, high rainfall areas; HTL, hot tropical lowlands; MUMZA, mid- and upper midland zone adaptation; SGS, short grassland savannah; SSZ, Sudano-Sahelian-Zone; STDL, subtropical dry land; TDL, temperate dry land; TGS, tall grassland savannah; WA, wide adaptation; WAD, wide adaptation to dry lands.

5. CIP-code: number or if not available '.' for missing value.

6. Maturity time: EM, early maturing in months (mths); MM, medium maturing in months (mths).

7. Resistance to SPVD: MRVD, moderate resistance to SPVD; RVD, resistant to SPVD; SVD, susceptible to SPVD; TVD, tolerant to SPVD; or if not available '.' for missing value.

8. Resistance to weevil: MRW, moderate resistance to weevils; RW, resistant to weevils; or if not available '.' for missing value.

9. Resistance to Fusarium wilt (*Fusarium oxysporum*): RF, resistant to Fusarium wilt; SF, susceptible to Fusarium wilt; TF, tolerant to Fusarium wilt; or if not available '.' for missing value.

10. Resistance to Alternaria: MRAB, moderately resistance to Alternaria blight; RAB, resistant to Alternaria blight; SAB, susceptible to Alternaria blight; TAB, tolerant to *Alternaria bataticola* stem blight; or if not available '.' for missing value. **11. Resistance to nematodes:** SN, susceptible to nematodes; or if not available '.' for missing value.

12. Abiotic stress resistance: RD, tolerant to drought; TMD, tolerates mild dry spells; TS, tolerant to salinity; or if not available '.' for missing value.

13. Comments about special uses, names, resistances or parental material: DC&T, direct consumption and table use; DPU, dual-purpose use as a food and feed; EBA, excellent to boil as 'ampesi'; EFB, excellent for baby-foods and FDP fortification of dairy

products; EFC, excellent for fried chips; EFF, excellent for French fries; EFS, excellent form and size for fresh market; EFU, excellent for *fufu*; FGT&MDMF, fairly good taste and moderate dry mouthfeel boiled roots; HF, heavy foliage; IT, industrial type; IU, industrial use (starch); LA, low adoption; OP, open pollination; RFB, moderate resistance to the sweetpotato flea beetle (*Chaetocnema confinis*); RSSR, resistant to Streptomyces soil rot (*Streptomyces ipomoeae*); WADLZ, wide adaptation to dry land zones; or if not available '.' for missing value.

Table A3. Breeding material in pipe-line for variety release in 2013.

Americas

Peru: Abigail [PE DO MDS HTL CIP-194540.5 RN . DPU&EFS(P: SR93.120 x OP)], Isabel [PE DO MDS HTL CIP-189153.18 RN . DPU& EFS(P: YM89.158 x OP)], Sumy [PE DO MS HTL CIP-105523.1 DPU&EFS(P: SR02.105 x INA100)], PZ06.120 [PE O MS HTL CIP-105058.2 . . RW . . RN . DPU(P: SR01.030 x INA100)], CIP-VJ08.330 [PE LO MS TDL CIP-107729.9 . RVD low_yields(P: PJ05.069 x DLP3163)], CIP-PJ07.057 [PE DO MDS HTL RN . DPU&EFS (P: 192131.12 x PJ05.099)].

USA: **Orleans** [US-LS O . TDL&HTL RFW . SN . RSSR], **04-175** [US-LS DO MS TDL&HTL RF RSSR], **07-146** [US-LS DO MS TDL&HTL RF . RN . RSSR].

West Africa

No breeding material in the pipeline for variety release

East Africa

Rwanda: 2002-155 [RW W DS HLA . . RVD RW RAB . . DPU], 2002-166 [RW W DS HLA RW . . RVD . RAB . . DPU], NASPOT-1 [RW C DS HLA CIP-191133.1 . RVD RWRAB . . DPU], NASPOT-9-0 [RW O MDS HLA CIP-100200.3 . RVD RW RAB . . DPU&(also named Vita)], NASPOT-10-0 [RW O MDS HLA CIP-100200.4 . RVD RW RAB . . DPU&(also called Kabode)].

Tanzania: Sekondari [TZ C DS WA . . MRVD (in TZ recorded as RAB)].

Southern Africa

Malawi: LU06/003 [MW C SS WA . . RVD RW], LU06/056 [MW C SS WA . . RVD RW], LU06/196 [MW C SS WA . . RVD RW], LU06/432 [MW C SS WA . . RVD RW].

Republic of South Africa: **Mvuvhelo** [ZA C SD&SS TDL&DST 1999-9-4 (round shape)], **2004-9-2** [ZA O M&SS TDL&DST SAB . TD (attractive roots)], **2003-23-6** [ZA O SD&SS TDL&DST (uniform, attractive skin)], **2004-9-1** [ZA O MSS TDL&DST SAB . . (uniform oblong, attractive skin)], **2004-16-1** [ZA O MSS TDL&DST SAB . . (uniform round elliptic, attractive skin)], **2002-8-2** [ZA O M&SS TDL&DST (long oblong, suitable for processing industry)].

Zambia: **Olympia** [ZM LO HD&MS WA DPU&(excellent form and size, P: V15 x OP)], **Kokota** [ZM . HD . . LM], **Twatasha** [ZM O HD WA . . MRVD (pink root skin)], **Chiwokoo** [ZM DO HD&MS WA (currently being grown by farmers, P: LUS-114 x OP)], **Kanga** [ZM Y HD WA . . .].

South Asia

Bangladesh: **BARI-SP-12** [BD O SD&DS WA CIP-440001 MM MRVD TMD (also called **Resisto**, from USA)].

India: **CO3-4** [IN W HS&MTS STDL], **CIP-440127** [IN O MDS&MTS STDL (also called **Tsurunash** or **Tsurunashi-genji**, from JP)], **CIP-440038** [IN O MS STDL IITA-TIS-2498 (high yields)].

West Pacific

China: Shang0829-1 [CN W DS&HD TDL RF], Ji-08088 [CN Y DST TDL RF . RN . (edible use, EFS & taste], Yushu-17 [SC Y DS&HD TDL RF], E3043 [CN Y MST TDL RF ... (edible use, EFS & taste)], Guangzishu-8 [CN PU DS TDL RF ... DPU(high anthocyanin, edible use)], Fushu-24 [CN PU MST TDL RF ... (EFS & taste)], Yanshu-0747 [CN PU MST TDL RF ... (edible use, EFS & taste)], Mianzishu-9 [CN PU MST TDL RF ... (high anthocyanin, high yields)], Ningcaishuf-18-1 [CN ... TDL RF ... (leaf-vegetable type, vegetable use, good taste)], Xushu-2001 [CN PU DS TDL (high anthocyanin, edible use, EFS&taste)].

East and South-east Asia

Indonesia: **BB20413.1** [ID W HD WA CIP-W0031-Op DT (recommended for low to midland, adapted to poor soil fertility)]; **Wolf366.18** [ID W HD . CIP-No.105365 DT (adapted to poor soil fertility)], **MSU-03028-10** [ID PU MD], **RIS-03063-05** [ID PU HD (tolerant to aphids, good quality storage root, good taste)].

Oceania

Papua New Guinea: 5-ML7e [PG Y DS&HD MUMZA&TDL], BL8d [PG LO DS MUMZA], NIB0801-001 [PG W MS], NIB0803-004 [PG W HD&DS MUMZA], NIB0806-017 [PG W MSS MUMZA], NIB0806-037 [PG W HD MSS MUMZA], NIB0808-026 [PG W HD&MSS MUMZA], NIB0812-005 [PG O MS MUMZA], NIB0812-018 [PG O MSS MUMZA], NIB0813-003 [PG LO MD MSS MUMZA].