ROOT CROPS IN EASTERN AFRICA

Proceedings of a workshop held in Kigali, Rwanda, 23-27 November 1980
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Résumé

Cette brochure traite principalement des deux tubercules alimentaires les plus importants en Afrique orientale, soit le manioc et la patate douce. Quelques communications portent sur la pomme de terre, l'igname, le taro et l'Enset - dont la consommation est considérable dans plusieurs pays de la région. Le rendement de ces cultures est limité par de nombreux facteurs. Aussi, la recherche effectuée dans le cadre de programmes agronomiques nationaux et internationaux est-elle orientée vers la correction de cette situation en Afrique. Les difficultés rencontrées en cours de travaux et les progrès réalisés sont décrits par des représentants et des consultants de l'Institut international d'agriculture tropicale d'Ibadan (Nigéria) et d'autres pays tel que le Cameroun, le Kenya, l'Ouganda, le Malawi, le Zimbabwe, l'Éthiopie, le Burundi, le Zaïre et le Swaziland.

Resumen

Esta publicación se enfoca en la mandioca y el camote — los cultivos de tuberosas más importantes del África oriental. Los trabajos tratan también del Solanum tuberosum, Dioscorea spp., Colocasia sp., Xanthosoma sp., y Enset sp., que son todos cultivos importantes a los países de esta región. La producción de cada uno es restringida por serios constreñimientos, y el alivio de éstos es el objetivo de varias investigaciones llevadas a cabo por los programas agrícolas nacionales e internacionales en el África. El progreso hacia y los problemas encontrados en llegar a este fin son delineados por especialistas representando al Instituto Internacional de Agricultura Tropical en Ibadan, Nigeria, y a los países de Camerún, Kenia, Uganda, Malawi, Zimbabwe, Etiopía, Burundi, Zaire, y Swazilandia.
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Historical perspectives of cassava breeding in Africa

B.D.A. Beck

The early records of the introduction of cassava to East and West Africa are reviewed, and the three major cassava-breeding programs that involved the use of interspecific hybridization to obtain resistance to cassava mosaic disease (CMD) are outlined. My earlier work to produce the interspecies hybrid clone 58308 is described; this clone has shown stable resistance to CMD for 22 years under continuous, high-inoculation pressure. Researchers at the International Institute of Tropical Agriculture have shown that this resistance is recessive, is polygenic, and is inherited in a largely additive manner. They have also shown that 58308 provides polygenic resistance to cassava bacterial blight (CBB) and that this resistance is also recessive and is inherited additively. The resistances to CMD and CBB are strongly linked, and this link may occur in the chromosome complement derived from the Manihot glaziovii parent. Clone 58308 has also been the principal parent in the production of lines with low cyanide in the roots. Resistance to both diseases and the presence of low cyanide have been incorporated into a large number of high-yielding populations at IITA, through a half-sib selection procedure with relatively large families. The future development and the distribution of new disease-resistant, low-cyanide cultivars for the smallholder and for large-scale producers as an industrial feedstock from these populations are discussed.

Cassava (Manihot esculenta) originated in South America, and Vavilov (1949) suggested that cultivated strains spread from a Brazilian-Paraguayan centre of origin. Cassava was widely grown in Brazil in the 15th century, where Pierre Matyr first described the use of cassava roots in bread in 1494 (Pynaert 1928).

Cassava meal was used by the Portuguese to provision their slave ships (Hawkins 1593) and was brought to the West Coast of Africa by slave traders who planted the crop at their factories to feed slaves in the barracoons. Lacourbe (1635) recorded cassava growing at Bissau, and Dapper (1668) reported the crop at Fourcados in the Niger Delta. Cassava was widely grown by farmers in Owerri by 1700, but "nowhere else was it a crop of more than

1 Brian Beck (Pvt) Ltd, Box 86, Zomba, Malawi.
local importance prior to the nineteenth century" (Jones 1957).

Cassava may have been introduced to Central Africa west of Lake Tanganyika along traditional overland trade routes from the Congo basin. The Portuguese brought manioc to the Island of Reunion from Brazil in 1739 and probably from there to Madagascar (IFAN 1951). Stuhlman (1909) quoted Strandes who stated that the first authenticated introduction to Mozambique was in 1750. Lacerda (1798) recorded buying cassava flour in Cazembe. Jones (1959, p. 84), discussing the reports of early travelers in East and Central Africa, suggested that, although there are many records of the occurrence of cassava in East Africa by 1850, it was at that time an unimportant crop, save on the coast and around Lake Tanganyika, to which it had been brought from the west.

The original importations of cassava to Africa were probably quite small and were obtained by the Portuguese from the Tupinamba Indians on the coast of Brazil who brought the crop from the high forest early in the 15th century (Jones 1959, p. 31). These cultivars were likely to have been adapted to the West African forest regions where slash-and-burn agriculture was widely established.

The fertility of forest soil cleared for cultivation falls rapidly during arable cropping. The ability of cassava, a highly efficient user of soil nutrients, to grow on soils exhausted by previous cropping led to its cultivation as the last crop of the rotation before the land was returned to forest. A well-established cassava crop competes well with weeds, freeing the farmer to work a newly cleared area, returning to the cassava garden to harvest small groups of plants as they are required. Cassava was left in the field for up to 30 months with the minimum of attention. During this period, it flowered and produced seed, and the seedlings had time and opportunity to grow in the areas recently cleared by harvests. When the farmer returned to the cassava garden to gather planting material for the next cycle of cultivation, he or she probably used only some of the seedling material, selecting the outstanding types.

Although the original importations were small, they were highly heterozygous; the system of agriculture in which they were used lent itself to natural outcrossing and seedling propagation with the development and selection of new types. Thus, when I commenced a cassava-improvement program in Nigeria in 1954, I was able to collect more than 450 morphologically distinct local cultivars from farmers' fields in the country. A similar range of diversity has been found by other workers in Africa. However, the yield of most of the African cultivars was low, less than 20 t/ha, and all the local selections have proved susceptible to cassava mosaic disease (CMD).

CMD is an African virus. It has not been reported from Latin America, where the crop originated. CMD was first described in East Africa in 1885 (Lefevre 1935) and first recorded in West Africa, in Nigeria, by Jones in 1926 (Golding 1936). Golding, writing in 1936, stated that mosaic had been reported in "the Belgian Congo, Ubangin-Shai, Moyen-Congo, French Cameroon, Nigeria, the Gold Coast, Ivory Coast, Liberia and Sierra Leone." Storey (1930) had recorded a similar disease in East Africa. Working independently, both Storey and Golding showed that CMD could be transmitted by a white fly, *Bemisia* spp., now known to be *B. tabaci* (Russell 1957). Storey also showed that the disease was further spread in the field by vegetative propagation, from stakes of infected plants.

It was the widespread occurrence and high incidence of CMD that caused governments to start cassava-breeding programs aimed at obtaining cultivars resistant to the disease. Breeding programs were launched in Nigeria (Faulkner 1932), in Ghana (Miles 1934), in Tanzania in 1935 (Storey 1936), in the Congo, and in francophone Africa by Institut de recherches agronomiques tropicales et des cultures vivrières (IRAT). This paper will discuss the three plant-breeding programs that have used interspecific hybridization within the genus *Manihot* to obtain resistance to CMD.

Storey (1935) introduced "resistant" material from West Africa that proved susceptible under the conditions of his trials. He suggested that the West and East African strains of the virus were different, although it was not possible to show symptom differences between them. He demonstrated differences in the symptom expression of mosaic from separate sources in East Africa and postulated the existence of mild and severe strains of CMD. He was also able to demonstrate the existence of a second viral disease, cassava brown streak (CBS), which did not occur in West Africa (Storey 1936).
Until the early 1950s, hybridization and selection in the West African programs were confined to the species *Manihot esculenta*; these failed to produce any cultivars resistant to cassava mosaic. None of the cassava lines tested in East Africa showed high resistance to CMD or to CBS, and, in 1937, Storey first crossed cassava with ceara rubber (*M. glaziovii*), which appeared to be resistant to the disease. By 1939, Storey widened his interspecies crosses to include *M. dichotoma, M. cathartica*, and *M. dulcis*. He obtained a high level of field resistance to both CMD and CBS in the *glaziovii × cassava* and the *dichotoma × cassava* hybrids. Later still, *M. melanobasis* and *M. saxicola* were included in the program.

Storey used the term “field resistance,” as do most plant breeders today. Field resistance is the sum of resistance of the plant to the virus per se and to infection from inoculation by the vector. Resistant plants are symptomless or show only occasional, mild leaf symptoms. Storey showed that none of his interspecies hybrids were immune to the virus, as he was able to infect field-resistant material by grafting.

This program was continued by Nichols and, later, by Jennings. Nichols (1947) reported that resistance to CMD was genetically controlled and that the *dichotoma × esculenta* interspecies hybrids showed the most promise for selection for mosaic resistance; these populations, however, showed a high degree of sterility. *M. glaziovii × cassava* interspecies hybrids and tree cassava × cassava hybrids both produced segregates resistant to CMD and CBS. In 1949 (EAAFRO 1949), it was shown that interspecies *M. melanobasis × cassava* hybrids had a high degree of resistance to CBS.

By 1951, the mosaic-tolerant ceara hybrids, notably 4332/2 and 46106/27, were available for testing and showed considerable promise (EAAFRO 1951). Jennings then started a program of intercrossing the resistant interspecies hybrids to release recessive genes for resistance and to recombine genes that had been dispersed in the earlier backcrossing program (Jennings 1976). This technique was successful, and considerable increases in stable resistance were obtained, notably in Jennings’ clone 5318/34. This program was terminated in 1957; 91 clones were retained, 5 of which were selected and distributed to farmers. These improved clones, which are now grown on a limited scale in East Africa, have not replaced the established local cultivars (Bock and Guthrie 1978). The reason, according to Bock and Guthrie (1978), is that the new cultivars proved to be less palatable than the traditional types. In addition, farmers found that, as the health status of the new cultivars declined, their mosaic resistance appeared to break down and seemed in no way superior to that of other types.

When I began a breeding program in Nigeria, I selected eight clones on the basis of the severity of mosaic symptoms in the field; yield; and contrasting agronomic characteristics such as branching, plant height, and root arrangement. These varieties were crossed together in a diallel program that produced some 25,000 seedlings. None of this material was field resistant to mosaic (Beck 1959).

In my opinion (Beck 1971), adequate resistance to African cassava mosaic virus does not occur within the species *M. esculenta*. In 1956, seed populations from the East African program, which had been continued by Nichols and Jennings, were introduced to Nigeria. From seed derived from Jennings’ selection 5318/34, I selected the CMD-resistant hybrid 58308 (Beck 1960); 58308 was selfed, intercrossed with other interspecies hybrids, and crossed to high-yielding local West African selections. In 1960, the cassava-breeding program was moved to the Federal Root Crops Research Station at Umudike in eastern Nigeria, and the progeny testing was continued by Ekandem. Unfortunately, almost all of the progeny and the records of this program were lost during the civil war in Nigeria. Most of the parent material, however, had been retained at Moor Plantation, and 58308 subsequently became the main source of resistance to CMD in the breeding program at the International Institute of Tropical Agriculture (IITA). The hybrid 58308 has remained resistant to CMD for 22 years under high-inoculation pressure (Hahn et al. 1980).

IITA commenced a cassava-breeding program in 1971. About that time, a new and serious disease of cassava was reported in West Africa. This disease, cassava bacterial blight (CBB), is caused by the bacterium *Xanthomonas manihotis*. The disease was first recorded in Brazil (Bondar 1912) and was first reported in Nigeria in 1972 (IITA 1972). Since that time, serious outbreaks of CBB have been reported in Zaire, Cameroon, Togo, Benin, Ghana, Congo, Uganda, Kenya, Tan-
zania, Burundi, Rwanda, and Central Africa (Terry 1978c). Most indigenous African cultivars have proved susceptible to the disease; infection can result in complete crop loss. Thus, the IITA program focused on both CMD and CBB. It was found that the interspecies hybrid 58308, originally selected for resistance to CMD, was also highly resistant to CBB.

Jennings, using the method of Gilbert (1967), showed that, in the East African material, resistance to both CMD and CBB was inherited in a predominantly additive manner, although there was a significant specific combining ability effect for resistance to CMD. Hahn and Howland (1972) confirmed this finding as well as showing that CMD resistance was under polygenic control and was recessive, with a heritability of about 60%.

This relatively high heritability, along with the polygenic control, meant that the resistance was likely to remain stable. Furthermore, a comparison of nine isolates of the CBB pathogen on resistant clones at IITA (1977) suggested that the resistance to CBB was race-nonspecific (Parlevliet and Zadoks 1977).

Hahn et al. (1980) showed that progenies derived from 58308 crossed with susceptible and moderately susceptible clones exhibited a significant genotypic correlation between resistance to CMD and resistance to CBB \( r = 0.90 \). The suggestion was that the correlation reflected links between the genes for resistance, controlled by a number of linked loci on a chromosome or on a set of chromosomes.

These workers have used the technique of population improvement with a half-sib family selection scheme, using relatively large families to break the linkage of the resistant genes and those controlling the poor agronomic characters of 58308, and to incorporate the resistance genes or groups of genes with those for high yield, good quality, low-cyanide content, and resistance to lodging. Because of the efficient field selection carried out by Hahn and his co-workers, this method has been brilliantly successful. Rapid improvements have already been made, and improved selections are in trial over a wide range of environments.

Resistance to the cassava green mite (CGM) *Mononychellus tanajoa*, a new pest in East Africa, has also been identified in these populations in trials in Tanzania.

Because of the rapid distribution of the IITA progeny for field testing by national programs, further information will be obtained on the stability of resistance to CMD and the race specificity of resistance to CBB. Efficient local selection within the IITA populations will lead to the development of well-adapted types either to be distributed to farmers or to act as parent material in national cassava-improvement programs.

**Discussion**

All the work described in this paper has been aimed primarily at producing cassava cultivars adapted to local African farming conditions for use as human food. In most African farming systems, cassava is grown by smallholders in fields less than 5 ha. It is harvested as required by the farming family, either for their own use or for processing as a cash crop into products such as chips, flour, or gari. There are marked producer and consumer preferences as to the type of cultivar grown, and these probably determine the uptake of new cultivars in peasant societies. For example, in Kenya, the mosaic-susceptible cultivar F279, introduced by Storey in his breeding program, has become popular in local areas, but the mosaic-resistant, improved cultivars are nowhere grown on a large scale and have not replaced the local types. Consumer preference is a local phenomenon and may be expected to limit the widespread use of otherwise outstanding cultivars.

However, the uses of cassava are now expanding. The recent increases in oil prices have made the development of synthetic fuels economically attractive. Zimbabwe and Kenya have commenced ethanol production programs using the molasses by-products of their sugar industries as a fermentable carbohydrate source. These, and other, governments are examining the possibility of using hydrolyzed cassava starch as a feedstock for synthetic fuels. Cassava is capable of giving a higher yield of calories per hectare than is any other crop. The mathematics of the utilization of cassava are attractive: 1 t fresh cassava roots will produce 180 L ethanol fuel compared with 70 L from 1 t sugarcane.

Kenya and other African states are also developing livestock-feed industries based on
cassava chips or cassava pellets, both for internal use and for export to Europe. The economics of using a food crop as an industrial feedstock, however, require careful examination.

To produce enough cassava to supply factories will require large-scale, plantation-type agriculture, and this type of cultivation requires mechanical assistance. Also, the types of cassava developed for large-scale agriculture will be markedly different from those adapted to peasant agriculture. For example, these cultivars will require much higher levels of disease resistance, because large-scale monocropping systems are more vulnerable to epiphytotic outbreaks of disease and, thus, more economically serious crop losses.

In my breeding programs, I sought to develop types that quickly formed a closed canopy and consequently reduced weeding. A minor heresy was invoked, for, in these closed canopies, susceptibility to *Cercospora henningsii* was an advantage. In Nigeria, this pathogen attacked only the older leaves in the lower strata of the canopy during the wet season and, in effect, hastened leaf fall; because they were densely shaded, these leaves contributed little to carbohydrate production and probably were respiratory sinks for sugars. *Cercospora* acted as a useful pruning agent. These cultivars would be of limited use in plantation agriculture. Densely interwoven branches in the canopy may cause serious problems in large-scale harvesting operations, and to use cultivars with no resistance to a potentially dangerous pathogen would be an unacceptable risk. A more erect, sparsely branched type, easy to clear from the fields, would be required. These types have a more limited leaf area; thus, resistance to fungal leaf diseases would be of considerable importance. Short, thick roots growing close to the original planting material would be essential for mechanical lifting. To enable harvests to be staggered for a continuous supply to the processing plant, it is essential that industrial cultivars have roots that are resistant to rotting when mature.

Most cassava-breeding programs have been designed to select cultivars adapted to the low-input systems of agriculture used by smallholder farmers. It is probable that large-scale, continuous cultivation for industrial production will require the use of fertilizers to maximize yields. The new cultivars must have the genetic background to permit economic responses to improved nutrition. In producing these cultivars, the breeders' work will be simplified in at least one regard: they will be selecting for an objective goal, fermentable carbohydrate per hectare, and will not be bedeviled by subjective considerations of local consumers' tastes.

The successful breeding programs of Hahn and his colleagues at IITA have provided a range of excellent commercial cultivars and sources of resistance to the major diseases and pests of the crop. The distribution, availability, and use of this valuable material are seriously restricted by the necessary plant-quarantine regulations of all cassava-growing countries. Successful genotypes have been a long time in the building. It has now been shown (IITA 1978) that the heat treatment for cuttings developed by Chant (1959) does not guarantee disease-free material, and, thus, the distribution of standard vegetative material is not possible. Persley (1979) has shown that CBB can be transmitted through the seed. The use of thermal inactivation of the bacterium by hot-water treatment of the seed requires further investigation before the plant-quarantine authorities will allow unrestricted movement of heat-treated seed. At present, most plant-quarantine stations do not have sufficient facilities to permit the growth and quarantine of the large seedling populations required by plant breeders. Perhaps the most promising technique for the rapid dissemination of improved cultivars is by the tissue-culture methods of Kartha and Gamborg (1975), coupled with the single leaf-bud cutting technique of Roca et al. (1980). The observation of Bock and Guthrie (1976) that CMD may be latent in vegetative material and may not produce symptoms until the third cycle of propagation should be borne in mind. This type of symptom masking will most likely be in cultivars with a high level of resistance to CMD.

Increasing population pressure on land and rapidly declining soil fertility make the rapid dissemination of IITA's improved cassava genotypes of paramount importance. The need is most urgent in areas where whitefly populations and the levels of infection with CMD and CBB are consistently high. A good case can be made for the establishment of an intermediate quarantine station, possibly outside Africa, using the new techniques of
chemical and thermal inactivation of seed-borne pathogens and tissue-culture and rapid-propagation techniques on a large scale. It is on the ready availability of improved genotypes that national programs will depend in future. The need for them is now.