CASSAVA BREEDING AT I.I.T.A.*

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SUMMARY

The breeding objectives in the Root and Tuber Improvement Programme of the International Institute of Tropical Agriculture (IITA) were laid down. Basic considerations in cassava breeding were reviewed and discussed. The paper attempts to produce a cassava breeding system applicable on a world-wide basis and describes the present state and the future development of cassava breeding.

RESUME

Exposé des objectifs du Programme de Sélection et d'Amélioration des Plantes à Racine et à Tubercule à l'Institut International d'Agriculture Tropicale (IITA). Examen critique des problémes fondamentaux de la sélection et de l'amélioration du manioc et tentative de formulation d'un système de sélection et d'amélioration du manioc ayant une application universelle. Présentation de la situation actuelle et des perspectives pour le développement de la sélection du manioc.

RESUMEN

Se establecieron los objetivos de hibridación del Programa de Mejoramiento de Raíces y Tubérculos del Instituto de Agricultura Tropical (IITA). Se discutieron las consideraciones básicas del mejoramiento genético en yuca. El reporte intenta producir un sistema de hibridación que sea aplicable sobre una amplia base mundial y describe el estado presente y el futuro desarrollo del mejoramiento genético de la yuca.

INTRODUCTION

Cassava is widely grown and used as a staple food in many parts of the tropics. World production amounts to about 100 million tons annually from 10 million hectares, of which Africa produces about 40 million tons from about 5 million hectares. In Africa, especially West Africa, cassava is the most popular of the root and tuber crops, and the trend in production shows a steady increase[15].

Cassava is potentially able to produce more food calories per unit area than any other lowland crops grown in Nigeria, owing to its high yielding ability, adaptation to diverse climatic and cultural conditions and ability to survive the four to six month's dry season. It requires less management input than cereal crops. Both root and leaf are valuable as human food and livestock feed, the leaf protein is high in quantity and of good quality in some cultivars, and the root is widely used for industrial production of starch and alcohol.

I.I.T.A. began its Root and Tuber Improvement Programme in 1971, and this includes cassava, sweet potato, yam and cocoyam, all of which are important food crops in many parts of Africa. However, in view of cassava's potential and its economic importance within the lowland humid tropics more generally, priority is being given to this crop. The main aims are to improve yield both in quantity and quality and to breed for resistance to the two major diseases, bacterial blight and cassava mosaic. At present the average yield of cassava in Africa is low, being about 8 tons per hectare per year fresh weight, equivalent to a little less than 3 tons dry weight. The quality criteria are not well defined, but some definite improvements can be made in advance of this knowledge. Cassava mosaic disease is a serious problem in Africa, as it is also in India and Indonesia. Nearly all plants are infected, resulting in an average yield reduction of 50 per cent[23]. Bacterial blight caused by *Xanthomonas manihotis* has recently been reported in Africa. In Nigeria[38] and Zaire[39] it causes severe tip die-back and defoliation, often resulting in the death of the plant. It is now thought that bacterial blight is potentially a more serious disease than cassava mosaic within the areas affected.

Although cassava is economically important in many other parts of the world, breeding for improvement in this crop has been given very little attention compared with many other crops. There is practically no information on the practical and fundamental approaches in breeding for the solution of many of the problems limiting or inhibiting the use of cassava. The breeding work during the period 1930 to 1950 in East Africa, West Africa, Brazil, Indonesia and Madagascar has for the most part not been sustained.

Our aim is to devise a breeding system that will be applicable on a world-wide basis and this paper describes the present state and future development of I.I.T.A.'s programme. We evaluate the possibility of in-

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corporating some of the methodologies already successfully used in breeding corn, alfalfa, sorghum and sweet potato.

BREEDING OBJECTIVES

The ultimate goal of cassava breeding is to incorporate into clonal cultivars all the characteristics, not yet fully explored, which appear to be associated with high yield expressed both in terms of quantity and quality per unit of area and time. Stability of the desirable characteristics is required over a wide range of environments and cultural practices.

Bearing in mind the limiting factors affecting cassava production in Africa, we regard the following objectives as realistic and our aim is to produce:

1. High yield in terms of dry matter per unit of land area and time.
2. Multiple resistance to diseases, especially cassava mosaic and bacterial blight and to pest attack.
3. Improved quality in terms of high starch (both quantity and quality), low or zero cyanide and high protein content, especially in the leaf.
4. Adaptation to a wide range of environments.
5. Improved plant types, especially in respect of canopy and root characteristics.

BASIC CONSIDERATIONS IN CASSAVA BREEDING

Breeding materials and evaluation

The acquisition and selection of superior breeding material is a primary necessity in any breeding programme. *M. esculenta* exhibits wide variation in form and there are about 128 other *Manihot* species[35], the genetic variation of which has not yet been fully explored or utilized.

Cassava is indigenous to the new world tropics and was probably domesticated in the drier parts of western and southern Mexico, northern Guatemala and also in northeastern Brazil[33]. It was introduced to the West African coast via the Gulf of Benin and the Congo river at the end of the 16th century and to Malava, Indonesia, Ceylon, India, Madagascar and Zanzibar during the 18th century[24].

Cassava in Africa shows considerable variation which is readily apparent in many local germplasm collections. This is not surprising as it flowers and sets seed freely, and new cultivars are established from volunteer seedlings which grow readily under optimum temperatures (30–35°C) and rainfall conditions which occur during some periods of the year. Cassava is rarely self-pollinated, since male and female flowers on the same inflorescence mature at different times. Thus, continuing recombination has occurred from outcrosses of genetically heterozygous cultivars. Some level of resistance to cassava mosaic has been established through intelligent selection by local farmers of superior seedlings for vegetative propagation, thereby developing new cultivars. Genetic fixation is not required in a vegetatively propagated crop since clonal cultivars can be produced from selected heterozygotes. Spontaneous mutation may also be a cause of additional genetic variation.

Genetic variability in Africa is not however expected to be as great as in Latin America where cassava originated. Original introductions may represent only a non-representative sample of the total germplasm available so that systematic introduction of new breeding material is important and is specially desirable from areas having similar ecological conditions. Introductions from countries where the crop is indigenous will be particularly valuable.

Manihot esculenta is the only edible cultivated species. Cultivars within this species have become extremely diversified during the process of clonal selection in different environments and their potential as sources of breeding material may be considerable, but is difficult to predict.

The IITA germplasm collection has not yet been thoroughly evaluated. Phytosanitary regulations require that introductions of new breeding material be confined to true seed which has had the appropriate fungicide/insecticide dressing, as the risk of introducing new diseases in vegetative material is considered too great. At IITA the Root and Tuber Improvement Program has adopted this procedure from the beginning, and Martin[30] has suggested that the germplasm banks of the future should be in seed form rather than as clonal collections. Cassava mosaic is not seed-borne[7], nor, so far as is yet known, is bacterial blight. Other pathogens of cassava, *Cercospora* spp., *Botryodiplodia theobromae*, *Colletotrichum* spp. causing stem anthracnose, and a *Phomopsis* sp. causing root rot and *Fusarium* spp. are endemic in Nigeria and therefore need be of no concern as far as phytosanitary regulations are concerned.

The large number of local clonal cultivars and plants grown from seed require evaluation in order to be of practical value. Their potential as breeding parents, as well as their own characteristics need to be screened. Their breeding value can be indexed by studying their general combining ability in test crosses to a low yielding local variety[11]. The testcross can be made by growing the germplasm collection and the local test variety in isolation, using the tester as a universal pollen parent and removing the male flowers from all plants of the germplasm collection. The following year evaluation of the testcrosses by growing the seed in replicated trials at several different locations and seasons would give the necessary information and useful agronomic traits should be noted at the same time.

Floral mechanism and cross-pollination

Cassava is diclinous, flowers of different sex being separated on the same inflorescence. Female flowers at the base of the inflorescence open first and apical male flowers normally open about a week later. During the flowering season there is great activity among nectar gathering insects and pollen collecting wild bees.

In India many cultivars rarely or never flower[28]. The same problem has been observed within the germplasm collection of several thousand entries at CIAT, Colombia. Cassava has a short day flowering response, but the effect of temperature and its interaction with day length on flowering has not yet been studied. At IITA most cassava clones flower during the period August to January with the peak of flowering occurring during the period October to December.

The stigma remains receptive for up to twenty-four hours, and dried pollen remains viable for six days. Eight to nineteen hours are required for fertilization to occur[6]. Structurally and functionally therefore the cassava flower is well adapted to cross-pollination. Both the stigma and pollen are sticky and pollination is effected mainly by insects, although wind and rain may also be agents. Wild bees are probably the principal pollen vectors as cassava nectar is very attractive to them. Some plants have been observed to attract more bees than others, and this has been found to be associated with greater nectar production which is sometimes so prolific that it can be found on the petioles. Wild bees are most active at high temperature, low humidity and high light intensity.

During the first breeding phases, selection was made among accessions of *M. esculenta*, *M. glaziovii* and *M. melanobasis* for early and profuse flowering characteristics that enhance the outcrossing potential. However, it has been observed that these characteristics are not associated with high yield, but depend on branching habit. Non-branching or indeterminate types flower relatively little since inflorescences, when they occur, develop at the point of branching.

Rogers[34] reported that *M. esculenta* is generally less fertile than other species, but we have not found, under Nigerian conditions, that this is apparently so. Seed matures in about 75–90 days[6]. The fruit has three locules and three seeds, and on average 100 seed weigh 10g.

Hand pollination

Flowers for crossing of both sexes are at the point of opening. Male flowers are collected early in the day and pollinations made during the remainder of the day. Bagging of female flowers before pollination is not practised, unless the particular population is very small and every flower must be utilized. Satisfactory results are obtained when a white paper bag (17 x 9 cm) is used to cover the pollinated flowers and this has proved much more satisfactory than the waxed narrow type commonly used by cereal breeders. Fruits and seeds set readily in most cultivars and families, but there was a 100 percent failure in hand pollinations to Llanera* which set seed only when naturally pollinated, but this could be used as the male parent in controlled crosses.

Germination of seed

Cassava seed germinates irregularly over a period of 2–4 months at ambient temperatures. The percentage germination is generally about 10–40 percent. In the past 'cracking' the seed coat was recommended and produced between 80–100 percent germination within 15–20 days. However, this method was very laborious and many of the seedlings were poor, due to damage to the embryo during cracking. The Federal Experiment Station of Nigeria has developed a most successful wet-heat treatment giving germination of a large number of seed of uniform stand over a short period of time[4,13]. However, at IITA we use unscarified seed, dressed with an insecticide/fungicide and planted directly in the nursery in January/March in shallow drills and kept well watered. At this time of the year, the soil temperature is within the required range and an irrigation regime ensures adequate moisture, resulting in an 80 percent germination within three weeks. By this technique about 12,000 seedlings were produced in 1972 and about 100,000 in 1973. The only problem with this technique is the profusion of weeds. To reduce weed competition, an experiment on preplanting treatments was conducted in order to shorten the days from planting in the field to seedling emergence. A presowing treatment, using wooden flats filled with sieved soil kept well watered and held outdoors resulted in a uniform 85 percent germination within 9 days after planting. A convenient and successful (80–90% germination) method for small experiments is to plant untreated seeds in peat pots

*The quoted use of this Colombian clone suggests that this must have been introduced to West Africa other than by seed. This supposedly high protein clone was for some time regarded as having great potential for improved nutrition in cassava eating areas.

held in black plastic or wooden seed trays. These, if kept well watered, grow equally well outside or in the hotter screen houses.

From a series of experiments on seed germination, it has been proved that light and drastic changes of temperature are not required for successful germination, but that a soil temperature between 30–35°C and regular moisture are essential.

Male sterility

Male sterility is common in cassava[5,8,23,28,31], and it has been suggested by Martin[30] that it could usefully be employed in the hybridization of cassava. We do not however agree, since incorporating this factor would take some time, and technical difficulties might arise. We prefer to produce the required hybrid seed by emasculation of the female plants which is easy because of dicliny. Also, since self pollination is rare, the required hybrids can be produced if a population consisting of a single plant of each clone is planted in several isolated breeding plots. Unlike corn, which requires a large amount of hybrid seed for economic production, cassava relies on vegetative propagation. However, male sterility might be worth considering if true seed was to be used in commercial cassava production on a large scale; but this neither seems feasible nor relevant at present.

Genetics in relation to breeding

There is little published information on cassava genetics. Cassava has the karyotype 2n = 36[1,9,14,28,32], and is probably alloploid (i.e. x = 9)*. Abraham[2] produced several 'tetraploids' (2n = 72) which gave a poorer yield than the original (2n = 36) parents: 'triploids' (2n = 54) were superior to the tetraploids.

Doughty[10] and Jennings[23] reported that resistance to cassava mosaic is multigenic. Based on data obtained from about 10,000 segregations in 72 families, it appears that resistance is under quantitative genetic control.[17] From our seven parent diallel cross, it appeared that resistance to cassava mosaic is recessive and has a high heritability of about 60 percent.

Cyanide content appears to be regulated by a complex of minor genes. A cross between two cultivars of low cyanide content produced plants having a much lower content than either of the parents, but the frequency of such transgressive types was very low.

Plot size and replications

Thompson and Wholy[37] have concluded by reviewing experimental work that a minimum of 16 and a maximum of 32 sample plants are needed to give a reliable estimate of yield and have suggested four replications as a minimum.

We applied the method employed by Hatheway[20] to decide by preliminary experimentation a convenient plot size and number of replications for the experimental determination of yield for subsequent work with this crop. Cassava was planted at 1 x 1 m. spacing. If the true difference among clones expressed as percentage of the mean is 13.7 percent in a trial employing four replicates of 16 m^2 than, in order to measure the same true difference, eight replicates would be required for a plot size of 8 m^2, or two to three replicates for a plot size of 32 m^2. We decided that to conduct yield trials for ten varieties in a convenient way, a plot size of 4 x 12 m will be used, but harvesting only the central 2 x 10 m, and using four replications would be satisfactory.

BREEDING METHODS

Introduction

Several methods have been used before in cassava breeding, but systems which have been recently developed and most successfully used by breeders of other crops have not previously been applied to cassava.

A breeding plan is required which will allow efficient selections from the variability and genetic potential of breeding populations.

Our short term objective is to collect and evaluate local clonal cultivars. This is to be followed by hybridizing amongst those selected ones. We need to find clones that will complement each other and produce good hybrids with each other that can then in turn be cloned. This should be easier than trying to break linkages and obtain all the favourable genes and gene combinations into one seed propagated variety, as is necessary in a non-vegetatively propagated crop.

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*Ed.

Conventional breeding systems

The early techniques, which were probably carried out by all the cassava growing countries which had facilities to do so, consisted of:

1. Collection and observation of a many local clones as possible.
2. Selection of the best of these for immediate use and for producing hybrids.
3. Selection of the best plants within hybrid populations.
4. Comparison of yield potential and other important agronomic traits of the cloned hybrids.
5. Evaluation of the best selections in local and district trials, followed by general distribution.

Such an approach would be followed by introducing additional germplasm from various sources and screening and using this in the same way as the local germplasm.

Intervarietal hybridization

When a desirable hybrid (heterozygote x heterozygote) plant is obtained, it can be issued as a clonal variety after testing. Genetic 'fixation' is unnecessary. If, however, a gene or genes which determine a desirable character is recessive, then as F_2 generation will need to be produced to bring such a gene into a homozygous state or further crossings may be made between selected plants to create desirable recombinations. It is necessary to have as large a population of clone x clone seedlings as possible because each plant will be genetically distinct at this stage and thus provide a source population for selection. In a vegetatively propagated crop, provided the first cross can be made, the parental material may come from many diverse sources, including wild species and those having different chromosomes or genomes.

Interspecific hybridization

Incorporation into cultivars of useful genes from related species appears to be of great possible value in a cassava breeding programme.[28] Since almost all the related *Manihot* species can be crossed with cassava[36] the entire genus *Manihot* can probably be considered as a common pool of germplasm from which desirable genes can be drawn for cassava improvement.[30] However only a few *Manihot* species have so far been used. *M. glaziovii, M. catingea, M. saxicola, M. melanobasis* and *M. dichotoma* have been used as sources of resistance to cassava mosaic and insect attack, for high protein content and for drought tolerance. Incorporation of resistance to cassava mosaic by crossing cassava with *M. glaziovii* has been particularly successful. It has recently been observed within our screening that this interspecific cross also produces a high degree of resistance to cassava bacterial blight (*Xanthomonas manihotis*). It is thus anticipated that a useful potential exists for obtaining from other *Manihot* spp economically desirable characteristics not found within *M. esculenta* itself.

However, the methodology of accomplishing the introduction of traits, which are frequently quantitative in inheritance, into cultivated cassava needs investigation. Backcrossing, followed by selection, has been used extensively[2,3,23,25,29], to introduce new genic sources from related species. Two or three backcrosses to adapted cultivars were made, in general, in order to incorporate the resistance to cassava mosaic disease of *M. glaziovii*, but except for this resistance, no overall improvement in cassava was achieved.

There is a great need for breeders to develop a methodology to introgress exotic germplasm most efficiently into their breeding populations, recombine simultaneously among genes from more than two germplasm sources but retain desirable gene complexes built up within the crop species during recent evolution and breeding.

The major problem of using exotic germplasm is how to effect the integration of the special features desired from the wild forms in a sufficiently short time to make the effort economically worthwhile.

Mackey[27] has proposed a modified convergent crossing that might be worth considering since it provides more opportunity for retaining good gene complexes and combinations already present in the current elite adapted varieties; and for the inclusion of any desired percentage of unadapted germplasm in the breeding population. The adapted germplasm in a given convergent cross may come from one, or many adapted varieties. This approach has been used in our breeding programme to incorporate the resistance of *M. glaziovii* to both cassava mosaic and bacterial blight into adapted local cultivars. Three-way crosses instead of single crosses have been effective for introgressing new germplasm into breeding populations[16]. Efron and Everett[12] suggested making a series of hand crosses between adapted and exotic material, and growing out the hybrids as a population, allowing natural random crossing in subsequent generations.

Population improvement

Several cassava breeders have already recognized the importance of improving base populations in order to provide more desirable sources of new genotypes. As cassava is normally cross-pollinated, uncontrolled crossing usually takes place accompanied by a high degree of seed setting. Nevertheless one might expect a certain degree of self-pollination in the absence of self incompatability. It should be borne in mind, moreover, since flowering times differ among individuals, complete parental representation might prove difficult and uncontrollable.

As we look ahead to the next decade, we believe that outcrossing will therefore not equate to 'random mating'. Our greatest yield advances in both quantity and quality in cassava are likely to come from the use of improved populations developed through cyclic selection and recombination.

Breeding schemes are needed which can provide continuous genetic upgrading of the breeding populations through new germplasm introgression, with opportunities for the selection of individuals from continuous improved recombinations.

Cassava breeders are fortunate in dealing with a plant with a flowering mechanism which makes it easy to achieve a large number of cross pollinations with minimum effort, and in the case of vegetative propagation which provides quantities of planting material for testing any particular genotype.

PROGRESS IN THE BREEDING PROGRAMME AT IITA

In 1972, about 12,000 seedlings were raised comprising three main groups:

1. Open-pollination among Nigerian local cultivars.
2. Hybrids among the selected Nigerian cultivars.
3. Seed introductions from Latin America and Asia.

The populations were screened for resistance to diseases, especially cassava mosaic and bacterial blight; evaluated for reaction to insect attack, plant conformation, and tuberous root characteristics. From these, about 1,200 promising individuals were selected and planted out as clones in rows for preliminary evaluation of yield potential, dry matter percentage, starch content and quality, and various other agronomic traits. Many clones resistant to cassava mosaic and bacterial blight were obtained from groups 1 and 2 but most of the plants from group 3 were highly susceptible. About 1,000 individuals representative of each selected clone, were planted in isolation to produce the base population for mass selection and comprehensive breeding schemes.

About 100,000 seedlings were raised in February-March of 1973, and screened for resistance to cassava mosaic and for acyanogenesis. A large number of individuals having resistance to the disease and low cyanide content were obtained. In September—October, about 50 promising families from various sources were selected and planted out in isolation to start a half-sib family selection scheme. These were planted in replicated trials interplanted with basal root-cuttings of those plants showing the best root characteristics (short, fat, compact and uniform). A second selection of about 3,000 individuals was made amongst all families, primarily on conformation. However, for certain exotics a considerable number of selections was made of the vigorous plants irrespective of conformation in order to provide as many different sources of genetic diversity as possible (in the population). These were planted in rows for evaluation in the dry season, and a further selection will be made in March—April for wet season evaluation. About 1,000 root stocks selected from the first 3,000 selections (chosen for desirable characteristics) have been planted out in isolation to provide a germplasm reservoir and to apply various selection schemes for population improvement.

It is now known that resistance to cassava mosaic is controlled by quantitative genes, appears to be recessive and has a high heritability of about 60%. Cyanide content appears to be regulated by a recessive minor gene complex, and resistance to cassava mosaic and bacterial blight appears to be associated, the resistance to both coming from *Manihot glaziovii.* It appears that tuberous root characteristics are highly heritable and that selection for them is possible at the seedling stage. Significant variety-season interaction and varietal competition have also been noted.

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