

REVIEW

Cassava improvement: challenges and impacts

N. M. A. NASSAR^{1*} AND R. ORTIZ²

¹Departamento de Genética, Universidade de Brasília, Brasília, Brazil

²Centro Internacional de Mejoramiento de Maíz y Trigo (CIMMYT), Apdo. Postal 6-641, 06600 Mexico, D.F., Mexico

(Revised MS received 6 July 2006; First published online 9 November 2006)

SUMMARY

Cassava (*Manihot esculenta* Crantz) is one of the two most important food crops in sub-Saharan Africa. This area accounts for most of the root harvest worldwide, followed by Asia and Latin America – the centre of origin for *Manihot* species. In Africa and Latin America, cassava is mostly used for human consumption, while in Asia and parts of Latin America it is also used commercially for the production of animal feed and starch-based products. Cassava is regarded as a crop adapted to drought-prone environments, where cereals and other crops do not thrive, and it also grows well in poor soil. There are about 100 wild *Manihot* species, which provide an important genetic endowment for cassava breeding. Professional cassava breeding started in the 20th century and was spurred on by increasing population demands. The main breeding goals are high yield per unit area, particularly in marginal or pest-prone environments. The most notable results from cassava breeding are seen today in sub-Saharan Africa, where it has been transformed from a poor man's crop to an urban food, and in Southeast Asia, where it has changed from a subsistence crop to an industrial cash crop. Long-term research by many international and national partners has led to breeding high-yielding cassava cultivars that increased crop yields up to 40%. Manipulation of genes from wild species has led to new cultivars that resist prevailing diseases and pests, allowing the avoidance of large-scale famine in sub-Saharan Africa. Cassava improvement continues to tap genetic variation through conventional breeding (including the use of wild species) and biotechnology, because many pathogens still take their toll and occasionally epidemics affect farmer fields significantly. However, new sources of variation are needed to genetically enhance the nutritional quality of this important food crop in Africa and other areas in the tropics of the developing world.

INTRODUCTION

Cassava (*Manihot esculenta* Crantz) is cultivated throughout the lowland tropics, typically between 30°N and 30°S of the equator, in areas where the annual mean temperature is greater than 18 °C. It provides efficient carbohydrate production (de Vries *et al.* 1967; Coursey & Haynes 1970), while tolerant of low soil fertility. It is the sixth major staple crop in the world after rice, wheat, maize, potato, and sweet potato with an annual production of 185 million t (FAO 2003). Africa accounts for more than half (0.51) of the world production, whereas Asia and Latin America harvest 0.29 and 0.19, respectively. The individual

countries of Nigeria and Brazil account for about one third of the global production (Table 1).

CLASSIFICATION

Cassava is a single species, *Manihot esculenta* Crantz (syn. *Manihot utilissima* Pohl) in the family Euphorbiaceae, and $2n=36$. Some aneuploids have been reported for certain cultivars (Nassar 1978*a*; Nassar *et al.* 1996) but this is not common and polyploids are rare. Magoon *et al.* (1966) suggested that cassava was likely to be an allotetraploid. Cassava cultivars have been classified according to morphology, e.g. leaf shape and size, plant height, stem colour, petiole length and colour, inflorescence and flower colour, tuber shape and colour, earliness, and content of cyanogenic glycoside in the roots.

* To whom all correspondence should be addressed.
Email: nagnassa@rudah.com.br

Table 1. *Cassava production, area harvested and yield in Africa and selected major producer countries*

Country	Area harvested (ha)	Production (million t)	Yield (kg/ha)
Angola	575 000	5 400 000	9391
Brazil	1 687 275	23 108 076	13 695
Colombia	208 377	2 214 990	10 629
Dem. Rep. Congo	1 839 962	14 929 410	8114
Ghana	794 440	9 731 040	12 248
India	270 000	6 900 000	25 555
Indonesia	1 290 000	16 723 257	13 963
Nigeria	3 455 000	34 476 000	9978
Tanzania	660 000	6 888 000	10 422
Thailand	1 030 000	16 870 000	16 378

Source: FAO (2003).

Cyanogenic glycoside has been used to classify cassava cultivars into two major groups: the 'bitter' cultivars, in which a high level (>100 mg/kg) of the cyanogenic glycoside is distributed throughout the tuberous root; and the 'sweet' cultivars, in which the glycoside is confined mainly to the peel and is at a lower level. The flesh of sweet cultivars is therefore relatively free of glycoside, although it always contains some (de Bruijn 1971). In general, sweet cassava cultivars tend to have a short growing season, their tuberous roots mature in 6–9 months and deteriorate rapidly if not harvested soon after maturity. The bitter cassava cultivars require 12–18 months to mature and will not deteriorate greatly if not harvested for several months (Bolhuis 1966).

CONSUMPTION AND USES

Approximately 0.57 of world cassava root production is used for human consumption, 0.32 for animal feed and industrial purposes, and 0.11 is waste (Bellotti *et al.* 1999). More than 700 million people consume cassava worldwide (FAO 2003). In Africa, cassava is used principally for human consumption due to its starchy roots; the leaves are also frequently eaten. Cassava roots contain 0.25–0.36 dry matter and the techniques and methods of preparation are designed to eliminate the poisonous cyanogenic glycoside from the tuberous roots of bitter cassava.

Cassava is also used as a raw material for producing cassava starch, which is an important raw material in food processing, paper, textile and adhesive manufacturing and in the oil drilling industry. It is also a raw material for many derived sugar products, such as glucose, maltodextrines and manitol.

MORPHOLOGY, COMPOSITION AND GROWTH

Cassava is a shrub, 1–3 m height with tuberous adventitious roots. The edible fleshy portion makes up 0.8–0.9 of the tuberous root. It is composed of 0.60–0.65 water, 0.30–0.35 carbohydrate, 0.01–0.02 protein, 0.000–0.002 fat, 0.01–0.02 fibre and 0.010–0.015 mineral matter of the tuberous root flesh (Nassar 1986; Nassar & Costa 1977; Nassar & Dorea 1982). The protein of cassava tuberous roots is rich in arginine but low in methionine and lysine. It seems that there is a relatively large amount of non-protein nitrogen in the tuberous root, so protein content estimated from nitrogen analysis tends to be higher than that estimated from amino acids. Some of this non-protein nitrogen originates from glycosides. Hence, caution must be taken when selecting high protein content cultivars, as it is possible that they are no more than high glycoside content cultivars (Nassar & Dorea 1982).

Stems, when planted, produce sprouts and adventitious roots within 1 week. Seeds are slow germinating and normally dormant. Scarifying the seed and filing the micropylar end does not break dormancy. The best treatment is thermal, i.e. temperatures of 18 °C for 16 h and 26 °C for 8 h to achieve seed germination (Nassar & Teixeira 1983). Seedlings ensuing from sexual seed are normally weaker than those from cuttings.

Cassava is indigenous to the lowland tropics, requiring a warm (25–29 °C), moist climate. It grows poorly in cold climates and growth ceases at temperatures below 10 °C. The plants grow best when rainfall is 1000–1500 mm per annum, but can survive when rainfall is as low as 500 mm p.a. When moisture availability is low, the cassava plant ceases growth and sheds some of its older leaves. When moisture becomes available, the plant resumes growth and

produces new leaves. The ideal soil for cassava is a light, sandy loam soil of medium fertility and with good drainage. On clay or poorly drained soil, growth is generally poor. Cassava can grow and yield well on soils of low fertility, where production of most other crops would be uneconomical. However, on highly fertile soil, cassava produces excessive vegetation at the expense of root formation. Cassava tuberous root formation is controlled by photoperiod. Under short day conditions it occurs readily, but at a day length of 12 h its growth is delayed and yield reduces (Bolhuis 1966). Vegetative growth and leaf area approach a maximum within 5 months (Williams & Gazhali 1969). The root enlarges, with deposits of starch accumulating by the eighth week after planting. The thickening of roots stops after 7–9 months in most cultivars (Beck 1960).

Cassava is usually harvested after 1 year, but can also be harvested after 2 years. However, because of its perennial nature it continues to grow for several years if left in the ground. Ffoulkes & Preston (1978) proposed that high yields of foliage might be obtained if cassava was managed as a semi-perennial crop with repeated harvesting of the foliage at 2–3 month intervals, and showed in the Dominican Republic that the fresh foliage could be used as a source of protein and for supplementing a liquid diet of molasses-urea for cattle.

REPRODUCTION

The flowers are monoecious. In each panicle a few basal pistillate flowers are protogynous. The staminate flowers are apical and numerous and open 2 weeks later. The plant is typically allogamous and consequently highly heterozygous. Sporadically, in certain environments, the male and female flowers of different plants open at the same time, and since plantations consist of only one clone, self-pollination occurs. Seed obtained from such pollination is considered partially inbred and would produce plants with reduced heterozygosity. Some such seed may drop and germinate in the next season. If this process were to be repeated for several generations it would change the genetic nature of the crop, shifting it from a highly heterozygous to a more inbred genotype (Nassar & O'Hair 1985). This observation was supported by Pereira *et al.* (1981), who worked with non-segregating progeny from Brazilian clones Guaxupe and Mantequeira.

Pollination is by insects and a survey by Nassar & Carvalho (1990) found various Hymenoptera and Coleoptera species effective, but honeybees (*Apis mellifera*) were the principal pollinator (about 0.7 of flowers). Outcrossing is therefore predominant and can be total, as demonstrated by using morphological markers in the progeny. A proportion of inbreeding, however, does exist (Pereira *et al.* 1981). Pollen varies

in fertility from almost sterile to 0.95 fertile. Pollen viability is reduced to about half the day after opening, and is lost after 2 days. Female flowers open 11 am to noon. Receptivity of the stigma occurs 6 h before flower opening.

Apomixis has been reported in cassava and the gene controlling this trait has been transferred from the wild to the cultivated species (Nassar 1994, 2000*a,b*, 2001; Nassar *et al.* 1998*a,b*). Farmers normally practice reproduction of cassava from cuttings, which leads to accumulation of viral and bacterial diseases that reduce productivity and may cause loss of superior genotypes. Stems produced through apomixis from a contaminated clone are free from viral and bacterial pathogens and can begin a new cycle of clonal life. Thus, the use of apomictic plants in propagation might lead to the avoidance of systemic pathogens and might assure preservation of superior clones. The use of apomixis for preserving superior genotypes also benefits international cassava programmes that routinely export their germplasm.

PATHOGENS AND PESTS

Many pathogens and pests reduce cassava yields, especially in Africa (Dixon *et al.* 2003; Oerke 2006). Diseases such as cassava mosaic disease (CMD), transmitted by a whitefly (*Bemisia tabaci*) vector and spread by infected cuttings, cassava brown streak virus disease (CBSD), bacterial blight (*Xanthomonas axonopodis* pv. *manihotis*), and anthracnose (*Colletotrichum gloeosporoides*) are among the most important diseases. Pests with a wide African spread are the cassava mealybug (*Phenacoccus manihoti*), African root and tuber scale (*Stictococcus vayssierei*), cassava green mite (*Mononychellus tanajoa*) and nematodes (particularly *Meloidogyne* spp.). Cassava breeders are broadening the genetic base and plant health researchers are using biological control and other crop protection options in order to continue to ensure food security in many tropical areas where this crop remains as the main staple.

WILD MANIHOT SPECIES

Relatives of cassava are perennial and vary in growth pattern from nearly acaulescent sub-shrubs to small trees. Decumbent sub-shrubs, semi-herbaceous sub-shrubs, shrubs and small trees are included in the genus (Rogers 1963). Many of the species are lactiferous, and some species, particularly *M. glaziovii*, have been grown (e.g. in Brazil and Nigeria) for rubber production (Rogers 1963, 1965). Many species, such as those in the group *tripartita* have stems adapted to marked dry periods, die back regularly to a root crown and shed their leaves during the dry season. Some species are found on limestone-derived and well-drained soils.

Most species are monoecious and a few are dioecious. Many species are protogynous and pollination is by insects. The formation of a large number of species has resulted from polyploidy, partial apomixis and weak pollination incompatibility (Nassar 1999, 2000*b*; Nassar *et al.* 2000).

All species of the genus *Manihot* are native to South America, particularly Brazil (Nassar 1978*c*, 1992*b*). The species of *Manihot* are all rather sporadic in their distribution and rarely become dominant over the local vegetation. The majority of species are found in relatively dry regions. Their typical habitats are forest clearings, as in the case of *M. anomala*; they are typically heliophiles growing only in the absence of shading. Many, such as *M. pohlii*, *M. zehntneri* and *M. grahamii*, are weedy types capable of invading newly disturbed areas. Many *Manihot* species are found on limestone-derived and well-drained soils. Almost all of the species are damaged by frost except, for example, *M. grahamii* and *M. neusana*, whose native distribution lies in regions with occasional frost.

Wild *Manihot* species can be used as a source of useful traits (Nassar 1978*d,e*, 1986). Use of the wild parent *M. oligantha* has produced a hybrid with increased root protein content (Nassar & Dorea 1982), which reached 0.04 of peeled roots (double that of common cassava), combined with low cyanide content (90 mg/kg) (Nassar 1978*a, b*). Apomixis was also transferred successfully from the wild species *M. neusana* (Nassar 2000*b*; Nassar *et al.* 2000). Important traits present in *M. glaziovii* can be incorporated into common cassava through interspecific hybridization (Nassar *et al.* 1995; Nassar 1997). Such interspecific hybrids can be polyploidized to restore fertility for further use in cassava breeding (Nassar & Freitas 1997).

High yielding cassava clones ensued from interspecific hybridization with wild species such as *M. glaziovii*, *M. pseudoglaziovii* and *M. cearulescens*. The resulting hybrid clones yielded three to four times more tuberous roots than common cultivars, and some of these hybrid clones showed longer vegetative growth.

CROP DIVERSITY

In general, cassava genetic diversity is shaped by both environmental and human factors. Genetic diversity within crops depends on farming practices, for example how long it takes for a farmer to change to planting a new cassava type and how many stems the household has in stock. Some farmers plant cassava every day for a week and then stop for 2–3 months. As a result, several months can separate the youngest and the oldest plants in a single farm system.

Human selection for productivity may reinforce natural selection (Salick *et al.* 1997). Stem cuttings of

cassava are widely exchanged between farmers of different villages, so a cultivar lost in one farm may be available elsewhere (Salick *et al.* 1997).

Cassava genetic diversity is enhanced by occasional natural crossing between types of cassava that have similar phenotypes (Nassar 1979*a*).

WILD RELATIVES AND WEEDINESS

Because of weak crossing barriers, hybridization can occur between plants of cassava and adjacent wild *Manihot* species. A large number of wild relatives are weedy types, i.e. they invade disturbed habitats. The progeny of such hybridization is a complex of cassava and wild species (such as *M. tipartita*, *M. nomala*, *M. zenerneri* or *M. grahamii*). These species complexes behave as weeds and can be detected in the margins of cassava plantations if these are near wild relatives. Over time, these hybrids develop into new weedy species. A number of new wild *Manihot* species could evolve as a result of chance hybridization between cassava cultivars and local relatives. The stability of these wild species is low. However, over time many phenotypic variations develop and could easily expand the species boundaries.

GENETIC ENHANCEMENT

For many years in the last century, clonal selection was the predominant method for cassava improvement at national centres in Africa and Brazil. The only exception was the pioneering work of Storey & Nichols (1938) in Amani (Tanzania), where they hybridized the wild species *M. glaziovii* with cassava to produce clones resistant to Cassava Mosaic Disease (CMD). Their work saved the whole of East Africa from this disease, which arrived there in the 1920s. Their hybrid clones were not only resistant to CMD but also productive and tolerant to drought (Otim-Nape 1993). They are still maintained at Amani and have been used by breeders of the International Institute of Tropical Agriculture (IITA, Ibadan, Nigeria) as a source for resistance to CMD, first in West Africa and later throughout the whole continent. Extensive testing and selection through several steps remains as the main breeding method after the initial cross to generate useful genetic variation in the population source (Phillips & Wolf 2005).

In the 1950s, Normanha Santana and Araken Soares of the Instituto Agronomico de Campinas (IAC, Brazil) began their programme by identifying the parental sources of new cultivars, which were selected on the basis of their productivity and resistance to diseases and insects. They carried out comprehensive tests of combining ability among clones collected from Sao Paulo and Minas Gerais. In these areas, wild species of *Manihot* normally grow in close proximity to cultivated cassava clones and natural

interspecific hybridization frequently occurs between them (Nassar 1984, 1989). Progeny seedlings of these natural crosses grow simultaneously and some of them are selected by farmers and reproduced vegetatively, giving rise to new clones. These clones grow in commercial plantations and are subject to selfing and inbreeding due to the monoclonal system of plantations (Nassar & O'Hair 1985). Emerging homozygous plants will have genes of wild species introgressed to their genomes. This cycle of hybridization is repeated in nature and inbred clones are enriched by highly adaptive genes of wild species brought to cultivation by farmers. These clones were the type collected by IAC breeders and used in their combining ability trials. Among them were the most successful clones ever known in the history of cassava in Brazil: Branca Santa Caterina and Engana Ladrao.

In the process of releasing new cultivars, IAC breeders established performance trials of root yield under suboptimal soil environments and mineral nutrition to broaden the scope of cultivar adaptation. This combining ability approach to production of superior progeny was highly effective and brought the State of Sao Paulo to the highest world yield levels in the 1960s, reaching 23 t/ha.

In the 1970s, the Centro Internacional de Agricultura Tropical (CIAT, Cali, Colombia) started cassava breeding with the aim of extending the benefits of the Green Revolution to the less privileged growers of cassava in Latin America and Asia. After 35 years, many cultivars have been released in many countries, mainly in Asia (Kawano 2003). However, cassava breeding for Latin America seems to have achieved only limited success, e.g. cassava yield in Colombia in 2003 was just above 10 t/ha – the same as in the early 1980s. Yield reduced in the whole continent from 13.8 t/ha in the 1960s to 12.8 t/ha in the 1990s (FAO 2003).

Nagib Nassar began a cassava genetic enhancement programme at the Universidade Federal de Goiás (Brazil) in 1974, continued at the Universidade de Brasília (Brazil) in 1979, aiming to utilize wild cassava for the improvement of cultivated cassava. Wild *Manihot* species were collected from South America and Mexico, thoroughly evaluated and hybridized with cultigens in order to incorporate their useful genes for high protein content, apomixis, tolerance to drought, resistance to bacterial blight and high yield into cultivars (Nassar 1979*b*, 1980, 1992*a*, 1994, 1997, 1999). To hybridize these species with the cultigen, interspecific barriers were overcome, and seed dormancy was broken using different methods and techniques (Nassar 1980; Nassar & Teixeira 1983; Nassar *et al.* 1996) that allow incorporation of useful genes into the ensuing hybrids (Nassar 1994, 1997; Nassar *et al.* 2000). Genetic enhancement produced trisomics, as well as triploid and tetraploid hybrid clones (Nassar 1992*a*; Nassar *et al.*

1996). Nassar shared the interspecific hybrids and other wild species with IITA cassava breeder Dr Sang Ki Hahn, who used this germplasm source to breed high-yielding TMS cultivars. Such cassava cultivars represent an important contribution to Africa's food security, especially among the poor (Nweke *et al.* 2002).

At the Central Tuber Crops Research Institute, India (CTCRI), scientists produced the highest world yields of cassava. There were trials of combining ability (Anonymous 1989; Rajendran *et al.* 2000). It is impressive that productivity of cassava in India increased from 7.2 t/ha in 1961 to 26.9 t/ha in 2000, while in South America cassava yield dropped from 13.8 t/ha to 12.8 t/ha in the same period (FAO 2003).

UNVEILING THE NEW AFRICAN CASSAVA

When Hahn arrived in Ibadan in 1971 to establish a root and tuber improvement programme at IITA, he recognized that no amount of research effort would increase cassava yields until the problem of cassava mosaic virus disease was solved. He recognized the enormous implications of an endemic disease aggravated by humans through the use of diseased cuttings, and he focused cassava research tightly on this disease problem. Together with Eugene Terry, Hahn began the arduous task of searching the germplasm for resistance characters and then combining those characters with lines having desirable yield and quality factors. Fortunately, Hahn had access to the mosaic resistant plant families developed from A. J. Storey's work in East Africa nearly 30 years before and that of Brian Beck at the Moor Plantation in the 1950s. However, these plant families had very poor root yields. He also brought cassava germplasm from Asia and South America. The latter incorporated wild *Manihot* genes that were initially bred by Nassar. It remained the IITA team's task, ably assisted by Audrey Howland, an outstanding breeding research associate, to cross, select, clone, challenge, rogue, and select, beginning each season with up to 10 000 seedlings, until the desired level of resistance was incorporated into 'elite' IITA cassava breeding materials.

The same IITA team made equally successful progress against cassava bacterial blight (Hahn *et al.* 1980). The IITA root and tuber improvement programme can now turn to research to increase yields in a broad range of agro-ecological zones and cultivation systems, to suit a wide variety of consumer preference. Deployment of this material in many African locations had a great impact (Dixon *et al.* 2003). In the 1990s, African programmes incorporated IITA-bred materials in 0.8 of their cassava-bred germplasm that led to gains in cassava yields of, on average, 0.5 (Manyong *et al.* 2000). The improved

Table 2. *Economic impact assessment of biological control of cassava pests in Africa*

Pest species	Year of first occurrence	Loss (%)	Successful biological control agent	Start of campaign	Redress (% reduction in loss)	Savings (US\$ million)	Discount rate (%)
Cassava mealybug	1973	40	The encyrtid wasp <i>Anagyris lopezi</i>	1981	90–95	7971–20 226 ¹	6
Cassava green mite	1971	35	The phytoseiid mite <i>Typhlodromalus aripo</i>	1983	80–95	2157 ²	10

¹ Based on 27 countries in Africa, depending on scenario.

² For Nigeria, Ghana, Benin.

Source: Neuenschwander (2004).

cultivars raised per capita output by 0.1 continent-wide, benefiting 14 million farmers.

BIOLOGICAL CONTROL OF CASSAVA PESTS

In the first 15 years of IITA, resistance breeding was the most frequently used method for combating disease and insect pests, as shown by the examples provided above. Since the late 1970s, in the case of the cassava mealybug and the cassava green mite, biological control research was conducted in parallel with resistance breeding that brought large-scale impacts in sub-Saharan Africa (Table 2). Led by Hans R. Herren, a significant contribution was made by the IITA team (Neuenschwander 2001). This contribution included identification of the cassava mealybug as a newly introduced pest into Africa, the location of the same mealybug species in its area of origin in South America, the successful rearing of cassava mealybugs and mites as well as their imported natural enemies in the laboratory at IITA, the migration and dispersal data assembled after the release of the beneficial parasite *Anagyris* (*Apoanagyris*, *Epidinocarsis*) *lopezi*, a predator wasp, and the development of a simulation model showing plant/pest/predator-parasite interactions (Herren & Neuenschwander 1991). Control of the cassava mealybug has been successful since its inception up by IITA in the 1980s (Norgaard 1988; Zeddies *et al.* 2000; Neuenschwander 2004).

After beginning control of the cassava mealy bug by the introduced predator wasp *A. lopezi*, IITA researchers undertook the biological control of cassava green mite (Dixon *et al.* 2003). The major achievements in cassava green mite research up to the late 1980s were the establishment of the mite's true identity, its behaviour within the cassava ecosystem, and its damage to the cassava plant (Mégevand *et al.* 1987). It was in the second half of the 1990s that IITA researchers J. Steve Yaninek and Rachid Hanna

succeeded with classical biological control of cassava green mite by identifying, introducing and establishing predatory mites (*Typhlodromalus aripo* and *T. manihoti*) and later an acaropathogenic fungus (*Neozygites tanajoae*) from climatically similar areas of Brazil. This cassava green mite biocontrol campaign is continuing in Central, Eastern and Southern Africa with the addition of strains of predatory mites adapted to mid-altitude agro-ecologies, and the emphasis on the integration of cassava cultivars suitable to predatory mites.

PROSPECTS OF IMPROVING CASSAVA NUTRITIVE QUALITY AND YIELD

Tuberous roots with protein content up to 0.04 were recorded in clones after hybridization of cassava with *M. oligantha* (Nassar & Dorea 1982). One such hybrid, ICB 300, had very high leaf lutein content; up to 9000 mg/kg compared with 700 mg/kg in common cassava cultivars (Nassar *et al.* 2004), which illustrated the potential use of wild species as a source of high protein content in tuberous roots and lutein in leaves.

There are other *Manihot* genetic resources that are rich in carotenoids. Screening some indigenous clones enabled selection of clones with high β -carotene content, as well as cultivars rich in lycopene (Nassar *et al.*, 2005). Excellent palatability and taste was added to their nutritive value and these new cultivars are being tested by small farmers in the Brasilia Federal District and adjacent states.

Chavez *et al.* (2005) found that carotene contents in the cassava tuberous roots ranged from 1.02 to 1.040 mg/kg fresh tissue. It appears that this trait is positively correlated with colour intensity and cyanogenic potential. Furthermore, the antioxidant properties of carotenoids in yellow cassava roots may help reduce or delay post-harvest physiological deterioration (PPD) because this trait is inversely associated with the total carotenoid content in roots

(Sánchez *et al.* 2006). Likewise, Chavez *et al.* (2005) reported average levels of 17.1 mg/kg for Fe and 7.5 mg/kg for Zn. The most promising genetic resources for Fe and Zn in the tuberous roots are from Meso-America, perhaps due to the introgression from wild *Manihot* species endemic to this region.

GENETIC ENHANCEMENT OUTLOOK

Although knowledge of cassava genetics seems to be rather limited, recent genetic research is providing more insight into trait inheritance, for example dominance plays an important role in complex traits such as root yield due to epistasis (Cach *et al.* 2005), which explains why specific combining ability effects are relatively more important than general combining ability effects in this crop (Jaramillo *et al.* 2005). On the other hand, general combining ability appears to be more important for dry matter content of the tuberous roots and plant type.

Similarly, the new knowledge gathered through genetic mapping, genomics, gene cloning and use of markers for aided breeding are improving the tool-kit

of cassava breeders. For example, the cloning of the peroxidase gene offers a potential marker for selecting cassava clones for resistance to bacterial blight (Pereira *et al.* 2003). Genetic engineering also provides complementary means for cassava germplasm enhancement, especially for traits in which conventional breeding still struggles for success, for example engineering cyanogen synthesis and turnover in cassava (Siritunga & Sayre 2004). However, for cassava growers to benefit from the use of potential uses of transgenic technology (Taylor *et al.* 2004), scientists should adopt a research-for-development mindset, which is geared towards the deployment of their research products to the farming systems where the crop thrives.

Thanks are due to the Brazilian National Council for Scientific Development (CNPq) for support to the senior author. The above mentioned living collection was established at the Universidade de Brasília, with the help of Canada International Development Research Center (IDRC, Ottawa) from 1976 to 1982 to whom the senior author of this article is grateful.

REFERENCES

- ANONYMOUS. (1989). *Annual Report*. Thiruvandrum: Central Tuber Crops Research Institute.
- BECK, B. D. (1960). *Cassava Trials on Moor Plantation 1958–1959 Report*. Ibadan, Nigeria: Department of Agriculture.
- BELLOTTI, A. C., SMITH, L. & LAPOINTE, S. L. (1999). Recent advances in cassava pest management. *Annual Review of Entomology* **44**, 343–370.
- BOLHUIS, G. G. (1966). Influence of length of the illumination period on root formation in cassava. *Netherlands Journal Agricultural Science* **14**, 151–262.
- CACH, N. T., PEREZ, J. C., LENIS, J. I., CALLE, F., MORANTE, N. & CEBALLOS, H. (2005). Epistasis in the expression of relevant traits in cassava (*Manihot esculenta* Crantz) for subhumid conditions. *Journal of Heredity* **96**, 586–592.
- CHAVEZ, A. L., SÁNCHEZ, T., JARAMILLO, G., BEDOYA, J. M., ECHEVERRY, J., BOLAÑOS, E. A., CEBALLOS, H. & IGLESIAS, C. A. (2005). Variation of quality traits in cassava roots evaluated in landraces and improved clones. *Euphytica* **143**, 125–133.
- COURSEY, D. G. & HAYNES, P. H. (1970). Root crops and their potential as food in the tropics. *World Crops* **22**, 261–265.
- DE BRUIJN, G. H. (1971). *A Study on Cyanogenetic Character of Cassava (Manihot esculenta Crantz)*. Wangeningen: Mededelingen Landbouwhogesschool.
- DE VRIES, C. A., FERWERDA, J. D. & FLACH, M. (1967). Choice of food crops in relation to actual and potential production in the tropics. *Netherlands Journal Agricultural Sciences* **15**, 241–248.
- DIXON, A. G. O. D., BANDYOAPADHYAY, R., COYNE, D., FERGUSON, M., FERRIS, R. S. B., HANNA, R., HUGHES, J., INGELBRECHT, I., LEGG, J., MAHUNGU, N., MANYONG, V., MOWBRAY, D., NEUENSCHWANDER, P., WHYTE, J., HARTMANN, P. & ORTIZ, R. (2003). Cassava: from poor farmer's crop to pacesetter of African rural development. *Chronica Horticulturae* **43**, 8–15.
- FAO (2003). *FAOSTAT, FAO Statistical Databases – Agriculture*. Available at <http://apps.fao.org>. Verified 17/7/06.
- FFOULKES, D. & PRESTON, T. R. (1978). Cassava or sweet potato forage as combined sources of protein and roughage in molasses based diets: effect of supplementation with soybean meal. *Tropical Animal Production* **3**, 186–192.
- HAHN, S. K., HOWLAND, A. K. & TERRY, E. R. (1980). Correlated resistance of cassava to mosaic and bacterial blight diseases. *Euphytica* **29**, 305–311.
- HERREN, H. & NEUENSCHWANDER, P. (1991). Biological control of cassava pests in Africa. *Annual Review of Entomology* **36**, 257–283.
- JARAMILLO, G., MORANTE, N., PEREZ, J. C., CALLE, F., CEBALLOS, H., ARIAS, B. & BELLOTTI, A. C. (2005). Diallel analysis in cassava adapted to the midaltitude valleys environment. *Crop Science* **45**, 1058–1063.
- KAWANO, K. (2003). Thirty years of cassava breeding for productivity. Biological and social factors for success. *Crop Science* **43**, 1325–1335.
- MAGOON, M. L., JOS, J. S. & APANN, S. G. (1966). Cytomorphology of interspecific hybrid between cassava and Ceara rubber. *Chromosome Information Service (Japan)* **7**, 8–10.
- MANYONG, V. M., DIXON, A. G. O., MAKINDE, K. O., BOKANGA, M. & WHYTE, J. (2000). *The Contribution of IITA-improved Cassava to Food Security in Sub-Saharan Africa: an Impact Study*. Ibadan, Nigeria: International Institute of Tropical Agriculture.
- MÉGEVAND, B., YANINEK, J. S. & FRIESE, D. D. (1987). Classical biological control of cassava green mite. *Insect Science and Its Application* **8**, 871–874.

- NASSAR, N. M. A. (1978a). Genetic resources of cassava: chromosome behaviour in some *Manihot* species. *Indian Journal of Genetics and Plant Breeding* **38**, 135–137.
- NASSAR, N. M. A. (1978b). Hydrocyanic acid content in some wild *Manihot* (cassava) species. *Canadian Journal of Plant Science* **58**, 577–578.
- NASSAR, N. M. A. (1978c). Microcenters of wild cassava *Manihot* spp. diversity in central Brazil. *Turrialba* **28**, 345–347.
- NASSAR, N. M. A. (1978d). Some further species of *Manihot* with potential value to cassava breeding. *Canadian Journal of Plant Science* **58**, 915–916.
- NASSAR, N. M. A. (1978e). Wild *Manihot* species of central Brazil for cassava breeding. *Canadian Journal of Plant Science* **58**, 257–261.
- NASSAR, N. M. A. (1979a). A study of the collection and maintainance of the germplasm of wild cassavas *Manihot* spp. *Turrialba* **29**, 221–224.
- NASSAR, N. M. A. (1979b). Three Brazilian *Manihot* species with tolerance to stress conditions. *Canadian Journal of Plant Science* **59**, 533–555.
- NASSAR, N. M. A. (1980). Attempts to hybridize wild *Manihot* species with cassava. *Economic Botany* **34**, 13–15.
- NASSAR, N. M. A. (1984). Natural hybrids between *Manihot reptans* Pax and *M. alutaced* Rogers & Appan. *Canadian Journal of Plant Science* **64**, 423–425.
- NASSAR, N. M. A. (1986). Genetic variation of wild *Manihot* species native to Brazil and its potential for cassava improvement. *Field Crops Research* **13**, 177–184.
- NASSAR, N. M. A. (1989). Broadening the genetic base of cassava, *Manihot esculenta* Crantz by interspecific hybridization. *Canadian Journal of Plant Science* **69**, 1071–1073.
- NASSAR, N. M. A. (1992a). Production of triploid cassava, *Manihot esculenta* Crantz by hybrid diploid gametes. *Field Crops Research* **18**, 173–182.
- NASSAR, N. M. A. (1992b). Cassava in South America: a plant breeder view. *Ciência e Cultura* **44**, 25–27.
- NASSAR, N. M. A. (1994). Selection and development of apomitic cassava clones. *Ciência e Cultura* **46**, 168–171.
- NASSAR, N. M. A. (1997). Development of cassava interspecific hybrids for savanna (cerrado) conditions. *Journal of Root Crops* **22**, 9–17.
- NASSAR, N. M. A. (1999). Cassava, *Manihot esculenta* Crantz genetic resources: their collection, evaluation and manipulation. *Advances in Agronomy* **69**, 179–230.
- NASSAR, N. M. A. (2000a). Wild cassava, *Manihot* spp.: biology and potentialities for genetic improvement. *Genetics and Molecular Biology* **23**, 201–212.
- NASSAR, N. M. A. (2000b). Cytogenetics and evolution of cassava (*Manihot esculenta* Crantz). *Genetics and Molecular Biology* **23**, 1003–1014.
- NASSAR, N. M. A. (2001). The nature of apomixis in cassava (*Manihot esculenta* Crantz). *Hereditas* **134**, 185–187.
- NASSAR, N. M. A. & CARVALHO, C. G. P. (1990). Pollinator insects and their behaviour in wild *Manihot* species (in Portuguese). *Ciência e Cultura* **42**, 703–706.
- NASSAR, N. M. A. & COSTA, C. P. (1977). Tuber formation and protein content in some wild cassava (mandioca) species native to Central Brazil. *Experientia* **33**, 1304–1306.
- NASSAR, N. M. A. & DOREA, G. (1982). Protein contents of cassava cultivars and its hybrid with *Manihot* species. *Turrialba* **32**, 429–432.
- NASSAR, N. M. A. & FREITAS, M. (1997). Prospects of polyploidizing cassava. *Manihot esculenta* Crantz, by unreduced microspores. *Plant Breeding* **116**, 195–197.
- NASSAR, N. M. A. & O'HAIR, S. (1985). Variation among clones in relation to seed germination. *Indian Journal of Genetics* **45**, 429–432.
- NASSAR, N. M. A. & TEIXEIRA, R. P. (1983). Seed germination of wild cassava species (*Manihot* spp.) (in Portuguese). *Ciência e Cultura* **35**, 630–632.
- NASSAR, N. M. A., NASSAR, H. N. M., VIEIRA, C. & SARAIVA, S. L. (1995). Cytogenetic behavior of interespecific hybrids of *Manihot neusana* Nassar and cassava, *M. esculenta* Crantz, and its backcross progeny. *Canadian Journal of Plant Science* **75**, 675–678.
- NASSAR, N. M. A., NASSAR, H. N. M., VIEIRA, C. & CARVALHO, A. (1996). Induction of a productive aneuploid in cassava, *Manihot esculenta* Crantz. *Brazilian Journal of Genetics* **19**, 123–125.
- NASSAR, N. M. A., VIEIRA, M. A., VIEIRA, C. & GRATTAPAGLIA, D. (1998a). Molecular and embryonic evidence of apomixis in cassava interspecific hybrids (*Manihot* spp.). *Canadian Journal of Plant Science* **78**, 348–352.
- NASSAR, N. M. A., VIEIRA, M. A. R., VIEIRA, C. & GRATTAPAGLIA, D. (1998b). Evidence of apomixis in cassava (*Manihot esculenta*) Crantz. *Genetics and Molecular Biology* **21**, 527–530.
- NASSAR, N. M. A., SANTOS, E. D. & DAVID, S. R. O. (2000). The transference of Apomixis genes from *Manihot neusana* Nassar to cassava, *M. esculenta* Crantz. *Hereditas* **132**, 167–170.
- NASSAR, N. M. A., ALVES, J. & DE SOUZA, E. (2004). UnB 033: an interesting interspecific cassava hybrid. *Revista Ceres* **51**, 495–499.
- NASSAR, N. M. A., VIZZOTTO, C. S., DA SILVA, H. L., SCHWARTZ, C. A. & PIRES JUNIOR, O. R. (2005). Potentiality of cassava cultivars as a source of carotenoids. *Journal of Food, Agriculture and Environment* **3**, 33–35.
- NEUENSCHWANDER, P. (2001). Biological control of the cassava mealybug in Africa: a review. *Biological Control* **21**, 214–229.
- NEUENSCHWANDER, P. (2004). Harnessing nature in Africa: biological pest control can benefit the pocket, health and the environment. *Nature* **432**, 801–802.
- NORGAARD, R. B. (1988). The biological control of cassava mealybug in Africa. *American Journal of Agricultural Economics* **72**, 366–371.
- NWEKE, F. I., SPENCER, D. S. C. & LYNAM, J. K. (2002). *The Cassava Transformation: Africa's Best-kept Secret*. East Lansing, USA: Michigan State University Press.
- OERKE, E. C. (2006) Crop losses to pests. *Journal of Agricultural Science, Cambridge* **144**, 31–43.
- OTIM-NAPE, G. W. (1993). *Epidemiology of the African cassava mosaic gemini virus disease (ACMD) in Uganda*. Ph.D. Thesis, University of Reading, UK.
- PEREIRA, A. S., LORENZI, J. O., MONTEIRO, D. A. & VEIGA, A. A. (1981). A study on the progeny of self-fertilized cassava clone Guaxupé (in Portuguese). *Bragantia* **40**, 217–219.
- PEREIRA, L. F., GOODWIN, P. H. & ERICKSON, L. (2003). Cloning of a peroxidase gene from cassava with potential as a molecular marker for resistance to bacterial blight. *Brazilian Archives of Biology and Technology* **46**, 149–154.

- PHILLIPS, S. L. & WOLFE, M. S. (2005). Evolutionary plant breeding for low input systems. *Journal of Agricultural Science, Cambridge* **143**, 245–254.
- RAJENDRAN, P. G., RAVINDRAN, C. S., NAIR, S. G. & NAYAR, T. V. R. (2000). *True Cassava Seeds (TCS) for Rapid Spread of the Crop in Non Traditional Areas. Technical Bulletin* 28. Thiruvananthapuram, India: Central Tuber Crops Research.
- ROGERS, D. J. (1963). Studies of *Manihot sculenta* Crantz and related species. *Bulletin of the Torrey Botanical Club* **90**, 43–54.
- ROGERS, D. J. (1965). Some botanical and ethnological considerations of *Manihot sculenta*. *Economic Botany* **19**, 369–77.
- SALICK, J., CELLINESE, N. & KNAPP, S. (1997). Indigenous diversity of cassava: generation, maintenance, use and loss among the Amuesha, Peruvian upper Amazon. *Economic Botany* **51**, 6–19.
- SANCHEZ, T., CHÁVEZ, A. L., CEBALLOS, H., RODRIGUEZ-AMAYA, D. B., NESTEL, P. & ISHITANI, M. (2006). Reduction or delay of post-harvest physiological deterioration in cassava roots with higher carotenoid content. *Journal of the Science of Food and Agriculture* **86**, 634–639.
- SIRITUNGA, D. & SAYRE, R. (2004). Engineering cyanogen synthesis and turnover in cassava (*Manihot esculenta*). *Plant Molecular Biology* **56**, 661–669.
- STOREY, H. H. & NICHOLS, R. F. W. (1938). Studies of the mosaic disease of cassava. *Annals of Applied Biology* **25**, 790–06.
- TAYLOR, N., KENT, L. & FAUQUET, C. (2004). Progress and challenges for the deployment of transgenic technologies in cassava. *AgBioForum* **7**, 51–56.
- WILLIAMS, C. N. & GAZHALI, S. M. (1969). Growth and productivity of tapioca (*Manihot utilissima*) 1. Leaf characteristics and yield. *Experimental Agriculture* **5**, 183–194.
- ZEDDIES, J., SCHAAB, R. P., NEUENSCHWANDER, P. & HERREN, H. R. (2000). Economics of biological control of cassava mealybug in Africa. *Agricultural Economics* **24**, 209–219.