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CASSAVA BREEDING.

A Multidisciplinary Review



**Proceedings of a workshop held in the
Philippines, 4-7 March 1985**

United Nations Development Programme (UNDP)
Centro Internacional de Agricultura Tropical (CIAT)
International Institute of Tropical Agriculture (IITA)
Philippine Root Crop Research and Training Center (PRCRTC)
Visayas State College of Agriculture (VISCA)

Cover photo: Microphotograph of cassava pollen grain germinating on a stigma.

CIAT, Centro Internacional de Agricultura Tropical, is a nonprofit agricultural research and training organization devoted to the goal of increasing sustainable food production in tropical developing regions. CIAT is one of 13 international agricultural research centers under the auspices of the Consultative Group on International Agricultural Research (CGIAR).

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CASSAVA BREEDING: A Multidisciplinary Review

**Proceedings of a workshop held in the
Philippines, 4-7 March 1985**

Technical editor: Clair H. Hershey



UNDP United Nations Development Programme



Centro Internacional de Agricultura Tropical



IITA International Institute of Tropical Agriculture



PRCRTC Philippine Root Crop Research and Training Center



ViSCA Visayas State College of Agriculture

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Foreword

Human population in tropical countries, at present somewhat over two billion, is expected to increase by about 50% by the year 2000. The concomitant need for increased food production is obvious. The dramatic contributions of the green revolution in the 1970s to rice and wheat production have not been extended to other crops to nearly the same degree. There is a growing consensus among agricultural workers that further quantum leaps in productivity of wheat and rice are unlikely in the near future, except in isolated areas, and that other major crops need to receive concentrated research emphasis to increase their productivity and/or extend their range of adaptation to new areas.

The fact that some of the most important tropical crops are grown under rainfed, variable, conditions precludes breeding for wide adaptability of single varieties across extensive geographic regions, as was accomplished for rice and wheat which were under irrigation, pest and disease protection, and high fertilization. Thus, the approaches to achieving increased productivity are likely to be different from those of the green revolution wheats and rices.

Although cassava breeding by national government agencies began in the first half of this century, the crop has received considerably less emphasis on genetic improvement than most other major food crops. This may be in part due to the early widespread perception that cassava had few problems requiring improvement through breeding. Also, since it is grown primarily by small farmers, government research agencies tended to give cassava little attention.

This workshop brought together, for the first time, cassava breeders and scientists in related fields from the three major cassava-producing continents to discuss the latest advances in cassava breeding research and exchange ideas on future priorities. As the cassava breeding literature is sparse, interpersonal communication in symposiums or workshops, such

as this one, plays an especially important role in information exchange. Although other international forums, such as the triennial symposiums of the International Society for Tropical Root Crops, also provide opportunity for updating on cassava breeding research, this workshop concentrated only on breeding topics, and therefore allowed much more intense discussion of issues specifically relevant to breeding.

Dramatic changes in cassava breeding research have come about in the past 20 years. To cite one example, the number of references to cassava in *Plant Breeding Abstracts* (PBA) in the five-year period from 1960 to 1964 averaged just seven per year. From 1980 to 1984, this increased to about 50 per year. Although other factors may be involved (such as the number of journals being searched) this is probably a reasonable reflection of the increase of interest in, and knowledge about, cassava breeding and related fields such as genetics and cytogenetics. To put these figures in a different perspective, however, the 1960 volume of PBA carried 160 references to rice, and in the 1980 volume, about 720.

Cassava is unique in its agricultural niche: the crop has very high yield potential under favorable conditions, but its marked comparative advantage is its ability to produce well in less favorable environments, especially drought-prone areas and on acid infertile soils. Most breeding programs now orient their research with a goal of breeding for efficiency in suboptimal conditions, in contrast to the emphasis on breeding for yield potential which was common just five or ten years ago. The concern for breeding for yield *stability* is equal to or greater than that of breeding for yield potential. In the same vein, a low-input philosophy of integrated pest-and-disease management, based on host-plant resistance, has come to the forefront in recent years. Basic knowledge of biology, epidemiology, and life cycles is contributing to setting breeding priorities and improving resistance evaluation techniques. Although still rudimentary, inheritance of important adaptation, yield, resistance, and quality traits is being elucidated.

Some of the novel approaches to plant germplasm management and breeding are already being applied, for example, germplasm conservation and international exchange of vegetative material as aseptic *in vitro* cultures. Other techniques are being researched, such as anther culture for haploid production, embryo culture, somatic embryogenesis, cryo-preservation of seeds and meristematic tissue, protoplast fusion, *in vitro* selection, and recombinant DNA and gene-transfer technology. These techniques are actual or potential tools in the total crop-improvement

picture. The present fascination with these techniques by the general scientific community should not detract from the need for breeders to make optimal use of all the tools available to efficiently solve specific problems and achieve designated goals. These goals should be determined by a combination of biological and socioeconomic criteria, and require an interdisciplinary approach to problem solving.

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Cassava Germplasm Resources

*Clair H. Hershey**

Introduction

Success in a crop-breeding program depends on a wide variety of preconditions. Among the most basic of these is a thorough understanding of the germplasm resources available. The basic genetic diversity available to the breeder is normally the consequence of natural selection over many centuries added to by the more recent selections by farmers. The breeder must know where this variability exists, its characteristics, how to access it, and how to utilize it in a productive breeding program. This set of knowledge is generally placed in the category of "germplasm resources" and includes the topics of origin and evolution, dispersal, collection, conservation, evaluation, documentation, and utilization.

This paper will review only briefly the origin and early dispersal of cassava, collection methods, and existing collections, as these aspects of cassava germplasm resources have been adequately reviewed elsewhere (Byrne, 1984; Gulick et al., 1983; Leon, 1977). The later sections will look in more detail at the evaluation and utilization of cassava germplasm, with an emphasis on applied breeding aspects.

Origin and evolution

The evolutionary history of cassava, like that of other root and tuber crops, has been difficult to trace. Archaeological remains are rare for fleshy plant parts, especially in the lowland humid tropics. The most apparent and basic conclusion is that cassava is a New World crop with origins in the lowland tropics. Studies of processing artifacts from Colombia and Venezuela give evidence of cassava cultivation as early as

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3000 to 7000 years ago (Reichel-Dolmatoff, 1957 and 1965; Rouse and Cruxent, 1963).

Recent reviews of the accumulated evidence have generally concluded that cassava has multiple origins (Renvoize, 1973). Harlan (1971) has suggested that cassava is noncentric, that is, with no obvious center of origin or of diversity. He also showed that areas of diversity need not correspond to centers of origin of a crop. Spath (1973) suggested four separate areas of origin: Guatemala and Mexico, the coastal savannas of northwestern South America, eastern Bolivia and northwestern Argentina, and eastern Brazil. Box and de la Rive Box-Lasocki (1982) postulate that types with high or low content of hydrogen cyanide (HCN) in the roots may have originated independently in Middle and South America. The high-HCN types were dispersed along the major rivers while the low-HCN types were found in drier areas (savannas). More recently, though, the low-HCN types have spread throughout South America.

Based on extensive studies from southern United States to Argentina, Rogers and Appan (1973) defined, within the genus *Manihot*, 98 species widely distributed throughout the lowland tropics of the Americas. Nassar (1978) defined four centers of diversity of the wild species: central Brazil (southern Goias and western Minas Gerais) with 38 species; western Mexico with 19 species; and two lesser centers, one in northeast Brazil and the other in western Mato Grosso and eastern Bolivia (Figure 1). The three Brazilian centers have some species in common, most notably from the heterophylla section which is closely related to the cultivated species (Rogers and Appan, 1973).

The groups of species from the northern and southern hemispheres are markedly distinct. With the exception of *M. esculenta*, none of the northern Middle American species are found naturally in South America, and only *M. brachyloba* occurs in both South and Central America.

Rogers and Appan (1973) hypothesize on the basis of taxonomic criteria that the genus *Manihot* is relatively recent in origin and that, in general, the species are still rapidly evolving. There appear to be no sharp genetic delimitations among species. They are variable with respect to vegetative structures, but relatively uniform in their floral organs.

The species of *Manihot* are perennial and vary in form from caulescent shrubs to trees with trunks 25 cm in diameter and a height of 10 to 12 m. They are generally sporadic in their distribution and never become dominant members of the local vegetation. Most are encountered in dry regions, with a few in rainforest ecosystems. Those found in rainforest

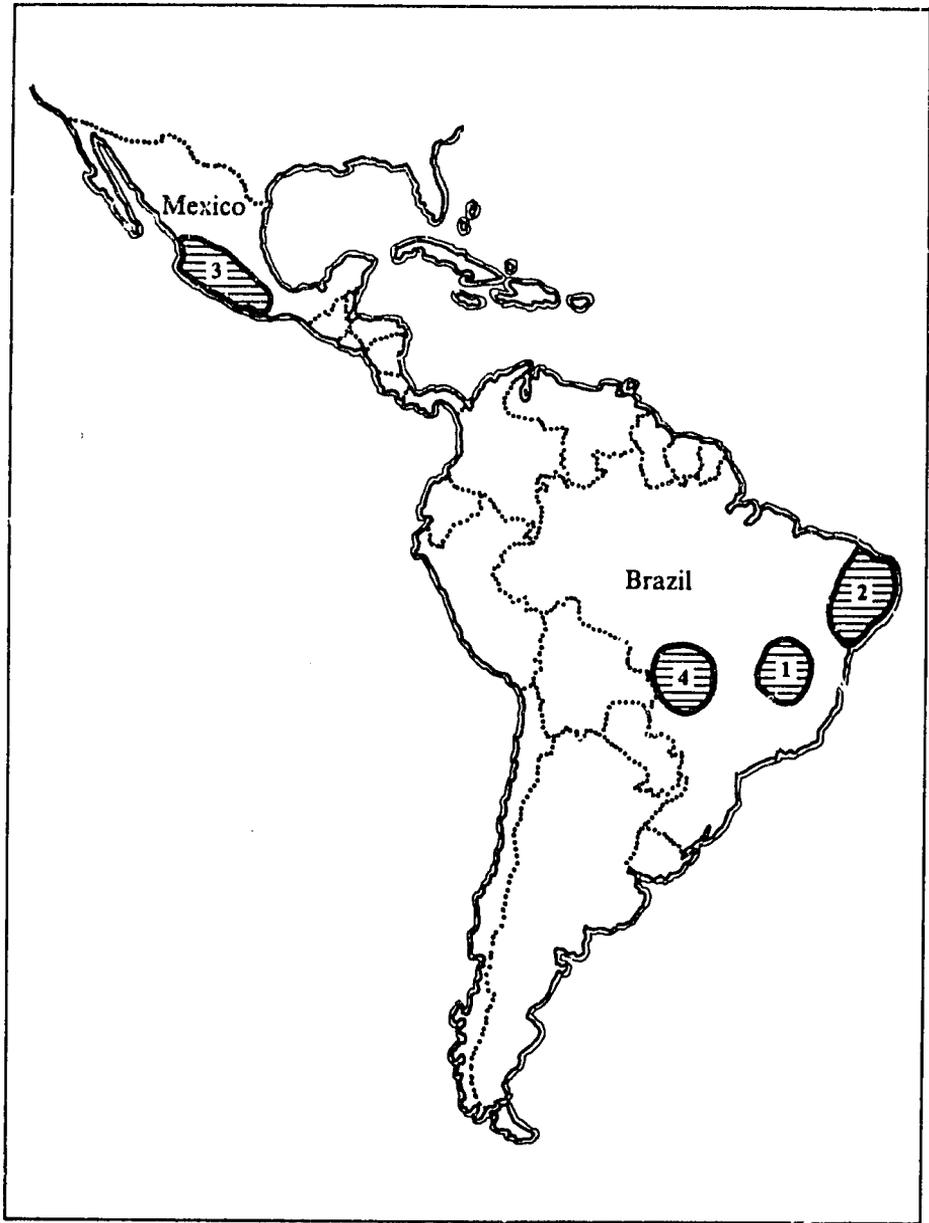


Figure 1. Centers of diversity of *Manihot* species. Numbers indicate descending order of species diversity. (Adapted from Nassar, 1978.)

areas are usually invaders after clearing of the forest. Thus, the species in *Manihot* appear to be shade-intolerant—capable of survival only with plenty of sunlight. They are not good competitors with vigorous intercrops or with weeds.

All the species are sensitive to frost, thus limiting their distribution to elevations below about 2000 m. Only two species (*M. grahami* and *M. anisophylla*) are found in regions of occasional, but predictable, frosts.

As many of the species are found where long dry periods are common, they have evolved mechanisms of drought avoidance or drought tolerance. One of the most notable of these mechanisms is the production of storage roots where large amounts of starch are accumulated. In all species studied, these storage roots also contain the glucoside linamarin, which breaks down after cell injury to release prussic acid (HCN). The evolutionary significance of HCN is not well understood. Theories that it may be associated with pest or disease resistance, or to higher yield potential have not been confirmed by experimental results. However, resistance to rodents and other rooting mammals through HCN production is likely.

Cassava appears to have evolved under highly localized biological and physical influences. Because of early and wide dispersal of the crop and relatively low levels of genetic interchange among regions, many distinct and locally adapted gene pools evolved. Although normally vegetatively propagated, cassava frequently produces seeds which give rise to new variability in traditional farming systems. The plants derived from these seeds may be recognized by farmers as being potential new varieties and given special care to compensate for their lower vigor at the initial stages. Thus, the farmer-breeder contributes to crop evolution.

Characterization of nearly 2000 cassava clones from Colombia illustrates what has no doubt occurred throughout the American tropics. The collection from the Centro Internacional de Agricultura Tropical (CIAT) was evaluated for a wide range of traits and then grouped according to area of origin within the country. Figure 2 illustrates the patterns that emerge for resistance to cassava bacterial blight, superelongation disease, cassava green spider mite, and concentric ring leaf spot; and for harvest index and root dry-matter content. Many other similar examples could be given. The patterns for disease-and-pest resistance closely correspond to their severity in a region: where the problem exists, resistance has evolved; where the problem does not exist, clones are generally susceptible. High dry-matter content is a general characteristic of the north coast clones and, to a lesser

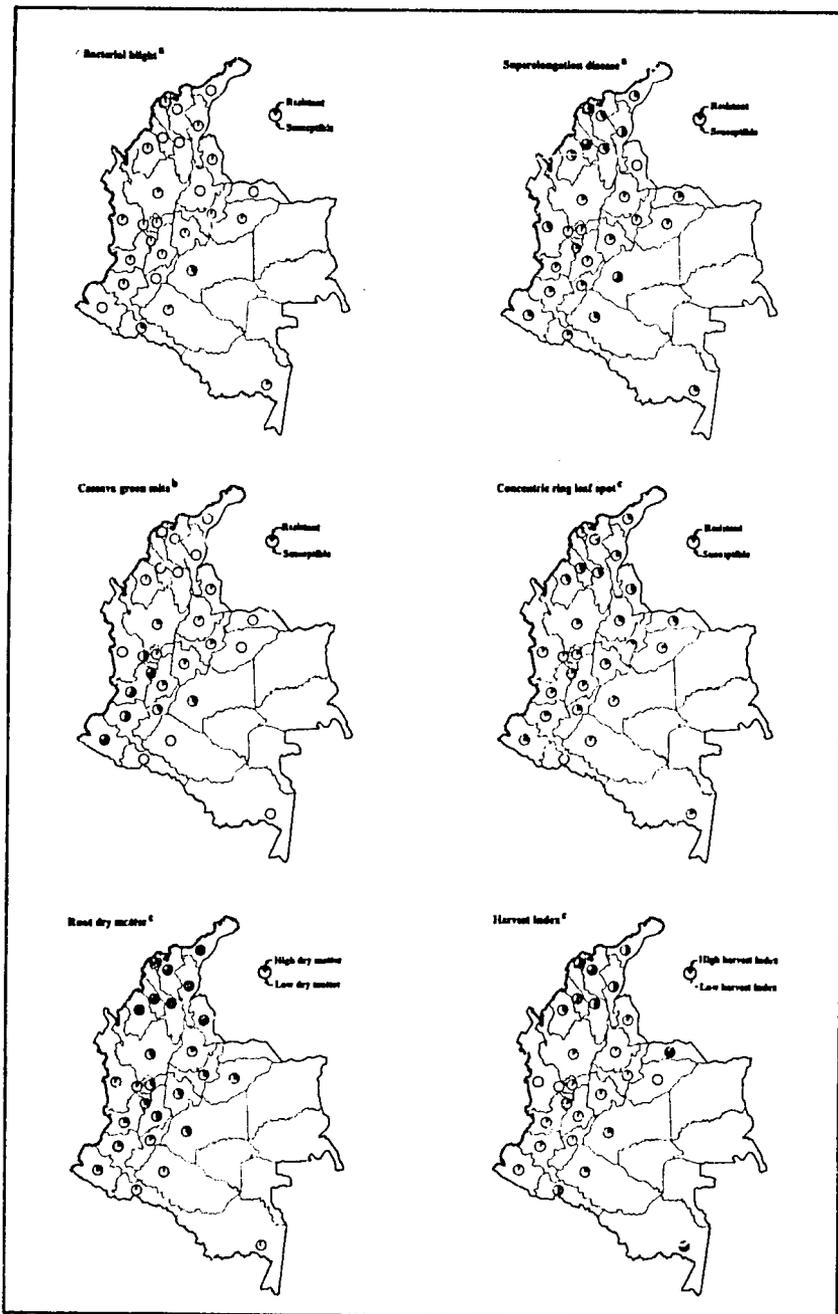


Figure 2. Classification of Colombian cassava germplasm for agronomic characteristics by area of origin. a = evaluation in Carimagua; b = evaluation in Popayan; c = evaluation in CIAT.

degree, of those from the Andean zone. In both areas quality for fresh consumption has been selected for over many years. High harvest index is also typical of the clones of the north coast region, which may be the result of evolution and selection under cropping systems and cultural practices where a high competitive ability (that is, large top growth) was less essential than in other regions. Knowledge of these and other patterns of evolution are critical to the efficient utilization of germplasm.

Dispersal

Cassava was widely distributed throughout the Americas and the Caribbean by the time the European colonists arrived in the 15th century. First exportations were made from Brazil to West Africa by slave traders in the 1500s. Cassava may have been introduced to Central Africa along trade routes from the Congo Basin. An independent introduction was made by the Portuguese to East Africa, first to the island of Réunion in 1739, probably from there to Madagascar, and then to the mainland (Jones, 1969). The original introductions were very limited in terms of genetic diversity. Nevertheless, in the slash-and-burn system widely practiced in the rainforest areas of Africa, it is likely that clones cross-pollinated and superior seedlings were selected and multiplied to become new varieties. Thus, when Beck began a cassava-improvement program in Nigeria in 1954, he was able to collect more than 450 morphologically distinct local cultivars (Beck, 1982). A similar range of diversity has been found by other workers in Africa. Although the number of clones introduced to Africa was apparently small, the high heterozygosity of these clones resulted in the possibility for good local selection for a range of conditions.

Early introductions to Asia are less well documented than those to Africa. One of the first introductions was apparently from Mexico to the Philippines in the 17th century, with later introductions to Indonesia and the Asian mainland. Introductions were probably made to India from East Africa sometime in the 19th century. With the establishment of breeding programs in South America, Africa, and Asia in the mid-1900s, the distribution among regions has accelerated.

Collection

The systematic collection of cassava germplasm did not begin until the mid-1900s and then only on a regional basis. The first large international collections were assembled only recently, with the largest of these now held

at CIAT in Cali, Colombia. Collection of cassava germplasm has been almost strictly based on collection of vegetative material.

A working group on cassava, sponsored by the International Board for Plant Genetic Resources (IBPGR), with representatives from Latin America, Africa, and Asia, recently defined collection priorities in cassava and wild *Manihot* species, with emphasis on the centers of diversity in Latin America (Figure 3). Collection in Asia and Africa may be less urgent because of the lesser genetic variability, but it is necessary to define existing variability, prevent genetic erosion of locally selected clones, and give breeders a broader genetic base for breeding. These priorities are based on the best available estimates of areas of genetic diversity, previous exploration, and potential for genetic erosion (Gulick et al., 1983; Patiño and Hershey, 1981). In recent years the IBPGR, CIAT, and various national programs have been collaborating to collect cassava and wild species on the basis of these priorities.

Conservation

At least 28 countries are known to have local, regional, or international collections. Table 1 lists the largest of these, which are at: CIAT in Colombia with 3680 accessions, Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA) in Brazil with 1960 accessions (at various locations), International Institute of Tropical Agriculture (IITA) in Nigeria with 1286 accessions, Central Tuber Crops Research Institute (CTCRI) in India with 1279 accessions, and Central Research Institute for Food Crops (CRIFC) in Indonesia with 700 accessions (Gulick et al., 1983). The Instituto Nacional de Investigaciones Agrícolas (INIA) in Mexico, the Centro Nacional de Recursos Genéticos (CENARGEN) in Brazil, and the Universidade de Brasília, also in Brazil, have the largest available wild *Manihot* collections. Conservation of the wild species is difficult because many are not easily propagated either sexually or vegetatively. Recent work on in vitro culture shows promise for the conservation of some of the species (CIAT, 1984).

Conservation of vegetatively propagated crops has always been laborious and costly relative to seed conservation. Nevertheless, it is often useful to maintain the specific gene combinations which have resulted from decades or even centuries of selection by farmers. Since cassava is highly heterozygous, the only means of conserving these specific gene combinations is through vegetative propagation. Alternatively, if the interest is

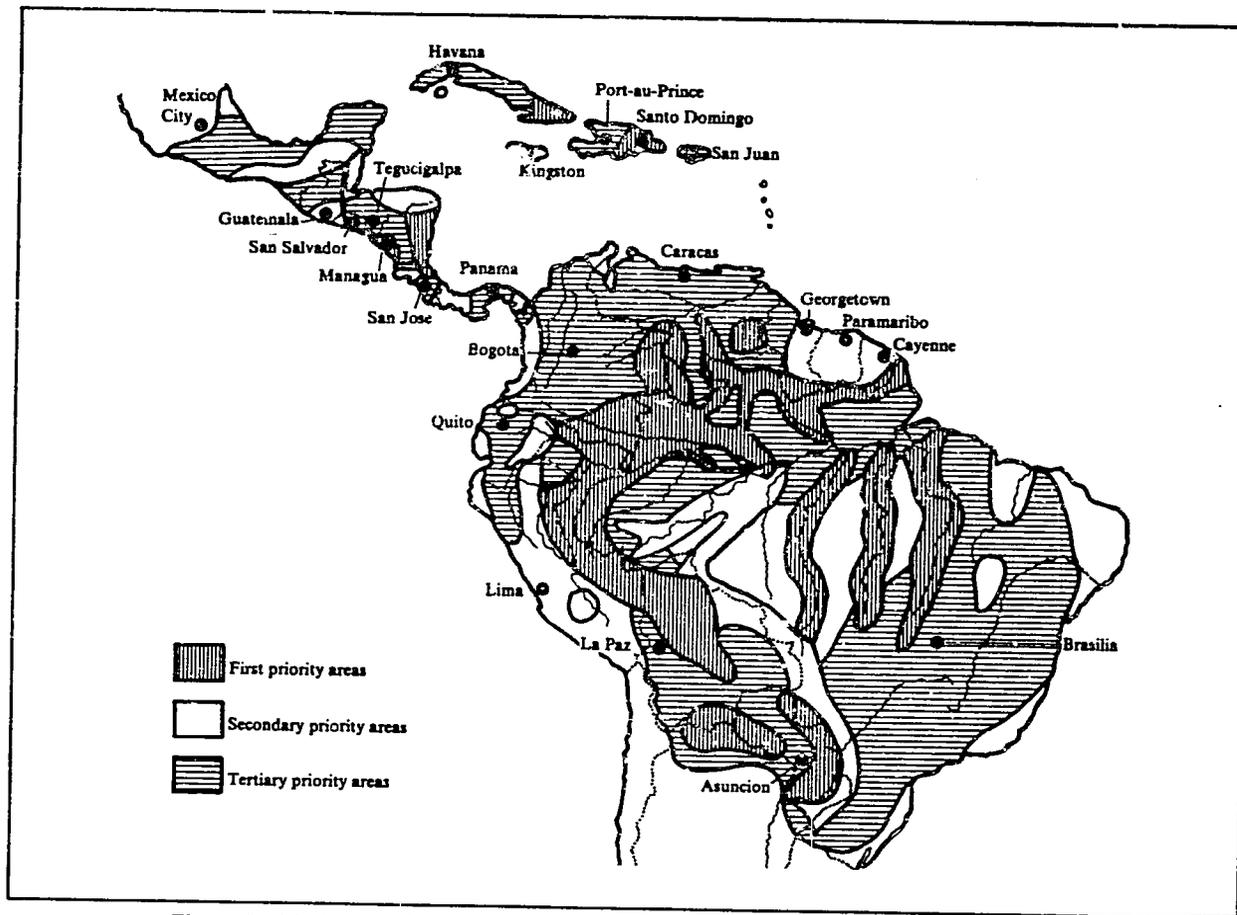


Figure 3. *Priority areas for collection of cassava in Latin America. (Adapted from Gulick et al., 1983.)*

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Table 1. Major cassava collections of the world.

Organization with collection ^a	Details of samples	Geographical representation	Maintenance
CNPMF/EMBRAPA	750 cultivars (cvs.), 12 species of wild <i>Manihot</i>	Brazil, Colombia	Plants
Dep. Agron., Univ. Brasília (Brazil)	21 species of wild <i>Manihot</i>	Brazil	Seeds
CIAT	3680 cvs., 7 species wild <i>Manihot</i>	Throughout Latin America and Caribbean	Plants, in vitro, some seeds
CTCRI	1279 cvs.	Mostly India, also S.E. Asia, S. America, Africa	Plants
CRIFC	700 cvs.	Mostly Indonesia	Plants
IITA	1286 cvs.	East and West Africa, Venezuela, Colombia, Brazil	Seeds and in vitro
National Cassava Center (Umuahia, Nigeria)	1060 cvs.	Mostly Nigeria	Plants and seeds

a. Acronyms of organizations are:

CNPMF: Centro Nacional de Pesquisa de Mandioca e Fruticultura, Cruz das Almas, Bahia, Brazil.

CRIFC: Central Research Institute for Food Crops, Subang, West Java, Indonesia.

CTCRI: Central Tuber Crops Research Institute, Trivandrum, India.

EMBRAPA: Empresa Brasileira de Pesquisa Agropecuária, Cruz das Almas, Bahia, Brazil.

IITA: International Institute of Tropical Agriculture, Ibadan, Nigeria.

SOURCES: International Board for Plant Genetic Resources (IBPGR), Rome, Italy.

Centro Internacional de Agricultura Tropical (CIAT), Cali, Colombia.

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the conservation of genes rather than of genotypes, germplasm could be maintained as true seed. Germplasm maintained in seed form would be useful principally as a source of genes in a breeding program and not directly as a source of varieties.

Cassava collections have traditionally been maintained in field plots. Stem pieces are used as the propagules just as in commercial production. Theoretically, such a germplasm collection could be maintained for many years without regeneration. However, in practice, maintenance problems often increase after a year or two, making replanting necessary at more frequent intervals. Common problems include lodging from excessive growth and buildup of pests and diseases. A major advantage of maintaining collections in field plots is that they provide continuous availability of planting material for evaluations.

Recently, techniques have been developed for *in vitro* maintenance of cassava. The basic procedure is to cut sterile meristem tips, place them in nutrient media in test tubes, and maintain the cultures under controlled light and temperature conditions. Under minimum growth conditions cultures can be maintained for 18-24 months before renewal (Roca, 1983). Facilities exist at CIAT with the potential capacity to hold 6000 accessions *in vitro* under the following conditions: 20 °C (day), 15 °C (night), 12-hr photoperiod, and 500-1000 lux illumination. Renewal can be done by planting stem pieces or meristem tips from the *in vitro* plantlet into new sterile media without the need for a field propagation phase.

Advantages of *in vitro* conservation are the small space requirements, low upkeep costs, and minimal possibility of loss through diseases, pests, climate, or soil factors. Disadvantages are the need for relatively sophisticated facilities for culturing sterile plantlets and maintaining reliable conditions.

A promising possibility for vegetative conservation is storing meristem tips in liquid nitrogen. Procedures are still at the experimental level, but successful regeneration of cryopreserved clones has been recently accomplished (Kantha et al., 1982). The major problem has been the low rate of recoverability—which should be possible to improve through further work with cryoprotectants and with freezing and recovery techniques. Genetic stability could also be a concern, but preliminary tests have shown no noticeable changes in plant characters after cryopreservation. The major advantage is the virtual freedom from maintenance problems during storage. Conservation could theoretically be done indefinitely with no need for renewal.

Seed conservation in cassava has received limited attention. Recent research, however, has shown that cassava seeds are probably orthodox in behavior and therefore can be stored under conventional conditions of low humidity and low temperature. IITA has reported storing seeds at 5 °C and 60% relative humidity for up to seven years with no loss in germination ability (IITA, 1979). CIAT has maintained a small collection of open-pollinated seed obtained from the field collection for five years under similar conditions. Preliminary observations suggest that cassava seed can also be preserved in liquid nitrogen, if frozen slowly and thawed in warm water (Mumford and Grout, 1978).

Apart from the mechanics of seed storage, further studies are needed to define appropriate methodologies for seed production. First, basic populations need to be delineated in terms of origin, morphological or agronomic characteristics, biochemical features, or other criteria. In order to preserve the integrity of these populations, care must be taken to: avoid contamination by foreign pollen through isolation; avoid random drift by using an adequately large number of basic plants; achieve random mating; avoid shifts through natural selection, particularly for high seed production; and ensure the highest possible yields of good quality seed to minimize subsequent regenerations.

These criteria are not easily met in cassava and much basic work needs to be done before even considering a seed germplasm storage system. The long-term advantages, however, warrant some work in this area.

Evaluation

A germplasm collection is useful as a resource to breeders only insofar as accessions are described in terms of characteristics of interest. Agronomic evaluation and selection are normally closely linked activities and therefore it is essential either that they are carried out within the same interdisciplinary team or that the persons carrying out the two activities have close communication. Most of the criteria developed for germplasm evaluation also apply to evaluation of breeding lines as there is no sharp distinction genetically between the two.

The IBPGR has developed, according to working group recommendations, a descriptor list for cassava as shown in Table 2 (Gulick et al., 1983). Descriptors are divided into two categories: characterization, that is, the recording of those characters which are highly heritable, easily seen by the eye, and expressed in all environments; and preliminary evaluation,

Table 2. Descriptors recommended by IBPGR for characterization of cassava.

Leaves and petioles	Stems	Roots
Color of unexpanded apical leaves	Stem color	Storage root surface color
Color of first fully expanded leaf	Number of levels of branching	Storage root pulp color
Shape of central lobe	Angle of branching	Root HCN ^a content
Petiole length	Height of first apical branch	
Petiole color	Height to top of canopy	
Pubescence of young leaves		

a. HCN: hydrogen cyanide.

SOURCE: International Board for Plant Genetic Resources (IBPGR), Rome, Italy.

which consists of recording a limited number of additional traits of lower heritability thought desirable by a consensus of users of the crop.

Although these descriptors cannot be considered definitive, the generalized use of this scheme will produce a rapid, reliable, and efficient means for information storage, retrieval, and communication, and subsequently augment the utilization of germplasm. Characterization is important, basically, as a tool for varietal description and for identification of duplicates in a collection.

Isozyme systems have now been identified for use in cassava characterization (Table 3). Electrophoretic techniques have been validated with 12 isozymes, two buffer systems, and two tissues (young nodes and root tips). These techniques will provide a powerful tool for duplicate identification, for monitoring genotypic stability of clones stored *in vitro* or in other nonconventional forms, and for varietal fingerprinting.

For purposes of discussion, preliminary evaluation can be divided into six aspects: general adaptation, resistance, plant architecture, yield, root quality, and other locally important traits.

Table 3. Isozymes and buffer systems for evaluation of cassava stored in vitro.

Isozyme	Buffer system	
	Standard ^a	PC ^b
Acid phosphatase	+	
Alcohol dehydrogenase	+	
Glutama-oxaloacetate-transaminase	+	
Glutamate dehydrogenase		+
Isocitric dehydrogenase		+
Malate dehydrogenase		+
Malic enzyme	+	
Peroxidase	+	
Phosphogluco-isomerase	+	
Phosphogluco-mutase		+
6-phosphogluconate dehydrogenase		+
Shikimic dehydrogenase		+

a. Extraction buffer: tris-malate; electrode buffer: lithium borate.

b. Extraction buffer: potassium phosphate; electrode buffer: potassium phosphate and citric acid.

SOURCE: Centro Internacional de Agricultura Tropical (CIAT), 1985b.

A first step is to define the objectives of evaluation. This should seem obvious, but it is in practice often inadequately planned. Collections are often maintained and evaluated by germplasm curators who may have little appreciation of the needs of plant breeders. The need for good communication between the two specializations is apparent. A general objective is usually to identify clones which can be used directly as recommended varieties or as parents in a breeding program. On this generalized objective hinge many other crucial decisions. If the objective of evaluation is to find material for a breeding program, further criteria depend on the objectives of the breeding program, vis-à-vis target production areas and their physical and biological characteristics, management practices to be employed, and market and consumption characteristics.

If large numbers of germplasm accessions are being evaluated, a multiple-stage evaluation may be advisable: small plots such as single, unreplicated rows, are used to discard obviously inferior material in the first cycle and, in later stages, selected clones are more thoroughly evaluated.

General adaptation. General adaptation includes the ability of the plant to germinate and grow reasonably under a given set of environmental conditions. This is basically a physiological adaptation to temperature, light and humidity conditions, and cropping system. Because genotype-

environment interaction is a universal phenomenon in crop plants, it is critical that agronomic evaluation be done under conditions reasonably similar to the target production area in terms of climate and soils. Management practices should be similar to those recommended for commercial production, in terms of land preparation, fertilization, stake treatment, planting system, and weed control, since genotype-environment interaction can be influenced by any of these components.

On a worldwide basis, cassava is generally cultivated on poorer soils and in more marginal areas, so for most programs it is appropriate to evaluate germplasm under the types of stress which are encountered in commercial production fields, rather than to seek maximum productivity under optimal conditions. If the target production area is edaphoclimatically diverse, various evaluation sites should be used. Experiment stations are usually located on the best land, in which case they may not be appropriate sites for agronomic evaluation of cassava germplasm.

Criteria for evaluation of adaptation are not always easy to define, as complex physiological systems may be involved. A methodology which evaluates general growth and vigor during the growing season and yield at harvest is probably most appropriate. Often it is not possible to separate an evaluation for general adaptation as described above from resistance to physical factors or from yield potential.

Resistance. Because pests¹ occur and develop in somewhat unpredictable ways, their evaluation is generally more complicated than the evaluation for adaptation to physical factors. Pest evaluations should concentrate first on those problems of known importance in the target production area (key pests) and, second, on those of potential importance based on edaphoclimatic conditions and geographic proximity of the pest or pathogen.

Many pest problems can be evaluated at the field level. Severity and/or uniformity of distribution within the evaluation field may have to be adjusted to achieve reliable evaluations (for example, by susceptible spreader rows or artificial inoculation). The long growing cycle of cassava facilitates multiple evaluations of pest: in many areas disease evaluations can be done during the rainy season and mite or insect evaluations during the dry season.

A common problem encountered in pest evaluations is the inability to

1. The term "pests" will be used throughout to refer to either arthropod pests or pathogens.

adequately differentiate reaction to individual pests when a complex of problems is present. Various alternatives are possible. If selective fungicides or insecticides are used during given periods, it may be possible to more effectively evaluate individual problems. For some pests, greenhouse or screenhouse evaluation can be used. However, this methodology must be chosen with great care to be certain that the results are highly correlated with field performance. Many reports of greenhouse evaluation techniques are available, but few have proven to be more reliable than field evaluations.

As a rule, the number of pest problems in Africa and Asia are limited (although sometimes severe), so evaluations may be relatively uncomplicated. In Latin America, where a wide range of pest problems evolved simultaneously with the cassava crop, defining an appropriate evaluation procedure can be more complex. Nevertheless, on a regional basis, a small group of the most serious problems can usually be defined and given priority for evaluation.

Plant architecture. Plant architecture in cassava is important for several reasons, including adaptation to specific cultural practices, production of vegetative planting material, and influence on carbohydrate distribution contributing to top growth versus root yield. Much has been written about the ideal plant type for maximum yield (Cock et al., 1979) and the effects of different stresses on yields in plants of differing architecture (CIAT, 1985a; Cock, 1978; Conner and Cock, 1981). The need for excess foliage as an insurance against partial loss to insects, diseases, or other stresses causing reduced leaf area, and the need to produce adequate numbers of high-quality stem pieces for reproduction must be balanced against efficient partitioning of carbohydrates to the roots under optimal conditions.

Plant architecture is also an important consideration for specific cropping systems. Nevertheless, a generalization seems to be that upright, later-branching types are preferable for both intercropping and monoculture systems (Leihner, 1983). Very vigorous plant types have a competitive advantage against weeds, but generally have a low yield potential due to low harvest index.

Yield potential. General adaptation and pest resistance must be combined with good yield potential. Yield potential can be defined in a number of ways. Physiologists tend to think of yield potential as the yield obtained under ideal conditions. However, this definition may have limited usefulness in cassava, where ideal conditions are rarely achieved or even approached under commercial production, for reasons described above. A

more practical definition would be to consider yield potential as the yield obtained under representative edaphoclimatic conditions and under improved management conditions which are economically within the reach of growers in the target area, but where pests and diseases are controlled. This definition allows a practical estimate of potential yields on a commercial scale, where pest-and-disease resistance is to be incorporated, and good (but not luxurious) agronomy is practiced.

Root quality. Requisites for cassava root quality vary considerably, depending upon end use of the product and regional preferences. Three broad categories can be defined as differentiating quality requirements: fresh for human consumption; processed for human consumption; and industrial use. A detailed analysis of different quality requirements for these markets is beyond the scope of this paper, but a few generalizations can be made in terms of evaluation procedures.

For the large majority of end uses, high starch content in the roots is desirable. Several rapid methods to evaluate starch content have been described, based on the high correlation between starch and dry-matter content. For fresh consumption, there are, as yet, no well-defined methodologies for quality evaluation apart from actual cooking tests. A preliminary elimination can, however, be based on dry matter (DM) and HCN content (those with either low DM or high HCN being unacceptable). Rapid qualitative methods of HCN analysis are adequate for a preliminary evaluation, while more sophisticated quantitative analyses can be used at the final stages.

For processed cassava for human consumption, quality requirements are less stringent. For some such uses high HCN is unimportant or even preferred. For industrial purposes quality requirements are generally even less stringent, but requirements do exist: for example, relative to dry matter, fiber, or HCN content, ease of peeling, root color, parenchyma color, and others.

A general suggestion before designing a germplasm evaluation program is that the quality requirements of the actual and potential markets in the region should be thoroughly studied to determine which quality parameters need to be evaluated and the range of acceptability for those parameters.

Locally important traits. In addition to the above generalized evaluation criteria, specific local and regional needs may define other important criteria. Some known examples of these types of traits are root surface

color (light or dark), root parenchyma color (white or yellow), plant type suitable to particular crop associations, characters associated with consumption of leaves as a vegetable, and many others. Only through a complete knowledge of local cultural practices and marketing and consumption patterns can the best evaluation strategy be defined.

Characteristics of landrace varieties

CIAT has done extensive evaluations of its germplasm collection under diverse soil, climatic, and pest conditions (CIAT, 1980, 1981, 1982, 1984, and 1985a; Hershey, 1983 and 1984; Kawano et al., 1978). Some generalized conclusions can be drawn from these evaluations relevant to setting breeding objectives and defining evaluation criteria. The following conclusions apply only in a general, overall sense to cassava germplasm and probably many exceptions could be cited.

Within cultivated cassava, a wide range of diversity exists for nearly all traits so far studied, including morphological, agronomic, and resistance traits. For virtually all pests studied, the resistance ranges from highly resistant to highly susceptible. Yield and quality traits and adaptation to soil conditions cover wide ranges. Although limited to growth in the tropics and subtropics, considerable variation exists in sensitivity to temperature and photoperiod. Variation in physiological processes is only recently being investigated, but indications are that high variability exists in photosynthetic rate, stomatal sensitivity to air humidity, and others (CIAT, 1984 and 1985a).

Although cassava as a species is adapted over a wide range of conditions, the range of adaptation of a given native variety is usually very limited. Most traditional varieties appear to be well adapted to traditional cultural practices but do not respond well to improvement in those practices. Local varieties tested in trials in Colombia have consistently responded less to improved cultural practices than have selected hybrids (Kawano and Jennings, 1980).

Most traditional varieties have evolved with multiple resistance to the pests of a given region (Figure 2). However, these resistance levels are generally low, since pest control in traditional cultivation systems is accomplished not only by varietal resistance, but also by isolation in space, intercropping, burning, and other cultural practices.

Yield potential of the majority of existing accessions is low and is manifested particularly as a low harvest index. Cassava evolved under

cultural systems where competitive ability was highly important both for survival and for reproduction, since stem weight is generally negatively correlated with productivity (Kawano and Jennings, 1980).

A significant number of accessions have favorable characteristics that have not yet been exploited in breeding programs. Genetic recombination will play the major role in the future for producing acceptable genotypes under conditions of improved cultural practices.

Documentation

Few cassava germplasm collections are well documented. Although certain minimal evaluations have been made in many collections, these data are generally poorly organized and difficult to interpret. Among the best documented collections are those of the Centro Agronómico Tropical de Investigación y Enseñanza (CATIE) in Costa Rica (Engels, 1981), CENARGEN, and Centro Nacional de Pesquisa de Mandioca e Fruticultura (CNPMP) in Brazil (de O. Silva, 1981), and CIAT. All have computerized evaluations which are either published or available on request. The extensive nature of the data on large germplasm collections limits the possibility for their wide distribution, but persons with specific interests can request computer searches for the relevant data.

Utilization

The eventual utility of germplasm collections is generally in breeding programs. Special importance will be given here to the principles and procedures for moving from basic germplasm to improved varieties. This is of course a broad subject area involving the whole gamut of plant breeding philosophy and methodology. Only some basic concepts will be discussed in this paper.

In crops with a long history of genetic improvement for modern agricultural conditions, there is generally a large genetic gap between bred varieties and landraces. This is the case for the world's major grain crops—wheat, rice, and maize. In these crops, apart from transferring single-gene or oligogenically controlled traits, the utilization of basic germplasm is a complex process. Along with transferring the desired trait or traits, a whole range of undesirable traits is carried along, and many cycles of recombination may be required to break linkages and return to the desired background genotype.

In cassava this is less of a dilemma. Modern breeding methods have a short history. Although significant gains have been made in breeding, the genetic differences between good landrace varieties and improved varieties are not extreme. Basic germplasm can therefore often be used as a source of any number of traits without major complications normally associated with exotic germplasm. Nevertheless, the efficient utilization of basic germplasm in cassava breeding requires good planning.

The generalized characteristics of cassava germplasm given in the previous section help define some of the basic breeding objectives. The methodology to meet these objectives is not necessarily self-evident. Given that most cassava will continue to be grown under suboptimal conditions, with an array of biological and physical stresses acting throughout the long growing cycle, it becomes clear that no single, simply inherited characters are likely to dramatically increase productivity, especially in the center of origin where biological constraints are many. Further, virtually all important agronomic traits appear to be multigenically controlled. With this situation, it becomes critical to consider a plant genotype as a complex, integrated gene system where it is virtually impossible to modify one character to the exclusion of others.

The most effective utilization of basic germplasm in breeding can often be made, not by looking exclusively for genotypes showing the highest expression of a single trait, but by looking for those showing moderate to high expression in a nearly acceptable genetic background. Through population improvement methods several characters can then be improved over time.

The use of wild species in cassava breeding has been limited, with the most notable exception being the transfer of resistance to cassava mosaic disease from *M. glaziovii* (Hahn et al., 1980). There seem to be few compatibility barriers among the *Manihot* species, however; so potentially greater use of wild species could be made without many of the incompatibility problems that plague other crops. As a general rule, use of wild relatives of crops for transferring individual traits should be a last resort, when insufficient variability is found in the cultivated species.

Some breeders have the concept that introduced germplasm must necessarily be better than local germplasm. But before introduction, a careful analysis of the defects of available germplasm and of the ability of introduced germplasm to correct or improve those characters, is necessary. Until locally available germplasm is well evaluated, introduced germplasm can probably not be efficiently utilized.

International centers and national programs can play complementary roles in promoting efficient germplasm utilization. National programs have the obligation to know first of all what germplasm is locally available, its characteristics, and which of these need to be improved. International centers have a similar responsibility to have their germplasm resources well evaluated and cataloged, and, in addition, available for international exchange. Major germplasm banks, either national or international, should have the ability to identify genotypes which can best complement locally available germplasm.

There is no sharp distinction between the management of basic germplasm and of breeding lines in terms of their utilization in practical breeding programs. In some cases the germplasm needs of a breeding program may be best met with germplasm accessions and in other cases with improved varieties.

A distinction can be made, however, in the manner in which germplasm is received—either as vegetative material or as true seed. By receiving vegetative material, a breeding program receives a clone of known characteristics and probably can identify a priori a methodology for making use of the clone—either testing for possible direct use as a variety or incorporating into hybridization blocks. Material received as true seed is highly variable and is often most appropriately first selected before use as parental material or, alternatively, used directly for selection of improved varieties.

The introduction of germplasm from one region to another, and especially across national boundaries, always entails some risk of pest dissemination. Virus indexing techniques, seed treatment methods, and *in vitro* techniques are all contributing immensely to improve the security of germplasm exchange. Nevertheless, quarantine regulations are highly variable across countries and may be either too stringent or not stringent enough with regard to cassava (Roca et al., 1982). Basic responsibility for assuring the phytosanitary status of materials lies ultimately with both the source and the recipient.

Summary

One of the most promising possibilities for improving productivity of cassava is through genetic improvement of yield potential and resistance or tolerance to physical and biological yield constraints. The immense genetic diversity of cassava has not yet been adequately collected, but is collected to a sufficient degree to provide variability to breeders for nearly all traits

of agronomic interest. Collection and utilization of wild species, however, has been limited, with a few notable exceptions such as transfer of resistance to cassava mosaic disease.

A prerequisite to successful utilization of germplasm is the full evaluation of the available germplasm base under conditions representative of the target production area. Introduced germplasm can have a large impact on genetic progress, especially if the locally available germplasm base is limited.

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Relationship between EMBRAPA (Brazil) and International Research Centers in Cassava Breeding and Germplasm Exchange

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Introduction

Agricultural research in Brazil is carried out by the Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA) which was established as a government enterprise early in the last decade. EMBRAPA coordinates a network of 24 national research centers, 14 of which concentrate on priority crops, 4 on natural resources, 1 on food technology, 1 on pesticides, and 2 on specialized services for basic-seed multiplication and soil surveys. Food crops research and genetic resources receive the highest priority.

Since cassava is a very important crop for low-income people in Brazil and cassava flour is widely used all over the country, the Centro Nacional de Pesquisa de Mandioca e Fruticultura (CNPMPF) was established in 1974 at Cruz das Almas, Bahia State, to develop research on breeding, agronomy, pest control, soils, and physiology to increase cassava yields. At the same time, the Centro Nacional de Recursos Genéticos (CENARGEN) was established in Brasilia to coordinate EMBRAPA's activities on germplasm exchange, collection, conservation, and evaluation, in order to increase the genetic variability of many crops, including cassava.

Cassava collection

CENARGEN, along with several state agricultural research organizations, has collected cassava from many regions around the country. The main goal is to collect specimens of the many cassava landraces and *Manihot* species found in Brazil. Priority collection areas have been established and

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collections are being made, especially in areas with indigenous communities, where crops such as sugarcane and soybeans are expanding, where flooding by large dams will occur, and other areas where *Manihot* germplasm is in danger of being lost. Apart from collection expeditions specific to cassava germplasm, collection expeditions for other crops may also obtain *Manihot* samples. These are brought to CENARGEN and then transferred to CNPMF in vitro.

At CENARGEN, 53 accessions of *Manihot* species are kept as living plants. The conservation of these species presents problems as some are short-lived and others produce few seeds. The collection must be regenerated periodically because it includes many species with interesting traits, such as vertically positioned leaves, high protein content in the roots, or very pubescent plants. To identify the various *Manihot* species, CENARGEN has employed a taxonomist.

Germplasm banks

A national cassava germplasm bank with about 288 accessions was set up at CNPMF in 1976. For this collection germplasm was obtained from the Instituto de Pesquisas e Experimentação Agropecuárias do Leste (IPEAL, now replaced by CNPMF) and the School of Agronomy, both at Cruz das Almas, Bahia. This collection has been increased to nearly 1000 accessions at present. Evaluation and characterization are being made for many traits according to the descriptors recommended by the International Board for Plant Genetic Resources (IBPGR), with some modifications. Plant reaction to diseases and pests is also being recorded. The data are sent to CENARGEN for computer processing and magnetic tape storage.

Because of the wide differences in Brazilian ecological conditions, four other satellite cassava germplasm banks were set up in 1981:

Unidades de Execução de Pesquisa de Ambito Estadual e Territorial (UEPAEs), Manaus, Amazonas (lat. 0°38' S and long. 59°52' W);

Centro de Pesquisa Agropecuária do Trópico Umido (CPATU), Belém, Pará (lat. 1°28' S and long. 48°27' W);

Empresa de Pesquisa Agropecuária do Ceará (EPACE), Pacajus, Ceará (lat. 4°10' S and long. 38°27' W); and

Empresa Capichaba de Pesquisa Agropecuária (EMCAPA), Linhares, Espirito Santo (lat. 19°23' S and long. 40°04' W).

The IBPGR proposed the establishment of an International Cassava Gene Bank in Brazil and suggested that it be included in the International Gene Banks Network coordinated by the Board. The proposal is now under consideration by Brazilian authorities.

Internal germplasm exchange

Brazilian institutions involved in cassava research may request specific accessions from CENARGEN. If, for some reason such as the presence of pests or pathogens, the accession cannot be sent directly from one place to another, it is sent by tissue culture in tubes—in particular to prevent the spread of cassava bacterial blight from the southern part of the country and of superelongation disease from the Amazon region.

In vitro germplasm conservation

A special chamber for cassava germplasm conservation in vitro is operating at CENARGEN. The plan is to have at least the CNPMF germplasm bank stored in vitro. This has several advantages—among them savings in labor and land and decreased danger of losing accessions. All germplasm evaluated and not used in the breeding program will be transferred to in vitro conservation. Germplasm imported in vitro is multiplied before being shipped elsewhere and duplicate samples are kept at CENARGEN.

International germplasm exchange

The cassava germplasm exchange between the Centro Internacional de Agricultura Tropical (CIAT) and EMBRAPA is made in vitro or in seed form. Through CENARGEN, about 72 accessions in vitro and 166 seed families for the CNPMF breeding program have been introduced from CIAT. Nearly 1000 accessions have been transferred in vitro from Brazil to CIAT, as well as seeds of 22 *Manihot* species for embryo culture. In collaboration with CIAT, two expeditions were carried out in Paraguay, with 166 samples collected, including landraces and 25 samples of wild *Manihot* species.

Using financial support from IBPGR and CIAT, 182 accessions were collected in Santa Catarina State by a team from the Empresa de Pesquisa Agropecuária de Santa Catarina (EMPASC). An IBPGR project to

collect cassava and *Manihot* species resulted, in 1984, in two expeditions which collected 98 cassava landraces and 33 *Manihot* species.

Because of the occurrence of cassava mosaic disease in Africa, introduction of cassava germplasm from that continent is prohibited, although 42 seed families and four *Manihot* species have been transferred from Brazil to the International Institute of Tropical Agriculture (IITA) in Nigeria. No more accessions have since been sent to IITA because of strict quarantine regulations which require that material be first sent through England. Work is being done to find natural enemies of the mealybug *Phenacoccus manihoti* and a team sponsored by IITA is set up at Campo Grande in Mato Grosso State. CENARGEN plays an important role in transferring collected insect species to IITA.

Conclusions

A better communication system for the exchange of information would improve relationships between the national cassava programs and the international centers working on cassava.

National and international breeding programs should use the data on germplasm characterization and evaluation to choose the most suitable parents. Progeny should be tested under conditions similar to those where the parents were selected. The breeding programs should also concentrate on producing specific crosses for different ecological conditions, using state agricultural research organization facilities for evaluation and selection.

Brazil is an important center of origin for cassava, and great genetic variability can be found. Cassava is grown between latitudes 5° N and 33° S in tropical and temperate climates. The adaptability of cassava germplasm in Brazil should be explored further to help increase genetic variability and solve problems within the world's cassava-growing areas.

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National Programs and International Centers: Developing an Optimal Working Relationship in Cassava Breeding Research in Africa

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Introduction

The international centers and national programs have the common task of helping farmers address the challenge of the rapidly growing need for food in various countries of tropical Africa. Throughout many parts of the continent drought, diseases, and pests are causing appalling crop losses and inflicting severe human suffering. While many national agricultural programs are aware of these problems, the efforts made to tackle them are, in many instances, limited because of inadequate resources. Complementary collaborative activities between national programs and international centers would be an effective way of facing this challenge.

Farmers in most of these marginal dry ecologies are already growing crops adapted to these conditions, and one of these crops is cassava. Its production is growing, especially in areas with drought periods too long for other crops. Despite the adaptability of this crop to adverse conditions and low production inputs, it is not without its problems of diseases and pests. Addressing these problems by breeding and improving yield potential will enhance the already competitive position of cassava.

This paper focuses on alternatives for collaborative relationships between international centers and national programs, with emphasis on the African situation.

Need for closer linkage

There is a growing trend towards intensifying contact and mutual exchange of information between national programs and international

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centers. However, despite the recognition that root crops may play a crucial role in the food economy of a given country, in most cases, they are not on the priority list for research. Besides the few minor efforts directed toward solving a particularly pressing problem, such as the sudden onslaught of a devastating pest or disease, there is usually no clearly defined research plan or goal.

Questionnaires returned by some root crops researchers in East and Central African countries showed that, of the tropical root crops, cassava is receiving the leading priority. However, the commitment of governments was not commensurate with the problems that need to be addressed. Table 1 summarizes some of the responses from the questionnaires from these 11 countries. There was also a general feeling that there was not enough incentive for some workers.

National programs that have formed strong linkages with the International Institute of Tropical Agriculture (IITA) in Nigeria have, in the majority of cases, strengthened their research capability and created

Table 1. Summary of research standing in root crops from 11 African countries.

	Level of training				Total
	B.Sc.	M.Sc.	Ph.D.	Other	
Personnel available, excluding field technicians	20	2	4	13	39
Persons in training	2	3	0	2	7
Priority of crops for research:					
Cassava	1				
Sweet potato	2				
Yam/cocoyam	3				
Top-ranked constraints of researchers:					
Training	23%				
Funds	20%				
Research facilities	20%				
Staff and research personnel	13%				
Need for more germplasm	13%				
Lack of research direction and linkages	10%				

impact with long-term benefits. For example, improved IITA cassava resistant to bacterial blight and mosaic virus is now grown on at least 750,000 ha in Nigeria, giving root yields 2-3 times greater than the local varieties which have been replaced, and with no new inputs. Collaborative efforts between IITA, the Nigerian Root Crops Research Institute, and the Nigerian National Seed Service have facilitated this massive multiplication and distribution system. Improved cassava has also been distributed and is being multiplied in 24 other African countries, again made possible through collaboration among national programs. IITA source material has been tested in the high-altitude dry ecologies of Rwanda and Malawi and has demonstrated its ability to withstand these conditions and sustain high yields.

Manpower training for root crops research has created a great impact by influencing the capacity of national programs. The collaboration remains strengthened by continuous training and exchange of information in terms of workshops, seminars, and short courses.

Focal point concept

Collaborative relationships between national programs and IITA are usually formalized by signing a "memorandum of understanding." In many cases, funds are obtained in order to appoint a collaborator or coordinator within the government research structure to serve as a focal point. In the case of a cassava-breeding research program, the collaborator would share the responsibility for supervising and ensuring that resources are allocated for the implementation of its objectives. This focal point person would also assist in coordinating the national cassava and root crops program. He would be an experienced cassava and root crops breeder who would be located within the governmental framework by the international center. His location would depend on such considerations as existing structure or staffing.

Another alternative would be a split appointment between the host national program and other national programs within the region. For example, a focal point person could carry a 60% research load for the host program and the rest of time consulting or coordinating for the other programs of the region.

Some of the functions of the person serving as a focal point would be to:

Serve as a link between the international center and national program;

Create an awareness of the scope and nature of the international center and the opportunities it offers;

Provide feedback to the international center on developments, performance, and constraints on genetic material and other products originating from the center. This flow of information is necessary in order for the center to improve and adapt future research;

Ensure that the defined cassava research goals are well integrated into the overall food development plan so that they can be recognized as priorities; and

Help in training skilled staff for the research program and inform the centers what special assistance is needed by the national program.

Undoubtedly, there are other workable alternatives with major advantages to both parties. However, care should always be taken to minimize potential sources for conflict of interest.

Impact of strong linkage

Close communication and cooperation between international centers and national programs would positively affect research programs by:

Offering guidance and direction to newly created national programs, which often start in a haphazard manner;

Facilitating the attraction of funds for root crops research at national programs;

Helping to build up a continuous flow of reliable and useful information between the center and national program;

Having a catalytic effect in stimulating government interest, and instilling confidence and respectability in young researchers in relatively little time. This will provide an impetus for national programs to carry on their own research projects; and

Bringing a level of specialized training to the national headquarters of the programs.

Conclusions

An optimal working relationship between national programs and international centers would facilitate the sharing of resources and technologies needed to tackle the food challenges of today. The strategy of promoting and establishing strong "focal points" as a link between the two types of entities strengthens the relationship through which clearly defined research programs can be implemented. Such linkages can also cushion the initial strain and costs that national programs have to undergo when setting up a cassava research program, and strengthen and broaden their research capacity. In the long run, the knowledge and experience gained by both national programs and international centers can facilitate the implementation of regional plans and ultimately make increased productivity at the farm level easier to achieve.

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Recent Advances in Cassava Genetics and Cytogenetics

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Introduction

Cassava, *Manihot esculenta* Crantz (syn. *M. utilissima* Linn.) belongs to the family Euphorbiaceae. The genus comprises 98 species. The species are confined, as wild plants, to the American tropics and no native species are found in the Old World. According to Muller (1873), cassava originated in Brazil and reached other tropical countries in the 16th, 17th, and 18th centuries (Greenway, 1944). Even though many varieties of cassava are now under cultivation, information on the wild forms is still meager. Rogers and Appan (1973) studied several species in order to classify and define their relationship with cassava.

Morphological criteria, geographical distribution, and other factors have been used to systematically classify the large number of so-called types, races, or varieties of *M. esculenta* (Magoon, 1967). As considerable morphological variation exists within the species, Rogers and Fleming (1973) have produced a computer-aided morphological classification of cultivars. However, genetic and cytogenetic evidence, which can additionally help in developing a more natural classification based on ancestral relationship, is far from adequate. Even though cytogenetics has been useful in solving some problems in breeding, through either increased knowledge of the genetic architecture of a species or the direct application of cytogenetic techniques to its improvement, such studies in the *Manihot* species have not received due attention and are still in their infancy.

Karyomorphology and chromosome pairing in *Manihot* species

A comparison of the chromosome morphology and the process of meiosis

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in different taxa is one of the ways of arriving at an estimate of the relationship between different taxonomic entities, especially at the species and lower levels. Unfortunately, cytological studies in *Manihot* species, perhaps because of a lack of suitable cytological techniques, were, until recently, confined to the determination of chromosome number in mostly cultivated types. Thus, information on the synaptic behavior of chromosomes in cultivated types, related wild species, or interracial or interspecific hybrids, is sparse. Although the analysis of the nature of pairing at pachytene stage in interspecific or interracial hybrids, or even in a population of a species, provides the best chance of scanning the different regions of the bivalents for structural hybridity, this information is negligible in cassava. Such an analysis can reveal cryptic duplications, inversions, deletions, or nonpairing segments, undetectable at diakinesis or later stages. Hence, the role played by some of these structural changes should be studied as they restrict the homology between the chromosomes of different taxa and so provide an effective control of genetic differentiation.

A knowledge of the internal mechanisms responsible for differentiation is of great importance if desirable genes are to be incorporated from related flora, especially the wild *Manihot* species, into cultivars, which at present face various handicaps such as hybrid sterility and inviability. Even when the hybrids are not sterile and are fully viable, it cannot at once be assumed that a free interchange of genes between the species will occur. Stebbins et al. (1946), considering the limitations for such a free interchange of genes, have utilized a recombination index calculated on the basis of pairing and chiasma frequency at metaphase-I (M-i).

A review of the literature shows that the *Manihot* species examined so far have a chromosome number of $2n = 36$ (Abraham, 1957; da Cruz, 1968; Ene, 1972; Magoon, 1967; Perry, 1943; Sohmer, 1968; Umanah and Hartmann, 1973). Graner (1935) and Doughty (1939) have recorded regular bivalent formation in the pollen mother cells (PMC) and no meiotic abnormalities were observed. Considering the chromosome number of other genera in the Euphorbiaceae, together with evidence from the meiotic studies in the species itself, an allopolyploid origin of cassava was suggested (Jennings, 1963). Magoon et al. (1969b and 1969c) have proposed a segmental allopolyploid origin for the cassava cultivars. These authors studied the pachytene chromosomes in a cultivar of cassava and individually identified all the 18 bivalents, using criteria such as total chromatin length, position of centromere, long arm to short arm ratio, the extent of pycnotic regions, and other landmarks such as chromomeres,

nucleolar organizers, and telochromomeres. The completely paired pachytene bivalents varied in length from 19.3 to 40.0 micrometres. The haploid chromosomal complement *inter alia* has three functional nucleolar chromosomes and six chromosomal types represented in duplicate. This suggests the possibility that the present-day cultivated types are allopolyploids of crosses between two closely related forms. Their two basic diploid parental taxa ($x = 9$), while possessing six chromosomal types in common, differ in three chromosomes of their complement. Hence the present-day cultivars may be considered as segmental allopolyploids (Magoon et al., 1969b).

Similar pachytene studies were extended to the species *M. glaziovii* (ceara rubber) and, employing the same criteria as in cassava, all the 18 bivalents were identified individually at pachytene (Krishnan et al., 1970). The completely paired pachytene bivalents varied in length from 21.2 to 37.0 micrometres. A comparative study of the pachytene karyotypes of the two species has shown the presence of several common features. In both species, three nucleolar chromosomes are present in the complement and exhibit similar length relationships. Despite the general agreement, a number of differences in the two karyotypes were noted, such as the relative position of morphologically similar chromosomes and the position of centromeres in the longest and shortest chromosomes.

The data on pachytene karyology of *M. glaziovii* corroborate the earlier conclusion, drawn from pachytene studies of *M. esculenta*, of the polyploid origin of the $2n = 36$ chromosome number of *Manihot* species. The higher number of nucleolar chromosomes has been adduced as evidence in support of such an origin and in both *M. glaziovii* and *M. esculenta* three nucleolar chromosomes are present in the complement. The presence of duplicated chromosomal types has also been a major consideration in support of polyploid origin (Krishnan et al., 1970; Magoon et al., 1969b). Based on the presence of two pairs of satellited chromosomes and the behavior of the chromosomes at M-I and A-I (anaphase-I), an allotetraploid origin for *M. esculenta* with a basic number of $x = 9$ has also been suggested by other workers (Ene, 1972; Jennings, 1970).

Meiosis has been found to be regular in a large number of the cultivated cassava types thus far studied (Magoon, 1969b; Sohmer, 1968). However, in a few types occurrence of meiotic irregularities such as laggards, delayed separation of bivalents, nonorientation and noncongression of bivalents, restitution nuclei, monads, dyads, and polyads have also been observed.

Recently, Jos and Nair (1979) studied the pachytene pairing in relation to pollen fertility in five cultivars of cassava and found that in the two highly pollen-fertile clones the pachytene pairing was normal, the chiasma frequency was above 29.6, and the later meiotic divisions were also normal. However, in the partially pollen-fertile clones different pachytene abnormalities like nonpairing, deletion, duplication, and inversion were found in different chromosomes. The chiasma frequency ranged from 27.9 to 29.2. In one clone as many as five bivalents showed aberrant pachytene pairing and the pollen fertility was only about 30%. It was suggested that the deletions noticed in chromosomes 9 and 15 may have played a significant role in reducing the pollen fertility. The chiasma frequency in this clone was the lowest.

If studied in conjunction with morphology, the identification of deletions in relation to specific chromosomes may open up new vistas for locating genes on particular chromosomes among the derived selfed progeny. Based on the extent of pachytene abnormalities in different clones, reduction in chiasma frequency, meiotic sequence, normal tapetal development, and microsporogenesis, it was concluded that pachytene behavior had a fixed role in determining the ultimate pollen fertility in cassava.

In crosses involving local and certain exotic types, cytological abnormalities indicating cryptic differences between the karyotypes of different geographical regions have also been observed: loose pairing, terminal and interstitial nonpairing, terminal deletion resulting in heteromorphic bivalent, and interstitial deletion and duplications resulting in loop formation.

Male sterility in cassava

Sterility is common in crops like cassava which have been propagated by vegetative means for thousands of years. Varying degrees of male sterility have been observed among the cultivars of cassava. Cours (1951), while studying the morphological variations in a large number of varieties, found that about 20% had deformed anthers and were male-sterile. Screening of a large number of cassava types led to the identification of varying degrees of male sterility and 35 types were completely male-sterile (Magoon et al., 1968). The mechanism of pollen abortion was determined in these male-sterile lines from a comparative study of flowers, microsporogenesis, and development of male gametophytes. Some of the

various causes that have been attributed to pollen abortion are described below.

Nondisjunction of microspores

A comparative study of external morphology, microsporogenesis, and development of male gametophytes in male-fertile and male-sterile lines has shown that in the two male-sterile lines, degeneration of individual microspores was a result of the failure of the microspores to separate from the tetrads which, in turn, led to the formation of empty anthers. The tapetum remained healthy and comparable with that of male-fertile lines and the abnormal behavior of microspores in the tetrad could not be attributed to any failure of the tapetum (Jos et al., 1966; Magoon and Jos, 1969). Consequently, the tetrads and, later the tapetum, degenerated and disappeared totally and the anther became empty, leading to complete collapse.

Abnormal behavior of tapetum

Another type of male sterility was encountered where the anthers contained only inviable pollen grains. Here the behavior of the tapetum was not normal. The tapetal cells coalesced at later stages and remained prominent even after the formation of pollen grains. Thus, failure of the tapetum to disorganize at the proper stage interfered with the regular supply of nutrition to the developing microspores leading to the production of inviable pollen grains (Jos et al., 1966; Magoon et al., 1968).

Functional male sterility

Functional male sterility was detected in a seedling from a tetraploid clone of cassava. Meiosis was normal with 18 bivalents at M-I and the microspores were disjunct in a normal way. There was complete absence of anther dehiscence and the pollen was never liberated in this clone. Seventy-three percent of the pollen grains inside the anther sacs were fertile. The cells of the endothelial layer remained parenchymatous without developing the characteristic fibrous thickenings as in normal fertile clones. The failure of dehiscence in the anthers was attributed to the absence of fibrous thickenings in the endothecium (Jos and Bai, 1981).

Cytological anomalies

Recently, male sterility due to cytological anomalies was also recorded. In a male-sterile clone the pollen was of variable size and 100% sterile. A

comparative study of this clone and a male-fertile clone revealed that in the male-fertile clone, 18 bivalents were present at M-I. On the contrary, in the male-sterile clone, chromosomes failed to pair and consequently 36 univalents were present at pachytene and M-I, thereby demonstrating it to be asynaptic and belonging to the category "complete" (Jos et al., 1984). Later stages of meiosis were highly irregular, resulting in the production of microspore tetrads with micronuclei and 100% sterile pollen.

Production of chromosomal races in cassava

Induced polyploids have great significance in crops where the economic product is a vegetative part (Stebbins, 1950) and especially where it can be clonally multiplied. Production of colchipooids as well as triploids deserves attention in cassava improvement programs. Triploids have been shown to be superior cultivars in several crop plants (Magoon, 1967). Their survival as cultivars means that they possess certain selective advantages, often concomitant with triploidy per se (Marks, 1966).

Induced polyploids

Production of induced tetraploids have two major uses: first, as improved strains and, second, in the production of other chromosomal races such as triploids. Graner (1941 and 1942) Abraham et al. (1964), and Magoon et al. (1969a) have described colchicine-induced tetraploids of cassava. The induced tetraploids have $2n = 4x = 72$ chromosomes. In general, these tetraploids exhibit the abnormal growth characteristics associated with polyploidy, such as increases in leaf breadth and thickness, stomatal size, length and girth of petiole, and flower size.

During meiosis in the PMCs, quadrivalent frequency was low. The mean chromosomal association in the variety M-4 was $2.1 \text{ IV} + 0.09 \text{ III} + 28.62 \text{ II} + 6.3 \text{ I}$. Subsequent meiotic stages were characterized by abnormalities such as lagging chromosomes (up to 14 univalents), belated separation of bivalents, division of univalents, irregular distribution of chromosomes to the poles at A-I, and micronuclei at the tetrad stage (Magoon et al., 1969a). Pollen sterility ranged from 62%-78%. Fertile pollen grains were much larger (180-196 μm) than in the diploids (125-140 μm). Seed fertility was also poor in the induced tetraploids under open-pollinated conditions.

During clonal propagation of the induced tetraploids, those of the variety H-602(3) and H-312 became very weak, exhibited stunted growth,

and failed altogether to get established in the field during fifth clonal multiplication. However, the tetraploids of the varieties M-4 and S-300 have undergone several generations of multiplication, suggesting the presence of variable genomic response to tetraploidy in cassava (Jos and Bai, 1974).

Abraham et al. (1964) found that some of the first generation polyploid plants were more vigorous and better yielders than the normal diploids. However, later polyploid generations were found to be poor yielders in yield trial experiments. Only one induced tetraploid gave a higher yield compared to its diploid progenitor. Magoon et al. (1969a) also found that the yield potential of diploids and induced tetraploids did not differ significantly. However, there was an increase in the protein content of the storage roots in the induced tetraploids. The average protein content was found to be 2.8% in the diploid and 3.8% in the tetraploid (Jos et al., 1972). Induction of tetraploidy may become a potent tool in the root quality improvement of promising cassava hybrids.

Production of triploids

Triploids are comparatively difficult to produce in cassava, as in the case of many other crop plants, presumably as a consequence of a "triploid" block (Marks, 1966). Abraham et al. (1964) and Jos et al. (1970) obtained triploids in cassava from crosses between colchicine-induced tetraploids and diploids. Recently, 11.5% fruit set and 8.4% seed set in crosses between a diploid clone (OP-4) and an induced tetraploid clone (S-300) were obtained when the former was used as the female parent (Jos and Bai, 1982). In the reciprocal cross the fruit set was only 6.0%. A total of 29 plants were raised from these crosses, of which two were from the reciprocal cross. Cytological screening of 18 of these plants revealed 15 of them to be triploids ($3x = 54$). A fruit set of above 30% and seed set of 17.9% was recorded when the induced tetraploid clones of H-2304 were used as the pollen parent and the diploid clone, OP-4, as the female parent. A total of 72 plants could be obtained from this cross (Jos and Bai, 1983) and cytological screening of 32 of these revealed them to be triploids with 54 chromosomes. These observations show that a very high frequency of triploids can be obtained in cassava.

Microsporogenesis was found to be highly irregular in the triploids (Jos et al., 1970). At M-I, the average chromosomal association consisted of 6.71 III + 12.23 II + 9.41 I per PMC. Meiosis was further characterized by different types of abnormalities resulting in high pollen sterility. The

triploids did not set seed on selfing and in the open-pollinated condition seed set was also low.

Abraham et al. (1964) found triploids to be superior to colchipooids in yield and sometimes they outyielded diploids. Jos et al. (1970) also reported similar observations. The diploid and tetraploid clones registered an average yield of 21.8 tons/ha and 19.9 t/ha, respectively, while triploids could yield as high as 29.1 t/ha under the same conditions. These results suggest that isolation of triploids could be an effective technique to achieve higher productivity in high-yielding varieties of cassava.

The storage roots of the triploid plants from the cross, OP-4 x S-300, were studied for rind thickness and dry matter content. The rind thickness varied from 13.0%-18.5%. When compared with the diploid roots of the same population, the triploid plants showed higher dry matter content. The diploids showed only 27% dry matter content whereas in the triploids it ranged from 34%-43%. The starch content was found to be the same in the two cytotypes, indicating that the increase in dry matter content in triploids is a result of fiber content (Jos and Bai, 1973).

Genome analysis

Interspecific hybridization and genome analysis in several crops have opened up new avenues of improvement in crop plants and have contributed to the development of new and better types. However, only a limited amount of interspecific hybridization has been done in cassava as compared with other crops, using only five or six species. This may be because there is a lack of extensive species collections at research centers.

There are no strong incompatibility barriers to interspecific hybridization, although considerable selection of cassava clones to be used as parents is necessary (Rogers, 1963). Koshy (1947), Cours (1951), Abraham (1957), and Magoon et al. (1966) reported successful crosses between cassava and ceara rubber. Crosses between *M. melanobasis* and cassava were very fertile and the fertility was maintained in the hybrids (Jennings, 1959). Several generations of backcrosses of these hybrids have helped to evolve cassava varieties highly resistant to viral diseases (Jennings, 1957 and 1963; Nichols, 1947). Bolhuis (1953) found that *M. saxicola* crosses freely with cassava. *M. saxicola* and *M. melanobasis* are valuable sources of new genes for increasing yields and both have high protein content in the roots. Based on the readiness with which these two species cross with cassava, it is doubtful whether their separation as distinct species is

justified (Bolhuis, 1953; Jennings, 1959). Koch (Jennings, 1959) reported successful crossing of cassava with *M. glaziovii* and *M. dichotoma* (Jacquie Manicoba rubber). Nichols (1947) and Jennings (1957 and 1963) described the uses of these species together with the species *M. saxicola*, *M. melanobasis*, and the tree-like species, *M. catingae*. The "tree cassava" is believed to be a natural hybrid between cassava and *M. glaziovii*.

In the *M. glaziovii* series, the early generation hybrids were of very low fertility, but improvement in both pollen and ovule fertility was observed in the backcross generations. In the series related to the tree cassava, the first cross itself was more successful. In the *M. dichotoma* series, there was moderate seed set in the original interspecific hybrids, but, with one exception, the F_1 hybrids were exceedingly poor and completely sterile. Although some of the first and second backcross hybrids were of improved fertility, the general level of both pollen and ovule fertility in the *M. dichotoma* series remained low. In contrast, *M. melanobasis* and its F_1 hybrids were relatively highly fertile—the ovule fertility being particularly high. From these results it was suggested that fertility in the early generations following interspecific crossing was limited by some form of interspecific incompatibility acting in addition to fertility-limiting factors inherited from the cassava parents (Jennings, 1963).

Although successful interspecific crosses involving species of *Manihot* have been reported, detailed cytogenetic studies are scanty. Doughty (1939) found that two univalents were occasionally present at meiosis in the F_1 hybrid related to *M. glaziovii*. Magoon et al. (1966) found that 18 bivalents were usually present at M-I, although occasionally two or three bivalents showed the tendency to separate precociously. Meiosis in the F_1 hybrid derived from tree cassava was apparently normal because tree cassava is probably a natural hybrid between *M. glaziovii* and cassava, and the F_1 between it and cassava can be considered as a first backcross (Doughty, 1939). Magoon et al. (1966) also found a high proportion of univalents at meiosis in some of the F_1 hybrids related to *M. dichotoma* but chromosome pairing in the others of this series appeared to be complete.

Similar observations were recorded for F_1 hybrids related to *M. dichotoma* (Bai, 1982). In a population of hybrid plants from the crosses of cassava and *M. dichotoma*, the pollen fertility was found to vary from 0% in 19 plants to above 70% in 34 plants. Chromosome number in all these hybrid plants was $2n = 36$. Interestingly, during meiosis in hybrids with 100% pollen sterility, the chromosomes remained as univalents at the pachytene and M-I stages and 36 univalents were present in both these

stages. Thus, these plants exhibit asynapsis of the category "complete." The asynaptic condition was attributed to gene dosage effect. In hybrids with 5%-50% pollen fertility, 18 bivalents were present at M-I and the mean chiasma frequency varied from 21.1 to 24.4 compared to the mean chiasma frequency of 26.4 in cassava and 22.1 in *M. dichotoma*. At A-I in these hybrids, a dicentric bridge and an acentric fragment due to a paracentric heterozygous inversion were discernible in 20%-30% of the PMCs. The hybrid plants with 70% or more pollen fertility exhibited normal meiosis with 18 bivalents at M-I. The fruit set percentage was low in these hybrids.

In the F_1 hybrids related to *M. glaziovii*, the nature of chromosome pairing at the early prophase stages was critically studied (Magoon et al., 1970 and 1971). The pachytene bivalents ranged in length from 15.3 to 35.3 micrometres. The parental chromosomes in general exhibited total synapsis along their entire length and only three bivalents were heteromorphic. Major chromosomal differentiation in the two species involved three chromosomes of their haploid complement which were represented by three heteromorphic bivalent associations in the F_1 hybrids, each probably consisting of a basic chromosomal type and a derived type. Since the three derived chromosomal types of the parents bear homoeology to the original chromosomal types in the F_1 hybrids, the independent origin of these types as a result of terminal deletion was adduced. The deletion must have occurred in both taxa, but involving different chromosomes (Magoon et al., 1971).

From the preceding brief survey it may be seen that considerable scope exists to intensify the work of interspecific hybridization and genome analysis in the genus *Manihot*, as a number of species possessing several desirable characteristics have been reported. However, as stated earlier, only a few species have so far been used.

Genetic studies

Male sterility

The genetics of male sterility resulting from the nondisjunction of microspores from the tetrads has been reported. A male-sterile clone was crossed with a few male-fertile clones. In some combinations the segregation of male-sterile plants occurred in the F_1 generation itself, showing that some of the apparently male-fertile clones were heterozygous. Among the F_1 progeny the segregation of male-sterility to fertility was 1:1, indicating

that it was only a backcross ratio. It was concluded that male fertility is dominant over male sterility and is monogenic (Jos and Nair, 1984).

Leaf shape

In cassava there are two distinct leaf types: broad and narrow. Jos and Hrishi (1976) concluded that the narrow shape is dominant to the broad shape and that the trait is monogenic.

Hydrogen cyanide content

Chandraratna and Nanayakkara (1948) reported that inheritance of hydrogen cyanide (HCN) content appears to be transgressive. Hahn et al. (1977) reported that 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.

Cassava mosaic disease

Doughty (1958) and Jennings (1970) reported that resistance to cassava mosaic disease (CMD) is multigenic. Hahn and Howland (1972) reported that resistance to CMD is controlled by quantitative genes and appears to be recessive with a heritability of about 60%. Jennings (1976) confirmed that additive genes are responsible for resistance to CMD.

Studies in cassava genetics should be intensified, as the inheritance of many important characters are yet to be determined.

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Hybridization and Breeding Methodologies Appropriate to Cassava

Alvaro Bueno*

Flowering behavior and pollination habit

Cassava (*Manihot esculenta* Crantz) is a monoecious species with a few large pistillate flowers borne basally and numerous smaller staminate flowers borne apically in the same inflorescence (Chandraratna and Nanayakkara, 1948). Flowering is always associated with branching points—an early-branching genotype may start flowering as early as three months after planting, while a nonbranching type does not flower (Conceição, 1979; Hahn et al., 1977).

Pistillate flowers have five petals and an ovary with three loci, each of which produces one seed. Staminate flowers have ten stamens arranged in two rings of five and do not open until after the last female flower of the inflorescence has bloomed (Graner, 1942a).

Anthers start dehiscence before the staminate flower opens, but complete it only by the time of opening. One male flower produces about 1600 pollen grains, of which only 50% are viable (Graner, 1942a). Pollen grains stored over calcium chloride were maintained viable for up to six days (Chandraratna and Nanayakkara, 1948).

Male sterility has been reported in cassava and several mechanisms for this have been described, including: early abscission of staminate buds, no pollen formation, nondehiscent anthers, and chromosomal pairing aberrations (Byrne, 1984).

The stigma is sticky and receptive at the time of blooming, becoming inviable within 24 hours. It secretes a sugary solution which is visible to the naked eye on the day the female flower opens. Changes in the size and

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format of the flower, and the nectar secreted by the stigma, aid in the identification of those flowers which will open the same day (Fukuda, 1980; Hershey and Amaya, 1980).

There seems to be a concentration of blooming around midday in most cassava-growing environments (Chandraratna and Nanayakkara, 1948; Conceição, 1979; Hahn et al., 1979; Hershey and Amaya, 1980). Flowers stay open only for a short period of time during the day (Fukuda, 1980).

Most genotypes flower preferentially during short days (Hershey and Amaya, 1980). In the northern hemisphere flowering occurs from July to January with a peak in October to December. In the southern hemisphere flowering occurs from January to July with a peak in April to June (Hahn et al., 1979). However, flowering time depends also on temperature and humidity. On cold and rainy days flowering is delayed and less intense (Fukuda, 1980). In environments deficient in soil moisture, flowering may be erratic (Byrne, 1984).

Prolific production of readily disseminated pollen grains suggests that wind may be an important pollinating agent, although this has not been confirmed experimentally. Profuse secretion of nectar attracts several insects, especially bees, which are also pollen disseminators (Chandraratna and Nanayakkara, 1948).

The flower biology and pollination habit of cassava make it a predominantly allogamous species. However, considerable selfing may occur because the protogynous flowering mechanism, especially in profusely flowering genotypes, prevents selfing in the same inflorescence, but not in the same plant (Kawano et al., 1978).

Hybridization methods

Because of the allogamous nature of the species, most cultivars are highly heterozygous. However, a field of a particular cultivar is composed of homogeneous genotypes, since cassava is normally propagated vegetatively with stem cuttings. Therefore, hybridization of selected parents is necessary to create source populations with high genetic variability.

Hand pollination

With large separate male and female flowers which do not open at the same time, it is very easy to hand-pollinate cassava flowers. Although the

procedure is simple, the cost of producing large quantities of hybrid seeds is considered high (Graner, 1942a). One successful pollination yields a maximum of three seeds, but this is seldom obtained and in most situations one seed per pollinated flower is a good average. Byrne (1984) estimated that one person can produce from 50 to 300 seeds per day, which compares unfavorably with other crops where just one pollination can produce that many or more seeds.

The pollination procedure begins in the morning when ready-to-open staminate flowers of chosen male parents are collected and put in small glass or plastic vials that are properly identified. Simultaneously, female flowers which will open that day are covered with a fine cloth or white paper bag before they open, to prevent their being contaminated by foreign pollen (Fukuda, 1980; Hershey and Amaya, 1980).

The actual cross is accomplished after midday when female flowers have opened inside the bag. Pollen is transferred by using the male flower as an applicator or a velvet-tipped pollen applicator. In either case pollen grains are deposited on the stigma by gently rubbing it with the applicator. When the velvet-tipped applicator is used, several female flowers can be pollinated without recharging it. If the applicator is to be used for other pollen parents, it should be dipped in alcohol before reuse. One staminate flower has enough pollen for three or four stigmas. Unopened female flowers, which have not been pollinated, should be eliminated from the inflorescence to avoid future confusions. Male flowers may be eliminated but it is not necessary, since they will not interfere with the pollinations (Conceição, 1979; Fukuda, 1980; Hahn et al., 1979; Hershey and Amaya, 1980).

After the cross is made it should be labeled with the name of the parents, date, and number of flowers pollinated. Flowers may be immediately covered with fine cloth or white paper bags, or they may be left uncovered for a few days and bagged when the ovary starts swelling. Developing fruits should be kept covered until maturity to avoid insect injury and to catch the seed upon dehiscence. Seed mature 2.5-3 months after pollination (Byrne, 1984; Chandraratna and Nanayakkara, 1948; Hahn et al., 1979; Fukuda, 1980; Hershey and Amaya, 1980).

The success rate of hand-crossing seems to vary widely. Fukuda (1980) reported that 80% of pollinated flowers set fruits. On the other hand, Conceição (1979) and de Albuquerque (1961) stated that only 15%-20% formed fruits. In Nigeria most cultivars set seed readily when hand-

crossed, but almost 100% failure was observed when the cultivar Llanera was pollinated. This same cultivar set seed satisfactorily when it was naturally pollinated by insects (Hahn et al., 1977).

A number of insects are known to reduce cassava's ability to produce viable seeds. The larvae of *Teleocoma crassipes* Aldrich bore into staminate buds and considerably decrease the amount of pollen formation. After pollination, larvae of *Anastrepha* sp. penetrate the developing fruit and damage the seed (Graner, 1942a). In environments which favor high populations of these insects, cassava seed production is almost nil under natural conditions. In the period 1978-1979, at the headquarters of the Centro Internacional de Agricultura Tropical (CIAT), seed production per pollinated flower decreased from 0.7 to 0.28 because of an increased population of fruit flies. Biweekly applications of fenthion increased the efficiency to 0.82 seeds per female flower (CIAT, 1981).

Open pollination

Observations made in CIAT's germplasm bank have shown that the yield potential of most accessions was low and very few genotypes had the necessary levels of combined resistance to disease and pest problems (CIAT, 1982a). This suggests that the frequency of desirable alleles in most accessions is low. Therefore, a cassava hybridization program will require a very large number of hybrid seeds from any particular cross combination for production of superior recombinant types (Kawano et al., 1978). Open-pollinated crossing fields are efficient mechanisms for economic production of large quantities of hybrid seeds.

Natural open pollination. Normanha (1971) and Conceição (1979) reported that the first cassava breeding efforts in Brazil were initiated by gathering open-pollinated seeds in germplasm collections. This procedure has the inconvenience of allowing a considerable number of undesirable pollen parents to participate in the crosses, reducing the probability of obtaining a superior segregant. Additionally, Kawano et al. (1978) reported that uncontrolled open-pollinated progenies of two cultivars included a large portion of selfed lines and that most of these did not yield even half that of the parent.

In environments where the population of fruit flies is high, the bagging of developing fruits is required. Application of insecticides is not recommended, since it will reduce the population of pollinating insects.

Controlled open pollination. Strategic location of plants within the field can increase the rate of natural crosses and reduce the problems of selfing.

Hahn et al. (1979) suggested that crosses among selected parents should be made in isolation. Each crossing plot should contain several parents, few plants per parent, and be replicated several times to maximize outcrossing. Conceição (1979) stated that isolated crossing fields should have one pollen donor row for every three female rows, which should be emasculated at regular intervals.

The installation of several isolated crossing fields has been recommended by da Silva (1971). The number of fields should be equal to the number of parents selected for crossing. In each field one different parent functions as pollen donor and all others are emasculated regularly.

Another scheme was used by Acosta-Espinoza (1984) who crossed nine progenitors. Each crossing plot consisted of nine plants and only the central plant, which was a different genotype in each plot, was used for seed collection.

Simple randomization of parents within the crossing plot and systematic arrangements such as Latin square designs may be used successfully.

Whatever the arrangement, the bagging of developing fruits is required for protection against fruit flies and collection of seeds after dehiscence. In sites where fruit flies are not a limiting problem, fruits in isolation plots may be left unprotected and collected when the seed coat begins to shrivel (Hahn et al., 1979).

Breeding methods

Cassava is grown under various stresses, such as little or no fertilizer, no irrigation, no chemical control of diseases and pests, and usually poor soils. Throughout its long growing cycle it is exposed to a wide range of physical and biological constraints. Considering this situation, the main objective of CIAT's breeding program is to exploit the ability of the crop to produce reasonable and stable yields under marginal conditions with low inputs (Hershey, 1984).

The major biological constraints for cassava production in Africa are diseases and pests. Major diseases are cassava mosaic disease (CMD), cassava bacterial blight (CBB), and cassava anthracnose disease (CAD).

Important pests are cassava mealybug (CMB) and cassava green spider mite (CGM). Because of limitations in the use of chemical products to control pests and diseases, development of resistant genotypes becomes the most appropriate and realistic approach for effective control (Hahn et al., 1980).

Although individual breeding programs have their own specific objectives, most programs aim at developing genotypes which combine the largest number of desirable traits associated with high root yield, disease and pest resistance, good root quality, and stability of production across environments.

Since cassava can be vegetatively propagated, superior genotypes identified in any phase of a breeding program may be maintained indefinitely. Vegetative propagation combined with sexual reproduction allows reliable estimates of environmental and genotypic variance. Given that inbreeding is deleterious (Kawano et al., 1978) and heterozygosity is essential for the maintenance of vigor, any breeding method should maintain heterozygosity and take into account both additive and nonadditive genetic variance (Byrne, 1984).

Introduction of cultivars

The introduction of a number of foreign cultivars into a region and the selection of the most adapted is a very simple and low-cost approach to crop improvement. Its classification as a breeding method may be contested, but it is indeed widely used. The method is generally practiced by programs which are initiating their activities.

Since introductions are usually in the form of stem cuttings, only a limited amount of genetic variation can be brought in and there is a risk of introducing diseases and pests. However, no special requirement is needed for the manipulation of the planting material. Cultivars may be introduced in the form of meristem cultures which will reduce the risk of introduction of diseases and pests, but will require some facilities for manipulation.

Each introduced genotype is initially planted in a single row of 5-10 plants without replication. All evaluations at this stage are preliminary and selection is usually very mild. In general, only genotypes which are extremely susceptible to diseases and pests and clearly show no adaptation to the ecosystem are discarded. It is recommended to include a row of a local cultivar every 5-10 rows as a check.

In the second and subsequent years each selected cultivar is planted in larger plots, with replications in one or more locations, depending on the amount of planting material available. Selection intensity increases and selection criteria become more rigid. If one or more introductions prove to be superior to the common cultivars of an ecosystem, they may be recommended for commercial use. Although the method is low cost, the probability of an introduced genotype being superior to locally adapted cultivars is low. Most introductions have been selected in ecosystems with different biological and physical constraints and therefore probably would not have all the characteristics necessary for good performance in the new environment.

Introduction of hybrid seeds

The introduction of seeds of selected crosses has the advantage of introducing a much wider genetic variability with reduced risks of bringing in diseases or pests. However, this approach requires some facilities for seed germination and seedling transplant, which may impose limitations for some programs.

The initial step is the germination of seeds directly in the field or in seed beds with subsequent seedling transplants. In either case irrigation may be necessary, because seedlings are very sensitive to water stress.

Since the number of seedlings is usually large, selection must be intense. The efficiency of selection depends primarily on the traits being selected. It is more effective for traits with high heritability, such as disease and pest resistance, and less effective for low heritability traits, such as root yield. Selection is practiced among progenies and within each progeny group (family).

Selected seedlings are cloned and planted in single rows of 5-10 plants. The best clones are selected and subsequently evaluated in larger plots with replications and in various locations. If a clone is judged superior to local checks it may be released as a new cultivar.

This procedure may be classified as low cost because it does not spend resources for parental evaluation and selection, and as more efficient than the introduction of cultivars because it selects from a much wider genetic base. However, its effectiveness is hampered by the fact that parents have not been selected within the target ecosystem and their progenies may lack

important alleles for good agronomic performance in the new environment.

Both CIAT and the International Institute of Tropical Agriculture (IITA) place strong emphasis on sending hybrid seeds, with appropriate adaptation and resistance, to national programs.

Intraspecific hybridization

Hybridization in cassava is used mainly for the creation of genetic variability. Most cultivars are heterozygous at the majority of their loci. Segregation will, therefore, occur at the first hybrid generation. Thus, each hybrid seed is potentially a new cultivar.

Probably the most common procedure for cassava breeding is the selection of superior parents within the species *M. esculenta* and the evaluation of hybrid progenies of selected crosses (Hahn et al., 1977).

The success of this method depends primarily on the choice of adequate parents and on the selection mechanisms used (Kawano, 1980). Selection of parents is normally practiced by phenotypic evaluation of cultivars and should be complemented by evaluation of the combining ability of the best parents (Hahn et al., 1979).

Some breeding programs give priority to field evaluation for the selection of superior parents. The choice of adequate selection sites becomes very important and a good site should include as many physical and biological constraints as possible, so that the final selections may have a chance of being widely adapted (Hahn et al., 1980; Lozano et al., 1984).

In each selection site evaluations aim toward the selection of genotypes with durable integrated resistance to most constraints. The best genotypes are evaluated for several growing cycles and those which prove superior enter the crossing blocks (Hershey, 1984).

After several years of evaluation of CIAT's cassava germplasm it was observed that the yield potential of most accessions was low, the frequency of accessions with combined resistance to all diseases and insects of a given region was still lower, and genotypes had a limited range of adaptation. It was concluded that only a few cultivars could be used directly as parents for the production of acceptable hybrids. More recently, new superior hybrids have entered the hybridization process and the parental base is continuously being upgraded (Hershey, 1984).

In Brazil, the evaluation and selection of superior parents is carried out by introducing a large number of cultivars into almost all states for local evaluation and selection of the most adapted. These activities are coordinated by the Centro Nacional de Pesquisa de Mandioca e Fruticultura (CNPMPF) and executed by state research units.

In Nigeria potential parents are selected from collections of local and introduced cultivars which are evaluated for disease and pest resistance, root yield and quality, consumer acceptance, and general adaptability to a range of environments (Hahn et al., 1979).

Ideally, the selection of hybrid progenies should be carried out in as many sites as is possible within a target region, but breeders are often restricted to a few sites. Therefore, the selected site should be carefully chosen and include as many of the relevant biological and physical constraints as possible. Very often clones give variable results when grown in places other than the original selection sites. This suggests that regional evaluation is necessary (Lozano et al., 1980).

Maximum adaptability to a given ecosystem should be achieved by initiating selection directly from the first hybrid generation within the target region. However, in sites with moderate to high stress conditions, seed germination is usually low, plant development is slow, and yield formation is delayed. This may cause serious problems in efficient selection (Hershey, 1984).

In order to assess the possibility of preliminary selection at CIAT headquarters for clonal performance in Media Luna, Colombia, hybrid seeds were planted in CIAT and Media Luna. At harvest, five stakes from each plant from both sites were planted in single rows in Media Luna. Correlation for root yield between seedlings grown in CIAT with stakes planted in Media Luna was very low. On the other hand, correlation between seedling and stakes grown in Media Luna was high and statistically significant, suggesting that *in situ* selection for root yield was more effective (Hershey, 1984). This is in agreement with results reported by Kawano (1980).

Considering these problems, the present selection scheme used at CIAT is as follows: all hybrid seeds are germinated at CIAT headquarters where adequate care is provided for the seedlings. Six months after germination each seedling is cut into two stakes—one remains in CIAT and the other goes to the selection site. This approach permits virtually all the genetic

variability created by a cross to be present for the initial selection in the target region (Hershey, 1984).

In Brazil, the first hybrid generation is grown in CNPMPF. One year after planting a mild selection is practiced among and within families and each selected genotype is cloned into five stakes. Each cutting is sent to a different selection site.

In Zaire, Singh (1980) suggested that seedlings should be initially selected for CBB and CMD resistance during the rainy season and the survivors be later screened for CGM and CMB during the dry season.

At IITA seedlings are first screened for disease and pest resistance and only the surviving genotypes are uprooted and evaluated for root yield and other characteristics (Hahn et al., 1979).

The first clonal selection is practiced when genotypes are planted in single rows of 5-10 plants. Kawano (1980) reported that single-row root yield had no correlation with bordered-plot root yield. Since the harvest index of single rows showed a higher correlation with root yield of bordered plots, it was suggested that harvest index in single rows was a better selection criterion than yield itself. Lozano et al. (1984) argued that under high-productivity environments, selection for harvest index in early stages could be more efficient, but in low-yielding environments selection for root yield, along with a reasonable harvest index, was a better strategy.

Row selection at CNPMPF takes into consideration root yield and quality, harvest index, disease and pest resistance, and plant architecture.

At IITA, the first clonal generation is evaluated in a preliminary yield trial with single rows of three to five plants. A standard cultivar is planted every ten rows as a check. Evaluation is for disease and pest resistance, plant architecture, and general vigor. Only selected clones are evaluated for dry matter and other traits (Hahn et al., 1979).

Bordered-plot selection begins at the second or third clonal generation and becomes more effective at later generations when the amount of planting material permits adequate plot size, number of replications, and number of test locations.

Hand-pollination and pedigree selection have some limitations, such as high cost (because of the large amount of hand labor required); relative inefficiency in breaking undesirable linkages (because only one cycle of

recombination is allowed); and inefficiency in combining a large number of desirable traits into a single genotype (because two particular parents usually do not have all the necessary genes and very often the number of hybrid progenies is too small to include all possible recombinants) (Byrne, 1984).

Interspecific hybridization

Since most species of the *Manihot* genus can be easily crossed with cultivars of *M. esculenta*, the entire genus may be considered a common gene pool from which desirable alleles can be drawn for cassava improvement (Hahn et al., 1977). However, it should be noted that only a limited range of possible interspecific crosses have been attempted.

Most programs of interspecific hybridization were conducted in Africa. Breeding for resistance to CMD was started in East Africa in 1937. No resistance was found in the cultivated species, but the progenies of *M. esculenta* x *M. glaziovii* showed promise (Hahn et al., 1979).

In Madagascar, breeding for resistance to CMD was initiated in 1940. Resistance was not found after repeated crosses between *M. esculenta* x *M. glaziovii* (Hahn, 1978).

In Nigeria, breeding for resistance to CMD started in 1955 with the introduction of clone 58308 from East Africa. This clone has shown stable resistance for several years, but also low root yield and poor root quality (Hahn et al., 1979).

A few other species have been used in crosses with *M. esculenta* with variable results. Jennings (1959) reported that hybrids between *M. esculenta* x *M. melanobasis* were often superior in seed set and root yield to intraspecific crosses.

In Brazil, an attempt to transfer CBB resistance from *M. glaziovii* was discontinued at the Instituto Agronômico de Campinas (IAC) in Sao Paulo. No resistant clones with good agronomic performance were developed.

The backcross method has been the most common procedure used to incorporate CMD resistance into cultivated cassava (Singh and Hahn, 1982). Although resistance was transferred, no overall agronomic improvement was observed in the hybrid progenies.

According to Hahn et al. (1977), a sound methodology for efficient introgression of exotic germplasm into cultivated cassava is needed, especially when traits to be incorporated are quantitatively inherited. The major problem is inclusion of a few special features of the wild forms, without disorganizing the desirable gene complexes built up in a superior cultivar.

Other methods such as modified convergent crosses and three-way crosses have been proposed, but results were not reported (Hahn et al., 1977; Singh and Hahn, 1982).

Population improvement

The probability of a superior recombinant type appearing in the progeny of a given cross increases when the parents have a high frequency of desirable alleles. As was stated before, very few genotypes within the cassava germplasm have this quality. Therefore, parental populations must be improved to increase the efficiency of breeding programs.

Recurrent selection has been reported to be the most efficient procedure for improving cassava base populations (Byrne, 1984; CIAT, 1982b; Hahn, 1978). The objectives of most recurrent selection programs are to increase the gene frequencies for traits such as high root yield, good root quality, disease and pest resistance, tolerance to soil and climatic stresses, and stability of production across environments (CIAT, 1981; Hahn et al., 1980).

The first step of a recurrent selection procedure is the synthesis of the original source population. Success in developing a good population depends on the selection of adequate parents with high breeding values. Parents for most existing programs have been selected according to clonal performance (Byrne, 1984; CIAT, 1982a). According to Hahn et al. (1979), two to three generations of random mating without selection are necessary for population synthesis.

Synthesis of original populations and later recombinations are performed in isolated open-pollinated crossing fields. At CIAT recombination is carried out in an isolated polycross with several replications (CIAT, 1981). Populations with larger genetic variability may be developed by using wild species in crossing plots (Hahn et al., 1979).

Cassava is not well suited for open-pollination schemes where random

pollination is required, because flowering time and pollen production differ widely among genotypes. For efficient recombination a good management of flowering is required (CIAT, 1981). Progenies resulting from each recombination cycle are evaluated and selections recombined again to form a new population.

Introgression of desirable genes, present in otherwise undesirable parents, into superior populations can be done by planting the unadapted parents as border rows of crossing blocks. They must be emasculated regularly to prevent the contamination of the gene pool. Progenies from the crosses are evaluated and the procedure is repeated with the selections (CIAT, 1981).

Hahn et al. (1979) reported that critical information is lacking on the population size and selection intensity necessary for recurrent selection in cassava. They suggested a selection intensity of 5%-10% for the first cycle and 25%-30% for subsequent cycles. The selected portion should contain 500 to 1000 plants to avoid loss of favorable genes.

In Brazil, there are no reported attempts of recurrent selection for cassava improvement. However, CNPMF's breeding program will initiate a half-sib recurrent selection scheme in 1985. The original population will be synthesized by intercrossing ten selected genotypes of different origins and good performance in Cruz das Almas. The experiment will be designed to also allow the estimation of important genetic parameters of the population, such as additive and dominance genetic variances, heritability, and genetic correlations. If the scheme proves efficient, the frequency of desirable alleles should increase in subsequent selection cycles, and the probability of identifying superior genotypes will also increase.

Nonconventional procedures

As nonconventional methods are treated more fully in the papers of Dr. William Roca and others in these proceedings, brief comments only will be made here.

Polyploidy. Graner (1942b) applied colchicine to the apical meristem of cassava and was successful in developing tetraploid plants ($4n = 72$) which exhibited larger stomata than normal diploids. However, the tetraploids had retarded plant growth and did not yield as well as diploids. Other reports state that tetraploids are more resistant to CMD and have higher protein content than diploids (Byrne, 1984).

Triploids ($3n = 54$), obtained by crossing female tetraploids with male diploids, seem to offer some hope of higher root yield than their parents.

Mutation. Radiation has been used in cassava cuttings, potted plants, seeds, and pollen grains to increase genetic variability. In general, the results were an increased mutation rate and reduction in plant growth, even though some vigorous mutants were observed. Most mutants produced have not been agronomically useful (Byrne, 1984).

Tissue culture. Embryo culture, as a propagation technique for difficult-to-germinate species, has been successfully performed with some wild *Manihot* species. As for pollen and anther cultures, only callus and root regeneration has been observed. Somaclonal variation and cell fusion still need a system for protoplast regeneration and selection of hybrid fusion cells (Byrne, 1984).

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Selection for Yield Potential in Cassava

*Tan Swee Lian**

Introduction

As a valuable source of carbohydrate, cassava has several important traditional and potential roles to play. It has long been a staple in various developing nations in Africa, South America, and Asia, and is widely used as an energy component in the formulation of livestock feed rations. Starch extraction is probably one of the oldest cassava-based industries from whence a whole host of related industries have developed, not the least important of which are the ones producing gasohol and high fructose-glucose syrups (HFGS). A substantial amount of interest was aroused in recent years in the potential of gasohol as a substitute for petroleum fuels, but it has since died down with the discovery of new oilfields. However, this potential with its renewable property may yet be exploited in the future. A growing amount of interest and enthusiasm is being shown at present in the sugar-substituting possibilities of HFGS. HFGS are particularly suited for use in soft drinks, canning, and the manufacture of confectionery. They will become significant in countries which produce little or none of their sugar requirements and hence have a price differential which makes HFGS attractive.

Whether destined for human consumption, livestock feed, or starch, high yield and, particularly, high production of root dry matter is the primary concern of both scientist and farmer. It has been reported that cassava has the highest potential production of calories per hectare per day among tropical crops (Table 1). However, it is not clear whether the yield of 71.1 tons/ha per year was achieved from experimental plots or from farm plots. Possibly the figure was a result of experimental yield,

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Table 1. Maximum recorded yields of some important tropical crops.

Crop	Annual yield (t/ha)	Daily energy production (calories in thousands per ha)
Rice	26.0	176
Wheat	11.7	110
Maize	20.0	200
Sorghum	13.0	114
Cassava	71.1	250
Sweet potato	65.2	180
Banana	39.0	80

SOURCE: de Vries et al., 1967.

considering that the world average yield is around 8.8 t/ha and the highest mean national yield is around 18.2 t/ha from India (Singh, 1986).

What is evident is that the full potential of existing cassava germplasm has not been realized. Experimental yields easily reach 50-60 t/ha (Chan and Ong, 1981; Cock, 1974; Kawano, 1978)—indeed, some farmers have reported such yield levels from first-season cassava crops on land newly cleared of jungle (Chan et al., in press). However, in general, root yields at the farm level often fall far below such expectations. This is hardly surprising as cassava is commonly grown in situations in which other crop species have difficulty in surviving, let alone producing economic yield (Cock, 1974, 1979, and 1983). A case in point is the huge cassava industry in Thailand, a large proportion of which is based on cultivation in the northeast region on highly leached gray Podzolic soils where other food crops cannot be grown (Sinthuprama and Tiraporn, 1986). Minimal or zero inputs are often associated with cassava cultivation among small farmers. In Malaysia, cassava growing is sometimes a part-time operation with the farmer devoting very little time to the maintenance of the crop between planting and harvesting (Chan et al., in press).

Economic yield in cassava almost always refers to the weight of the thickened storage roots, specified either as fresh or dry weight. The formation of these thickened storage roots (or storage root initiation) and their subsequent growth in weight (storage root bulking) are both dependent on intrinsic (physiological/genetic) factors as well as on environmental factors.

Environmental factors influencing root yield

Environmental factors such as temperature, rainfall, solar radiation, and soil conditions have strong influences on the physiological processes of a cassava plant and, ultimately, its yield (Cock, 1983). In selecting for yield potential in cassava, it is essential therefore that such environmental factors as are within the control of the experimenter be kept as constant as possible. These factors include mainly the agronomic and cultural practices. It has been shown by various workers throughout the tropical belt where cassava is grown that yields vary considerably according to soil nutritional conditions (Chan, 1980; Chew et al., 1978; Godfrey-Sam-Aggrey, 1977; Mohan et al., 1977; Obigbesan and Agboola, 1977; Takyi, 1974a and 1974b). Similarly, cultural practices have varying degrees of influence on yield, for example, length of cutting (Chan, 1969), stem part from which the cutting is taken (Chan et al., in press), age of the plant from which the stem is cut, length of stem storage prior to use as planting material (Chan et al., in press), planting density (Chan et al., in press; Enyi, 1972a; Gurnah, 1977; Mandal et al., 1973), depth of planting, orientation of cutting (Chan, 1969; Takyi, 1974a), degree of weed control (Chan et al., in press; Doll and Piedrahita, 1977; Godfrey-Sam-Aggrey, 1978), and length of crop cycle (Obigbesan and Agboola, 1977; Takyi, 1974b).

Intrinsic factors influencing root yield

Intrinsic factors are those which result from the physical or genetic endowment of a particular clone. While physiological characteristics are governed by the genetic makeup of a clone, they are also subject to influence by various environmental factors. Understanding how a certain physiological characteristic or parameter contributes to final root yield in cassava will provide pointers as to what constitutes an "ideal" cassava plant in terms of high-yielding capacity. Indeed, some of these parameters, if under strong genetic control, may serve as selection criteria in the search for high-yield potential in a cassava clone.

Leaf area index

Total dry matter production in a cassava crop is dependent on leaf area—the photosynthesizing surface. The rate of dry matter accumulation, or crop growth rate (CGR), has been found to have a parabolic relationship with leaf area index (LAI), reaching a maximum at an LAI of around 3.5, as shown in Figure 1 (Cock, 1983; Cock et al., 1979; Enyi, 1972b). LAI, on the other hand, is a composite resulting from the product

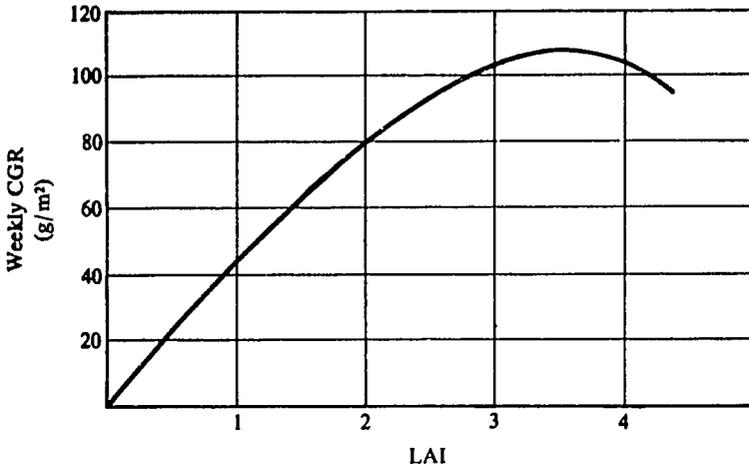


Figure 1. Relationship between crop growth rate (CGR) and leaf area index (LAI) in cassava. (Adapted from CIAT, 1976.)

of total leaf number per plant, individual leaf size or area, and planting density.

Planting density. Cassava is normally planted at a spacing of 1 x 1 m, which is near the optimal spacing for root yield in most genotypes under relatively favorable growing conditions (Chan et al., in press).

Leaf size. Individual leaf size is a varietal characteristic with a wide range. One study of six varieties shows how leaf size differed among the varieties, as well as how it changed through time within each variety (Figure 2). Leaves formed early in the crop's growth tend to be larger than those formed at the end of the season in branched varieties, whereas leaf size in unbranched varieties is less drastically reduced as the crop ages (Tan and Cock, 1979b). Some external effects such as drought (Conner, 1980), thrips infestation, mosaic disease (Hahn et al., 1979), anthracnose, and nutritional disorders (for example, zinc and copper deficiencies) are known to reduce leaf size.

Leaf life. Total leaf number on a plant at any one time is largely dependent on the difference between the rate of leaf production and the rate of leaf abscission (a characteristic which can simply be described as leaf life) and branching intensity. Leaf life, like leaf size, is another varietal characteristic which varies with the age of the plant when the leaf was formed (Tan and Cock, 1979b). Leaves formed in an older plant are shorter lived. However, unbranched varieties are better able to maintain a constant leaf life throughout the crop cycle (Figure 3). It is also recognized

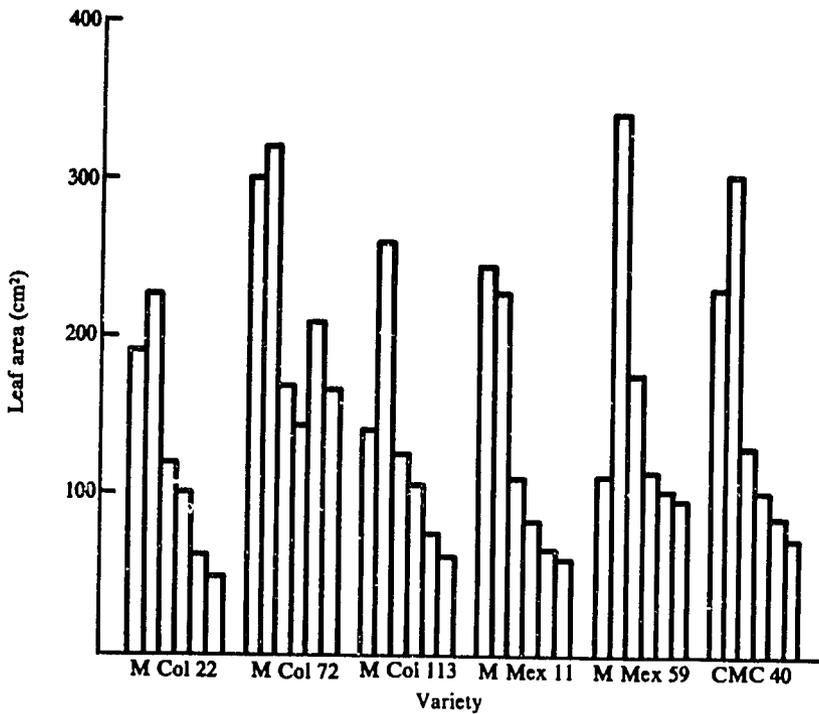


Figure 2. Leaf size changes through time in different varieties. Each column represents a 2-month interval. (Adapted from Tan and Cock, 1979b.)

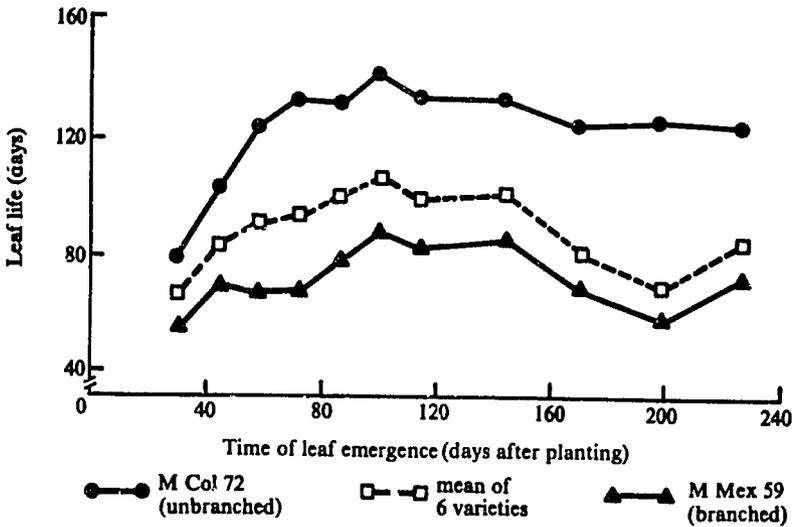


Figure 3. Leaf life in relation to time of leaf emergence. (Adapted from Tan, 1980.)

that shade has drastic effects on leaf life (Cock et al., 1979; Tan, 1980) which may explain why, in highly branched varieties, leaf life drops considerably in the later growth stages of the plant when there is a greater degree of intershading among leaves. Leaf life may be shortened by drought (CIAT, 1977) or disease, but prolonged by cooler temperatures (Irikura et al., 1979) (Figure 4).

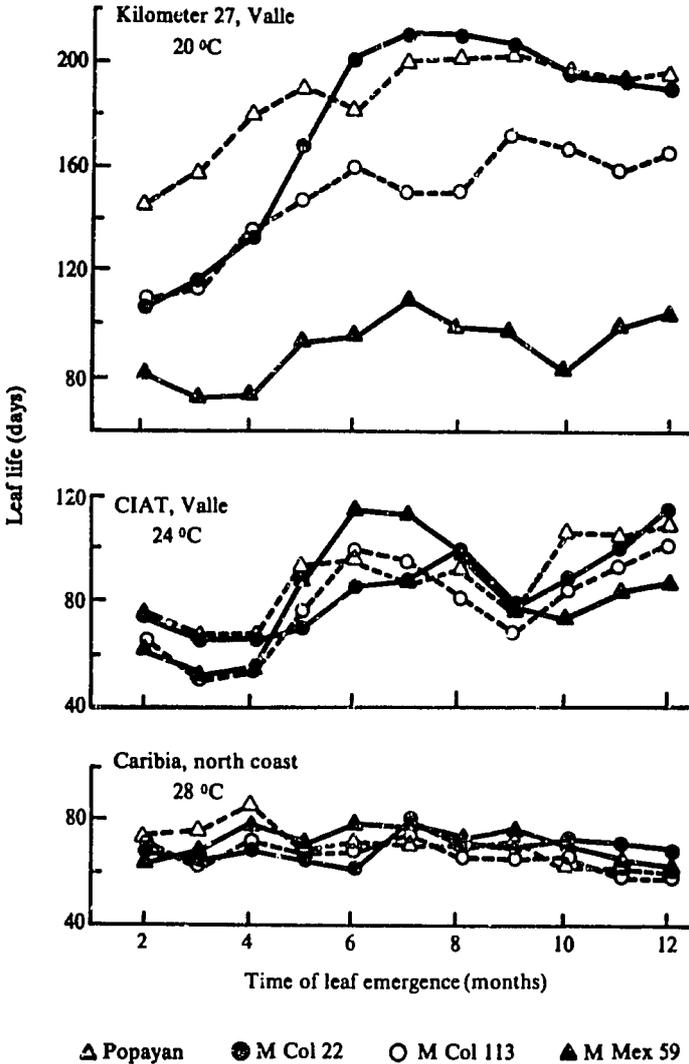


Figure 4. Effect of average temperature on leaf life. (Adapted from Irikura et al., 1979.)

Leaf production per apex. This factor remains fairly constant in unbranched varieties but shows a gradual decline in rate with time in branched varieties with little difference among varieties (Figure 5). However, total leaf production (leaf production per apex multiplied by the number of apices per plant) changes the picture: heavily branched varieties have many apices and so will have a very high rate of leaf production per plant, whereas an unbranched variety (unless more than one stem is allowed to develop per cutting) with its single apex will have a total leaf production equal to the leaf production rate of that apex.

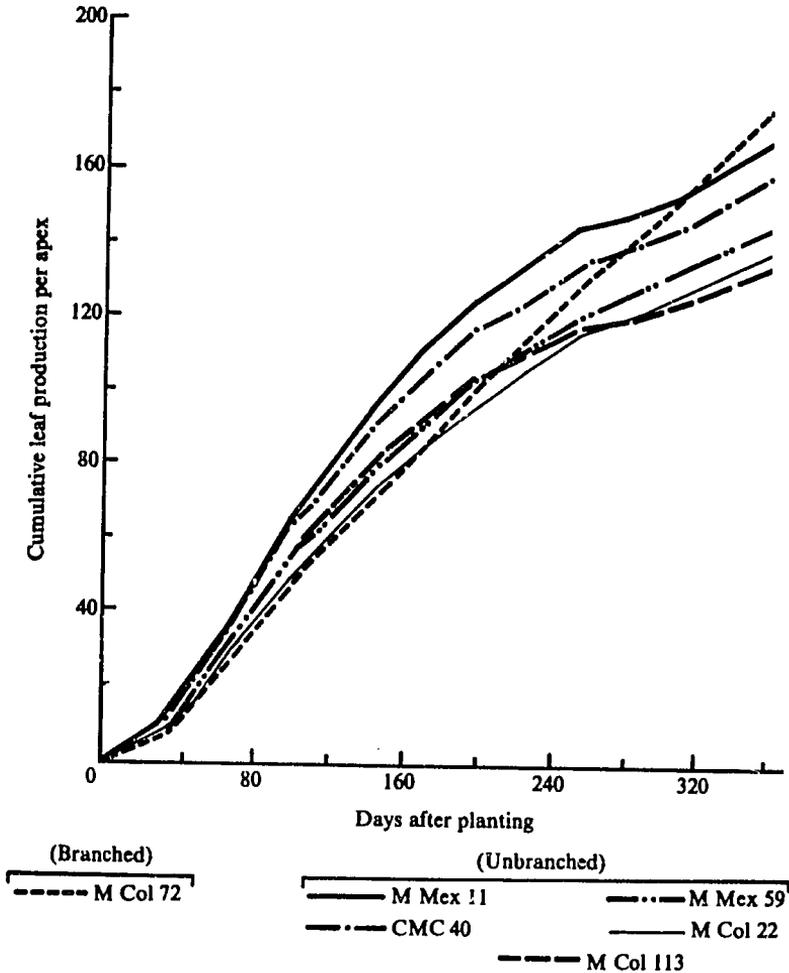


Figure 5. Leaf production rate per apex in different varieties. (Adapted from Tan and Cock, 1979b.)

Branching. Another varietal trait, branching, is defined by three parameters: the time of first branching; the rate of subsequent branching; and the number of apices formed per branching. A variety which branches early, often, and forms three or four apices at each branch point gives rise to a heavily branched form with dense foliage.

CGR has a parabolic relationship with LAI because at very high LAIs, leaf life becomes shorter and shorter as a result of shading. Although the number of leaves per unit land area may be high, this is maintained by a high turnover rate of leaves.

Harvest index

Total dry matter production or biological yield does not define the economic yield which, in cassava, usually refers to the root yield. Although root yield is highly correlated with total plant weight within a single genotype at various stages of plant growth (Boerboom, 1978b; de Bruijn, 1982; Tan, 1980), this relationship does not always hold true across genotypes. In other words, a large plant does not necessarily promise a high root yield. The harvest index, which is the ratio of root weight over total plant weight, is therefore a parameter which reflects the dry matter distribution within the plant in favor of root yield. In a crop such as cassava where the economic yield comes from a vegetative part—specifically, the adventitious roots which are modified into storage organs—the harvest index is generally much larger than may be expected from a crop whose economic yield results from fruits or seeds, such as grain legumes or cereals. Also, structurally speaking, higher harvest indexes are possible in root crops since the plant is not required to “hold up” a heavy yield (Coursey and Haynes, 1970).

Harvest index has been found to be one of the most important parameters in the selection for yield potential in cassava. Early work by Kawano (1978) has shown that selecting for high harvest index in seedling plants as well as in clones in single-row evaluation (that is, the first generation of clonal evaluation) is more effective in identifying high-yielding genotypes than using root yield itself as a selection criterion. Seedling and clonal yields are generally unrelated, partly because of the different nature of their storage root systems: the seedling plant has a tap root system whereas the clonal plant has an adventitious root system. Furthermore, clones in single rows respond differently from those in a stand or population because of differences in plant spacing and competition effects among and within genotypes (Kawano et al., 1982).

Priority of top growth. A clone with a high harvest index may be assumed to be physiologically more efficient, since most of its dry matter production is channeled towards storage in the roots. However, root storage takes a lower priority to top growth within a cassava plant. Dry matter storage in the roots results from any surplus over dry matter requirements for the production of new leaves (an energy-consuming physiological process), maintenance of existing leaves, and maintenance and weight gain of stems and branches. This was experimentally demonstrated by topping plants to arrest leaf production, resulting in increased dry matter storage in the root (Tan and Cock, 1979a).

The priority that top growth holds over root storage suggests that in a heavily branched clone with profuse top growth, the sheer mass of leaves, stems, and branches, as well as the high turnover rate of leaves (short leaf life due to heavy shading within the canopy), precludes as much dry matter left over for root storage as would be the case in a lightly branched clone. This supposition is borne out by an experiment in which a densely branching clone had varying number of branches removed to simulate different degrees of branching. The highest yields came from the lightly branched simulated plant types (Table 2). That an improvement in leaf life might have something to do with these better yields was also evident (Tan and Cock, 1979a). More directly, CIAT (1979) showed that when leaf life was shortened by artificial removal of leaves, root yield was similarly reduced (Figure 6). Indirect evidence is also to be found in the depressive effects of defoliation on root yields (Dahniya et al., 1981; IITA, 1976).

Selecting for high harvest index therefore ensures that genotypes with excessive top growth are avoided. Nevertheless, recent examination of top

Table 2. Dry root yield of M Col 113 with different branching patterns.

Times of branching (no.)	Apices per branching (no.)	Dry root yield (t/ha)	Root yield over control (%)
Control = 4	3-4	5.5	
4	3	7.3	33
4	2	10.3	87
0	1	8.4	53
1	3-4	8.5	55
2	3-4	9.8	78
3	3-4	9.3	69

SOURCE: Tan, 1980.

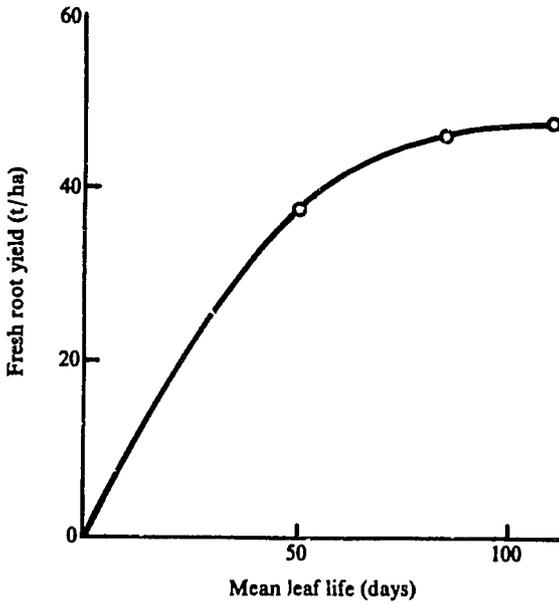


Figure 6. Effect of mean life on fresh root yield. (Adapted from CIAT, 1978.)

growth data in improved new clones (Table 3) shows that while harvest indexes and yields in those clones were higher, their top growth remained virtually unchanged from that of local control cultivars. This seems to emphasize the need to maintain a certain amount of canopy to provide an adequate photosynthetic apparatus for dry matter production. In other words, in striving for a higher harvest index, it is still necessary to ensure enough leaves remain to produce the dry matter for storage in the roots.

Root number. Assuming a lack of other limitations to root storage, sink strength is also determined by root number. Total root number has shown high correlations with root yield (Tan, 1981). When root number was reduced to less than seven or eight per plant by clipping at 6 and 12 weeks, root yield declined (Cock et al., 1979). Top growth was unaffected by the size of the root sink. In most clones, root number is fixed early during the plant's growth (Wholey and Cock, 1974). It can therefore be used as an early selection criterion. There is, of late, a great deal of interest in genotypes which are able to produce a root yield as early as nine or even six months. Such short-term cassava varieties will make more productive use of a given piece of land and provide a faster rate of return from planting cassava.

Table 3. Comparison of root yields, total fresh plant weights, fresh top weights and harvest indexes between improved clones and controls in three varietal trials.

Trials	Fresh root yield (t/ha)	Total fresh plant weight (t/ha)	Fresh top weight (t/ha)	Harvest index
Trial 1^a				
Five best clones	41.6	61.5	20.0	0.68
Control (local cultivar: Rayong 1)	28.9	49.8	20.9	0.58
% advantage over control	44	23	-4	17
Trial 2^b				
Five best clones	59.3	86.5	27.2	0.69
Control (local cultivars: Golden Yellow and Kadabao)	32.0	60.8	28.7	0.52
% advantage over control	85	42	5	33
Trial 3^c				
Four best clones	28.3	48.0	19.7	0.59
Control (local cultivar: Black Twig)	21.3	41.0	19.7	0.52
% advantage over control	33	17	0	14

- a. Conducted at Rayong Field Crop Research Center, Thailand, in 1983-1984 with 16 clones. (SOURCE: Kawano, K. and Tiraporn, C., Dept. Agric., Thailand.)
- b. Conducted at PRCRTC in Leyte, Philippines, in 1983-1984 with 74 clones. [SOURCE: Apilar, E. and Kawano, K., Philippine Root Crop Research and Training Center (PRCRTC).]
- c. Conducted at Ubiyu Plantation, Sitiawan, Malaysia, in 1982-1984 with 13 clones over two seasons. [SOURCE: Tan, S. L., Malaysian Agricultural Research and Development Institute (MARDI).]

In harvesting for early yield, more often than not a high harvest index at six or nine months is indicative also of that which may be expected after 12 months (Boerboom, 1978a; Tan, 1980). Harvest index changes with time, increasing rapidly in the first six months of growth, thereafter leveling off in its rate of increase towards the end of 12 months (Figure 7). A high-yielding variety at six months therefore tends to be high-yielding at 12 months as well, except in cases where the rate of increase in harvest index is low but relatively constant throughout the crop growth season.

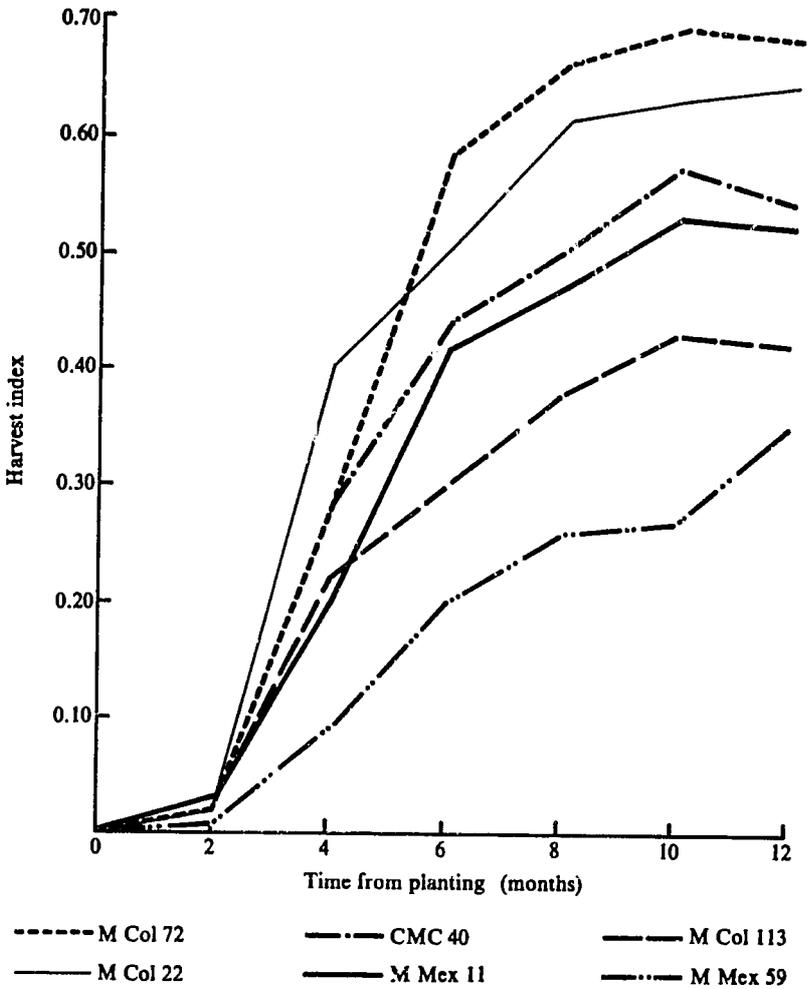


Figure 7. Relationship of harvest index with time in six varieties of cassava. (Adapted from Tan, 1980.)

Other yield indexes

Boerboom (1978b) postulated the use of two parameters to describe the efficiency of dry matter distribution in cassava: the efficiency of the plant in storage root production (ESRP), and the initial plant weight at which storage root production starts (ISS) (Figure 8). Since cassava is harvestable between 6 and 24 months after planting, the harvest index may not have reached its constant value at the time of harvest, whereas the ESRP as

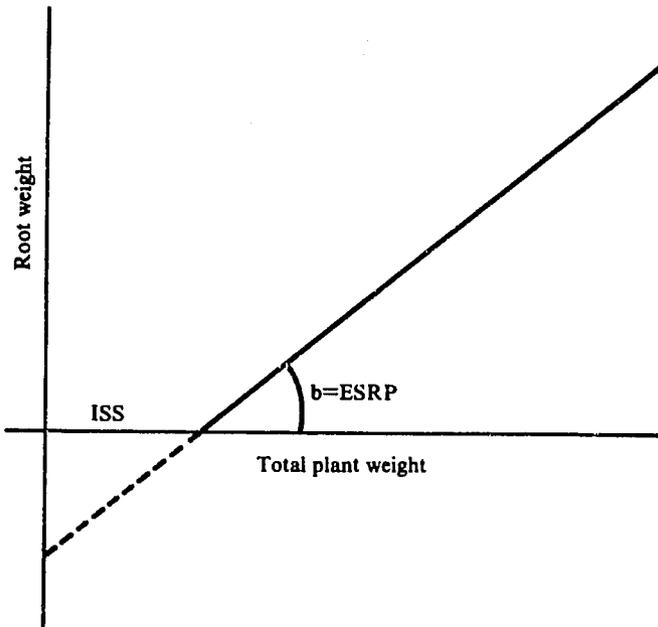


Figure 8. Relationship between dry weight of whole plant versus dry weight of roots. (ESRP = efficiency of storage root production; ISS = initial plant weight when root storage starts.) (Adapted from Boerboom, 1978a.)

proposed in the dry matter distribution model is a constant throughout time. Thus, the ESRP and ISS may be determined at early stages of the growth cycle, for example, before six months after planting. The ESRP was also found to be stable over different locations (de Bruijn, 1982).

It cannot be denied, however, that the harvest index is a more practical tool in selecting for high yield potential since the ESRP requires data from three or four harvests to plot the regression slope between root weight and total plant weight.

To complete the picture of intrinsic yield factors, it should be mentioned that there is, as yet, no direct evidence that the photosynthetic rate of single attached leaves is related to total dry matter production. This is probably because the relationship, if it exists, is confounded by the total number of leaves in the canopy, the degree of their intershading, and hence the differences in photosynthetic rates at various levels within the canopy. Indeed, Mahan et al., (1976) found that crop growth rate was related to the product of leaf photosynthesis and total leaf area. The rate of photosyn-

thesis of single attached leaves is not only a complicated parameter to measure, requiring apparatus of some sophistication, but also a questionable criterion in terms of practicality and efficiency in the selection for yield potential at present.

It would be appropriate to mention in passing that diseases and pests are known to be notorious reducers of yield (Hahn et al., 1979), and that incorporating resistance against these biotic factors would further remove limitations to the yield potential of any genotype. Indeed, yield was improved 2-18 times when resistance to bacterial blight was incorporated into new clones (IITA, 1976).

Towards realization of yield potential

What, then, are the parameters of practical importance in the selection for high yield potential? Little information on the genetic control of various physiological parameters and yield components in cassava is available in published literature. Heritability estimates on some characteristics of agronomic significance are listed in Table 4. Although broadsense heritability values (h^2_b) are generally high for root yield and harvest index, the narrow-sense value (h^2_n) is higher for harvest index than for root yield. This bears out the finding that harvest index in seedling populations is highly correlated with yield in clones, and that harvest index in clones under single-row evaluation relates strongly to yield in clonal populations.

While harvest index without doubt is a highly useful tool in selection, it would also be advisable to pay some attention to root yield itself. It is not uncommon to find genotypes of low vigor (and therefore low total plant weight because of short stature and poor top growth) having very high harvest indexes when obviously their root yields are much too poor to consider for selection. It would be inappropriate to use the harvest index blindly without consideration of root yield. It is, therefore, a good idea always to include controls, such as local cultivars or best available commercial cultivars, to set the level of yield that is to be improved. It will then be a simple matter to pick out those genotypes which exceed this yield level or at least attain it while having a higher harvest index than the controls.

Dry matter content of roots, total root number, and plant height have similarly high h^2_b values. Mean root weight is less highly heritable. The strong genetic component controlling total root number suggests its possible application as a selection criterion, especially since it is strongly

Table 4. Heritability estimates of some important agronomic traits in cassava.

Trait	h^2 value (%)	b/n ^a	Source
Root yield	76	b	Birader et al., 1978
	79-94	b	Kawano et al., 1978
	87	b	Tan, 1984
	40	n	Kawano, 1977
Harvest index	79	b	Birader et al., 1978
	75	b	Tan, 1981
	89	b	Tan, 1984
	68	n	Kawano, 1978
Dry matter (or starch) content	80	b	IITA ^b , 1981
	93	b	Tan, 1981
	92	b	Tan, 1984
	62	n	Kawano, 1978
Total root number	69	b	Birader et al., 1978
	81	b	Tan, 1981
	92	b	Tan, 1984
Plant height	37	b	Birader et al., 1978
	86	b	Tan, 1981
	91	b	Tan, 1984
Mean root weight (or root size)	40	b (?)	Hahn et al., 1977
	54	b	Birader et al., 1978

a. b = broadsense heritability; n = narrow sense heritability.

b. IITA = International Institute of Tropical Agriculture, Nigeria.

associated with root yield (Birader et al., 1978; Holmes and Wilson, 1977; IITA, 1982; Magoon and Krishnan, 1977; Tan, 1981). From a physiological point of view, selecting for higher root number (more than 8-10 per plant) would ensure that the size of the root sink is not limited to root bulking and yield. Where cassava is grown for direct human consumption, commercial root number (referring to roots of at least 15 cm in length) is an important consideration. This character appears also to be highly heritable with a value $h^2_b = 85\%$ (Tan, 1984).

The highly heritable nature of dry matter content (or starch content) is encouraging since economic yield in most cases strives for high dry root yield. As a selection criterion, starch content of roots is practical as it can

quite easily be estimated as dry matter content (to which it is highly correlated) or converted from the root specific gravity value (again highly correlated with starch content). Moreover, starch content has been found to be a very stable trait over different environments (Tan, 1984).

Plant height is a strongly inherited character and has shown positive correlation with total plant weight (Tan, 1981). It is, therefore, an indirect indication of total dry matter production, although it must be remembered that high total dry matter need not reflect high harvest index. Plant height together with the appearance or condition of top growth can therefore indicate plant vigor.

Although the heritability of leaf life and canopy characteristics still remain to be investigated, observations tend to suggest fairly strong genetic control. The use of leaf life as a selection criterion on its own has doubtful practicality—first, because one has to determine which is the best stage of growth at which to measure leaf life, and, second, because leaf life is only one of the physiological traits contributing to root yield and so may be expected to be relatively ineffective if selected for by itself. To ensure an adequate top growth for dry matter production, long leaf life helps to reduce waste of dry matter in abscised leaves and consumption of more dry matter to produce new leaves. Perhaps, as a temporary measure, until a fuller understanding of the inheritance of canopy characteristics and on how they can best be exploited is available, the condition of the canopy throughout the crop cycle may be used as an index of its adequacy. While the canopy must not be excessive (as in densely-branched forms where leaf life is reduced drastically because of intershading), enough foliage should be maintained throughout the cropping season to ensure a net production of dry matter for root storage (Doku, 1965). The ideal LAI of around 3.0-3.5 probably calls for intermediate- or late-branched forms with light branching, since completely unbranched forms often have difficulty in realizing the optimal LAIs for maximal crop or root growth.

Selections for high-yielding genotypes should as far as possible be carried out in those environments in which they will ultimately be cultivated. While for early stages of evaluation involving large numbers of seedlings and clones, this may not always be possible for reasons of costs and distances, such trials should be located at least in areas representative of production regions in terms of soils and climate. The final test for adaptability will still be regional trials in the final stages of clonal evaluation of the most advanced selections. This will help in reducing the gap between yields achieved at experimental stations and in farmers' fields.

As more and more comprehensive information is gathered to provide a better understanding of the physiological basis of yield in cassava and how individual traits are inherited or influenced by the environment, we may begin to fully exploit the yield potential of cassava through genetic as well as cultural manipulation. The day may come when yields in excess of 90 t/ha per year, as has been estimated to be physiologically sound and possible (Cock, 1974), will be realized with ease, not only under experimental conditions but also in actual farm situations.

Frontiers for cassava cultivation

The future of cassava is dependent to a considerable extent on its traditional ability to survive in relatively harsh or hostile environments where it faces little competition from other more economically important crops. It would therefore be unwise to select for genotypes which respond to a highly favorable environment such as high fertility and irrigation. We should even look towards extending the frontiers of cassava cultivation into special environments, such as:

Particular nutrient environments. There is evidence of physiological variability in different genotypes in their mineral nutrition with regard to responses to calcium and ammonium nitrogen and nitrate nitrogen (University of Queensland, 1981).

Different climatic and edaphic conditions. Unfavorable climatic conditions may be bypassed by selecting for short-duration or early harvestable varieties, for example, to avoid the hot and dry climate in central India in certain months of the year (Deshmukh et al., 1977). Varietal differences in adaptability to acid peat soils have been observed in Malaysia (Chew, 1974).

Intercropping with plantation crops. It would be necessary to select for some degree of tolerance to shade. Screening studies of 100 cultivars under coconut at the Central Tuber Crops Research Institute (CTCRI) in India (1973) have identified five with root yield reductions of only about one-third as compared to yields under full sunlight.

Mechanized cultivation. To reduce labor costs (a major component in production costs for cassava, particularly for harvesting), it would be necessary to select for suitable plant forms to facilitate cultivation, such as unbranched as suggested by Magoon and Krishnan (1977). Another factor of plant form to select for is root shape amenable to mechanical lifting.

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Selection for Improved Root Quality in Cassava

*Nzola Meso Mchungu**

Introduction

In cassava improvement, the breeder's primary concern is to increase the root yield of varieties that are resistant to major diseases and pests. Root quality should also be considered as an important selection criterion as this is the final factor in acceptability to consumers. Farmers often prefer a variety of good quality to a higher yielding variety of poor quality. In this light, some improved varieties have failed in the market because they could not meet other requirements of the consumers.

Selection for root quality is normally carried out at advanced stages of yield trials, as the tested lines are reduced in number. At the Zairian Programme National Manioc (PRONAM), screening for nutritional value is done simultaneously with other quality factors. These are measured both in fresh roots and in transformed products. In addition, leaf quality is evaluated since cassava leaves constitute the main vegetable of the Zairian diet.

Root quality characteristics often considered are the cyanide content, starch quality, protein content, and dry matter percentage. However, despite the improvement of quality in cassava roots and transformed products, the market value of these roots and products is not based upon the nutritional value alone, but also upon several other criteria such as color, flavor, cooking time, texture and consistency, taste, and storage ability. These criteria vary according to the product and the ethnic group of the consumer.

Cyanide content, dry matter, starch, and crude protein show wider variation in the hybrid population than in the parents, and character

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association studies for these four traits indicate their independent inheritance (Magoon et al., 1972). The breeder, therefore, can expect to be able to achieve simultaneous improvement for each.

Cyanide screening

Cassava is known to be toxic to humans because of the presence of cyanogenic glycosides: linamarin (up to 96% of the cyanogenic glycosides), together with much smaller amounts (up to 4%) of the closely related glycoside lotaustralin (Conn, 1973). Linamarin and lotaustralin hydrolyze under the influence of the endogenous enzyme linamarase to liberate hydrogen cyanide (HCN).

Although cassava is often described as "bitter" or "sweet" according to the amount of cyanide present, the sweetness or bitterness is not always associated with HCN (Coursey, 1973). Environmental conditions have a very important influence on the cyanogenic glycoside content of cassava plant organs. de Bruijn (1971) noted that different clones do not react in the same way to changing ecological conditions with regard to HCN content. Although the glycoside content increases with an increased rate of nitrogen fertilizer application, potassium and farmyard manure applications tend to decrease it.

Part of the variation in the levels of HCN production which exists among cyanogenic plants is genetically controlled, as observed in *Sorghum*, *Lotus*, and *Trifolium* spp. (Hughes, 1973). Hahn et al. (1977) reported that low cyanide content in cassava appears to be regulated by a recessive minor gene complex. A low broadsense heritability of 35% was found for root cyanide content (Mahungu et al., 1984).

To reduce the incidence of chronic toxicity associated with continued ingestion of cassava products, there is a need to develop improved varieties of cassava with low cyanide content (Sadik and Hahn, 1973). Screening of genotypes by estimating the cyanide content in the roots is laborious and time-consuming. Suggestions have been made to utilize cassava leaves, which are the site of cyanogenic glycoside synthesis (de Bruijn, 1971), for cyanide determinations to identify potentially low-cyanide cultivars (Sadik et al., 1974). Cassava could then be rapidly and conveniently screened at the seedling stage, since leaves are more accessible than roots. Furthermore, several workers (Cooke et al., 1978; Mahungu, 1983; Moh, 1976) have reported significant correlations between cyanide in leaves and in roots.

There is often a belief among farmers that the bitterness in cassava is associated with high yield. Holleman and Aten (1956) reported a positive correlation between root cyanide content and root yield and pointed out the difficulty of breeding cassava for low cyanide and high yield. This has been disputed by Cooke et al. (1978) and Sadik and Hahn (1973) among others. In a detailed study, using six cassava populations, Mahungu (1983) found that a weak but statistically significant genotypic correlation ($r = 0.20^*$ and $r = 0.26^{**}$) existed in only two populations. Other relationships found were a consequence only of the environment. This is an indication that there is no genetic barrier to develop high-yielding cassava clones with low cyanide levels. At the International Institute of Tropical Agriculture (IITA), several low cyanide clones have been developed (Table 1). The clone LCN 6063, which had the highest yield, had the lowest HCN content with 3.3 mg/100 g of fresh root. LCN 6068 and LCN 518 are relatively resistant to cassava mosaic disease (CMD) and cassava bacterial blight (CBB).

For large germplasm evaluations, it is advisable to use the sodium picrate test for hydrocyanic acid screening because it is faster and less

Table 1. Performance of clones with low cyanide levels, International Institute of Tropical Agriculture (IITA), 1979-1980, Ibadan, Nigeria.

Clone	Fresh yield (t/ha)	Dry matter (%)	Disease resistance			Total HCN (mg/100 g) ^b
			CMD ^a	CBB ^a	CGM ^a	
LCN 6068	31.8	30.2	2.5	1.5	2.0	3.3
LCN 518	22.7	34.4	2.3	1.5	2.3	8.9
LCN 6086	20.1	31.2	—	2.5	1.5	5.0
LCN 30474	17.1	33.6	3.5	1.8	2.0	7.2
LCN 3109-N-7	16.4	38.8	3.8	1.8	2.5	6.3
LCN A/41369	11.3	33.9	2.3	1.5	2.0	4.1
LCN 6051	8.9	25.7	4.0	1.5	2.0	9.2
LCN 3109-N-17	8.8	32.5	4.5	1.5	2.3	4.4
LCN 50067 B	6.7	31.9	3.8	1.5	2.0	5.3

a. CMD, CBB, and CGM are, respectively, cassava mosaic disease, cassava bacterial blight disease, and cassava green spider mite damage, which were scored on a scale from 1 to 5.

b. Hydrogen cyanide (HCN) content of fresh roots was tested, using an enzymatic assay.

expensive. At PRONAM in Zaire, large populations of cassava are screened each year. Clones established in the preliminary yield trial in 1983-1984 were screened and about 9% were found to be very low or low in HCN content (Table 2). Further testing with the quantitative enzymatic assay will help in determining the amount of HCN in selected low-HCN clones.

A major constraint in quantitative screening of large numbers of breeding lines for low cyanide content has been the lack of a rapid and reliable analytical technique. An automated method has recently been developed (Rao and Hahn, 1984) following the enzymatic assay as outlined by Cooke (1978 and 1979). The automated method can handle 300 analyses a day (40 samples/hour), as compared to 40 samples a day by the manual method.

Using the automated enzymatic assay, routine screening for HCN is carried out at IITA each year and low-HCN clones are identified (Figure 1). About 65% of the clones screened contain less than 5.0 mg HCN/100 g of fresh weight in the peeled roots.

Cyanide toxicity does not pose a serious problem in some parts of Africa where the roots are transformed into other products before consumption. A study conducted at IITA (Mahungu and Hahn, 1981) of fresh roots from four IITA-improved clones and two local varieties showed that the total HCN content was reduced from a range of 4.4-17.2 to a range of 0.1-0.6 mg/100 g of fresh weight after complete fermentation and peel removal on the third day of soaking in water (Table 3). More than 95% of the total cyanide was removed after fermentation—a significant amount, considering that fermentation is the first step of processing for many cassava products.

Table 2. Hydrogen cyanide (HCN) level in roots using the sodium picrate test, M'vuazi, Zaire, 1983-1984^a.

HCN level	Plants	
	(no.)	(%)
Very low	29	4.0
Low	34	4.7
Medium	84	11.5
High	583	79.9

a. HCN screening study at PRONAM is partly financed by the International Foundation of Science (IFS), Sweden.

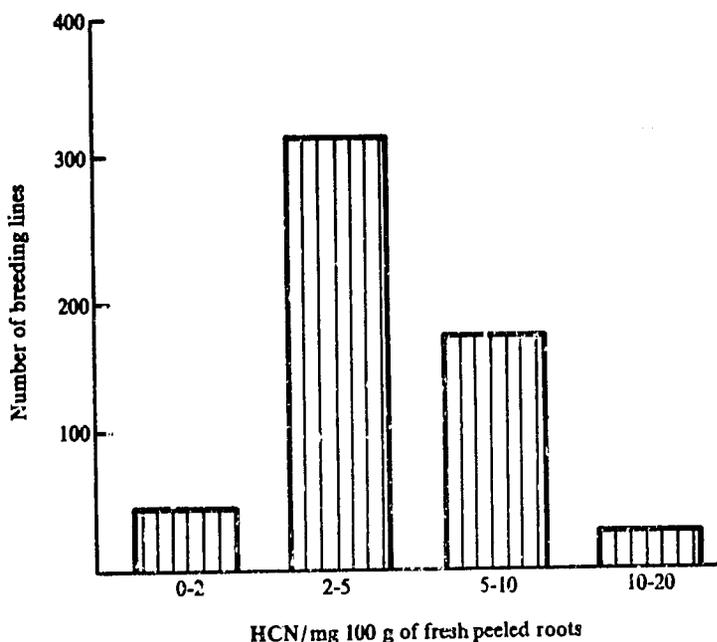


Figure 1. *Distribution of low-HCN cassava breeding lines screened by the automated method. (Adapted from IITA, 1981.)*

Table 3. Total cyanide (mg/100 g of fresh weight) reduction following cassava root fermentation in water, International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria.

Clone	Days after soaking				Peeled
	0	1	2	3	
30572	11.6	6.8	2.1	1.3	0.4
20395	9.5	6.9	3.2	0.9	0.1
50395	17.2	7.7	5.1	2.9	0.8
30001	5.1	2.3	1.0	1.0	0.6
Isun	4.4	3.1	2.0	0.9	0.3
60506	11.6	7.6	4.7	1.2	0.5
Mean	9.9	5.8	3.0	1.4	0.5
% ^a	100	58	31	14	5

a. Relative to 0 days after soaking.

In the Kasai region of Zaire where roots are not fermented, qualitative determination of HCN with the sodium picrate test (Kiala, 1983) has indicated that most of the flour still contained high amounts of HCN (Table 4). The results show that the amount in flour was generally proportional to the HCN content in fresh roots. In such cases, breeders' efforts should be to develop very low cyanide, but high-yielding clones. Most likely it is easier to introduce a new variety than to change food habits.

Table 4. Hydrogen cyanide (HCN) in flour from unfermented roots, Gandajika, Zaire, 1983.

Clone	Fresh yield (t/ha)	HCN in fresh roots ^a	HCN in flour ^a
30085/28/10	34.0	2.7	3.0
Kabongolo	27.3	2.7	2.0
30085/28/4	25.5	3.0	2.7
A 56/1	25.5	3.0	3.0
MSB	25.3	1.0	1.0
30093/6	25.0	2.7	1.7
CB 5065/1	24.0	2.0	2.0
MWP	22.3	1.0	1.3
HI 61	22.0	2.3	1.3
30085/28/8	21.3	2.0	2.0
S 097	17.0	3.0	3.0
30280/7/6	16.5	2.3	2.0

a. HCN rating: 1 = low; 2 = medium; and 3 = high.

Dry matter content

Dry matter determination is very useful in root quality evaluation because of its association with other root quality characteristics. Moderate to high heritability was reported (Mahungu et al., 1984) for dry matter in roots

(52%), while a high broadsense heritability of 80% was reported by IITA (1980). This high heritability indicates that selection of breeding clones for dry matter content may be effectively carried out at an early stage. However, low expected genetic gain was observed (29%), mainly because of its low (9%) genetic coefficient of variation (Mahungu et al., 1984). This indicates a somewhat limited scope for further improvement by selection.

Dry matter is also important in evaluating the quality of the roots for making *gari*, a common West African food made from grating and fermenting the roots. A significant genetic correlation coefficient ($r_g = 1.35$) was obtained between the percentage of dry matter and the garification rate¹ (IITA, 1980). This relationship indicates that selection at a preliminary stage based on dry matter percent may lead to a higher garification rate. However, other *gari* quality characteristics need to be evaluated at an advanced stage of breeding.

A strong genetic association ($r = 0.63$) between dry matter and starch was reported (Mahungu, 1983) using six cassava populations. In another study involving 205 clones, a correlation of $r = 0.81$ was observed (IITA, 1975). This suggests that both traits can be improved simultaneously by selection. Since the estimation of starch content is a more laborious procedure than for dry matter, initial screening can be carried out on the basis of dry matter content.

High dry matter percentage in roots has been observed in some cassava clones developed at M'vuazi research station in Zaire (PRONAM, 1984) (Table 5). Clone 30572/172 had 43% dry matter in its roots. High dry matter is the criterion used by most Zairian women for selecting cassava varieties, as high dry matter leads to higher flour production.

Starch formation

Initiation of starch formation in cassava roots was investigated in 10 clones at 1, 2, and 3 months after planting (Mahungu and Almazan, 1983). Starch granules stained by iodine were observed under the microscope. Agronomic factors that may influence starch formation such as plant height and number of roots and leaves, were also noted. It was evident that, even in the first month of growth, starch formation was initiated in the storage roots.

1. Garification rate is defined as: the rate of the processed *gari* over the total fresh tuberous roots in terms of weight (IITA, 1980, p. 52).

Table 5. Performance of selected cassava clones from an advanced yield trial, M'vuazi, Zaire, 1983-1984.

Clone	Fresh yield (t/ha)	CMB ^a	CBB ^a	Dry matter (%)
30572/175	23.4	3.0	3.0	37.7
30572/172	22.7	2.8	3.2	43.1
30572/4	16.8	2.0	3.0	39.2
Mpelo-longi	15.9	3.0	3.2	40.2
02865	19.3	3.0	3.2	36.6
30085/28	16.8	3.0	3.2	30.6
Trial mean	14.1	2.8	3.1	39.0
LSD (5%)	7.3			

a. CMB and CBB are, respectively, cassava mealybug and cassava bacterial blight disease, the incidence of which were scored on a scale from 1 to 5.

Effect of root size on cassava products

The effect of root size on the quality and yield of various processed products was investigated (Hahn et al., 1981). Twelve cassava clones from a yield trial at IITA were used for the investigation. The experimental design was a randomized complete block with two replications. Cassava roots from each replication and from each clone were divided into three marketable size classes: roots with a diameter less than 3 cm (small); those with a diameter between 3 and 5 cm (medium); and those with a diameter more than 5 cm (large).

Fresh roots were processed into two products: *gari* and *chikwangué*. *Gari* is derived from fresh roots after grating, fermenting, drying, and roasting. *Chikwangué* is made by fermenting, sieving, drying, pounding, parboiling, wrapping in leaves, and boiling. *Gari* is widely consumed in West Africa and *chikwangué* is consumed in Zaire and other central Africa countries. The total HCN content was estimated, following the enzymatic assay method (Cooke, 1978 and 1979).

The mean total cyanide estimation in *gari* (Table 6) for the 12 clones was 0.79, 0.70, and 0.75 mg/100 g for the small, medium, and large roots,

Table 6. Total hydrogen cyanide (HCN), (mg/100 g) in *gari*, according to root size, International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria, 1982.

Clone	Small	Medium	Large	Mean
30001	1.1	0.5	0.3	0.6
50207	0.5	0.3	—	0.4
50548	0.7	0.9	—	0.8
50193	1.0	0.9	1.0	1.0
U/1421	0.4	0.8	—	0.6
30572	1.1	0.6	—	0.9
50392	0.9	0.9	0.8	0.9
30337	0.5	0.6	0.6	0.6
60506	0.9	0.8	0.8	0.8
4(2)1443	0.5	0.4	0.6	0.5
4(2)0762	0.6	0.8	0.9	0.8
60444	1.2	0.9	1.0	1.0
Mean ^a	0.8	0.7	0.7	
CV	25.3	35.7	33.3	

a. Means are not significantly different at the 0.05 level.

respectively. There was no significant difference among the means. This suggests that root size has no influence on cyanide content in *gari*. The yields of *chikwangue* and *gari* according to root size are reported in Table 7. There was no difference in *chikwangue* yield according to root size, but the small roots gave less *gari* yield.

This study showed no difference in the quality of *gari* from different sizes of cassava roots. However, the quality of *chikwangue* from the small roots was not as good as that from medium and large roots.

Protein enhancement in roots

It is increasingly being recognized that an inadequate intake of food, with an insufficient calorie or energy intake, and not merely protein deficiency, is the cause of widespread protein-calorie malnutrition. Comparing some starchy roots, Oke (1977) found that cassava roots differed from yam and potato in containing fewer free amino acids in fresh samples. However,

Table 7. Percent conversion of fresh cassava roots to processed products according to root size, International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria, 1982.

Clone	Chikwangué				Gari			
	Small	Medium	Large	Mean	Small	Medium	Large	Mean
30001	18	28	—	23	12	14	16	14
50207	32	16	36	28	10	12	—	11
50548	16	22	24	21	10	10	—	10
50193	28	24	20	24	6	11	10	9
U/1421	26	30	33	30	11	14	—	12
30372	28	38	30	32	10	12	—	11
50395	18	28	18	21	9	11	12	10
30337	24	25	26	25	10	13	13	12
60506	14	40	20	25	10	10	10	10
4(2)1443	32	36	36	35	10	10	14	11
4(2)0763	28	34	28	30	9	12	10	10
60444	16	14	14	15	4	6	6	5
Mean ¹	23.3a	27.9a	25.9a		9.3 b	11.3a	11.4a	
CV	19.8	32.1	57.5		23.7	20.8	13.6	

1. Means followed by the same letter are not significantly different at the 0.05 level.

cassava is biologically a highly efficient producer of calories, and if it could be made a more efficient producer of protein, it could make a greater contribution to nutrition in the tropics. Protein malnutrition is prevalent, particularly among low-income families in the developing regions where cassava is an important food.

Some attempts have been carried out to improve the protein content of cassava roots through conventional breeding methods involving selection, hybridization at both intra- and interspecific levels, induced polyploidy, and mutation. A large germplasm collection comparison of about 1400 entries was screened for quality characteristics but no significant variability in root protein content was found (Hrishi and Jos, 1977).

However, using interspecific hybridization, a wild species, *Manihot saxicola* (claimed to contain 11% protein) was crossed with *M. esculenta* in an attempt to transfer high protein content to the cultivated species (Jones, 1959). The few successful seedlings obtained from this cross showed relatively high protein content in the roots, but when these selections were

propagated vegetatively, the protein content fell back to typical levels (Jones, 1959).

Polyploidy has been reported to be successful for quality improvement of some crops (Allard, 1960). Thus, Jos et al. (1972) compared the protein content of the diploid and tetraploid plants and found that the average crude protein in the tetraploid was 42.3% more than in the diploid. Storage roots of diploid parents showed a range of 2.26%-3.30% crude protein, while in the corresponding tetraploids, the range was 3.30%-4.86%. Jos et al. also reported that the roots of diploids and tetraploids did not differ significantly in shape or size, so that the variability in protein content was not merely a characteristic related to the overall size of roots, as noted in some other crops, but rather that the protein per se increased. The age of the plant is very important in selecting for root protein because storage proteins, which are relatively low in sulfo-amino acids, are formed at a later stage of development.

Selection procedure for root quality

Following the breeding scheme as reported by Hahn (1982), root quality evaluation can be performed as follows:

The cyanide in the leaves of seedlings (20,000-100,000) established in the nursery is evaluated, using the sodium picrate test. This simple and fast test is appropriate at this stage. However, attention should be placed on the number of samples evaluated. One sample per plant is taken during the first run. Those plants detected as having low cyanide are rerun for confirmation by assessing five samples per plant.

The above method is again used in reevaluating the roots and leaves of the first clonal evaluation comprising 500-3000 clones. About 100 clones in the preliminary yield trials are evaluated for cyanide (both roots and leaves), using the enzymatic assay. In the advanced yield trials with about 40 clones, cyanide content in roots and leaves is again assessed, using the enzymatic assay. Additionally, root dry matter content is determined.

Other root quality characteristics are assessed in the uniform yield trial, comprising about 15 clones. The roots are transformed into local products and a panel of about 30 persons are invited for quality testing. The color, flavor, texture and consistency, and taste are evaluated by the panel and this information helps in identifying the causes of consumer appreciation or rejection of a variety.

General considerations

The nutritional status of different cassava varieties suggests that there is no theoretical reason why cassava with increased amounts of root and leaf protein should not be developed by breeding. Screening methods must be fast, use little material, and not require expensive equipment. In general, such methods are likely to be simple chemical procedures. If stable relationships are identified between agronomic traits and any of the root quality characteristics, these also can be efficiently used in selecting good root quality at preliminary stages.

In many parts of those developing countries where cassava is eaten, grain legumes are the principal source of protein nitrogen in people's diets. In such circumstances the sulfo-amino acid content of the grain legumes is of significant importance, since the cyanogenic glucosides present in cassava combine with and reduce the absorption of methionine and other sulfo-amino acids (Hulse, 1975). In some other areas (for example, Zaire and Uganda), cassava roots are often eaten together with sesame, which has been reported to have a high content in methionine.

In addition to these various aspects of nutritional quality, there is a need to describe more precisely the contribution of cassava to the diet of the people living in the humid tropics. Knowing what and how people eat will give breeders considerable insight as to how new cassava varieties will improve their nutrition. However, cassava roots are not to be considered as a protein source like beans, but must be regarded as good suppliers of daily energy.

There is a need to standardize the manner in which analytical results related to root crop quality are reported. For example, some workers use ppm for HCN content while others use mg/100 g of fresh weight. Another question is whether to screen protein as the absolute amount per weight of roots or as a percentage of root weight. There should also be a standardized methodology by which the biochemical composition of root crops is determined and rationally presented.

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Techniques and Advances in Breeding Cassava for Disease Resistance in Africa

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Introduction

Cassava is commonly referred to as a "poor people's subsistence staple" in many areas, particularly in Africa, where it is grown as a major food crop. Cassava roots, which are prepared in many different ways (depending upon local custom and preference), form the basic starchy element of the diet. In some African countries, the leaves are also consumed as a green vegetable, thus providing an additional source of much-needed protein.

Cassava has the ability to adapt to diverse environmental conditions and when it is incorporated into complex farming systems can produce relatively high yields despite adverse conditions. Cassava is relatively drought tolerant and can survive 4-6 months of dry weather. It requires few production skills and can be grown with limited inputs. Planting and harvesting are not seasonal. It is usually harvested as required for consumption and can be kept in the ground for up to 24 months. It continues to play a vital role in alleviating famine conditions in Africa where drought often occurs, by producing a constant food source when other crops fail. For this reason, cassava cultivation is continuously being expanded. In many parts of Africa, where populations continually increase, soils have become progressively poorer because of heavy and continuous overuse. Cereals cannot be successfully grown under these conditions, but cassava can often give reasonable yields. Before the last 15-20 years, cassava was believed to be a hardy crop with few or no major disease problems. However, the low average yield of 6.4 tons/ha in Africa (in comparison to the world's average of 8.8 t/ha) is primarily a result of heavy disease and pest infestation in addition to poor soil and crop management practices.

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A number of cassava diseases have been reported to be of economic importance throughout the world (Lozano and Booth, 1974; Terry, 1982). However, this paper discusses cassava breeding for resistance to only those diseases of major importance in Africa: cassava mosaic disease (CMD), cassava bacterial blight (CBB), and cassava anthracnose disease (CAD).

Major economic diseases of cassava in Africa

Cassava mosaic disease (CMD)

CMD is a foliar disease and has been observed in Africa and India, causing 20% to 40% reduction in root yield. The disease is readily transmitted by an insect vector (*Bemisia tabaci* Genn.). The causal agent (a geminivirus) of CMD was first sap-transmitted from CMD-infected cassava to *Nicotiana clevelandii* by Bock and Guthrie (1976) and to *N. benthamiana* by Rossel (IITA, 1979). The CMD virus was sap-retransmitted from cassava onto CMD-susceptible cassava clones from Latin America (Bock and Guthrie, 1978). The geminivirus was successfully transmitted back to cassava from the inoculated host *N. benthamiana* (Bock and Woods, 1983; Rossel, 1983). It thus appears that the epidemiology of CMD, which has been a mystery to virologists for some 50 years, has finally been understood.

The incidence of CMD in cassava is based on the availability of inoculum, which in turn is dependent upon both the density and activity of its vector, the whitefly (*Bemisia tabaci* Genn.). Environmental conditions that apparently favor whitefly population buildup and activity are: 150-280 mm of rain/month, temperatures within the range of 27-32 °C, and solar radiation of 400 g-cal/cm² (SI units: 1673.6 J/cm²) (Leuschner, 1978). Detopping shoots also enhances CMD symptom expression. The young leaves are more susceptible than older ones and CMD symptoms decrease with increasing plant age.

Environmental conditions affect CMD symptom expression: temperatures greater than 35 °C suppress symptom development (Chant, 1958; Terry, 1978). Disease incidence is also altered by the application of lime. Liming at a rate of 0.5-1.0 t/ha was shown to increase the incidence of CMD (Edwards and Kang, 1978). In acidic soils, CMD is less severe. Soil nutrient levels, particularly those of nitrogen, phosphorus, and sodium, are highly correlated with the severity of CMD: $r = 0.58, 0.54, \text{ and } 0.51$, respectively (Ambe-Tumanteh, 1980). The incidence of CMD is less during the dry season, at elevations higher than 500 m, and in those areas where annual rainfall is either less than 900 mm or more than 1500 mm per year.

Cassava bacterial blight (CBB)

Four species of bacteria are known to infect cassava (Lozano et al., 1981), two of which are present in Africa: *Xanthomonas campestris* (Pammel) Dowson pv. *cassavae* (Arthaud-Berthet and Bondar) Dye and *X. campestris* pv. *manihotis*, the former being less important. The latter, the causal agent of CBB, has been reported in many countries throughout Africa and results in complete yield loss under favorable conditions for its development and spread.

As plants become older, the tip dieback symptom of CBB increases (Hahn, 1978), and older, lower leaves exhibit more serious symptoms than younger ones. However, the young shoots are more susceptible than older shoots.

CBB severity is higher in cooler areas where day and night temperatures average 20-25 °C than in warmer areas where temperatures average 25-30 °C. It is more severe in areas where night and day temperatures are 15-20 °C and 28-30 °C, respectively, than in areas where night and day temperatures are 22-25 °C and 30-33 °C, respectively (Takatsu et al., 1979). The optimal temperature for growth and development of both *X. campestris* pv. *cassavae* and *X. campestris* pv. *manihotis* has been shown to be 30 °C (Maraité and Meyer, 1980). CBB incidence appears to be higher in poor sandy soils during the rainy season.

Cassava anthracnose disease (CAD)

CAD, caused by *Colletotrichum gloeosporioides* pv. *manihotis* Henn., has been reported in many countries (Muimba, 1982) and attacks mainly the stem. *C. manihotis* is a weak pathogen. When the cassava host is injured by storm, animals, insects, or other diseases, severe infection may occur. A sap-sucking insect (*Pseudotheraptus devastans*) has been reported to be responsible in part for disease spread and infection (Muimba, 1982).

The succulent parts of young cassava stems are more susceptible to CAD than older parts. CAD incidence and severity are higher in the later part of the wet season than in the early rainy season (IITA, 1976). The suitable relative humidity for both growth and spore germination of the pathogen was found to be between 91%-98% (Chevaugéon, 1956). Among the temperatures tested, the optimal rate for growth and sporulation of

the fungus was found to be between 20-27 °C (Muimba, 1982). The highest spore germination rate was observed within a range of 20-30 °C (Muimba 1982).

Identification of sources of disease resistance

Breeding for CMD resistance was initially carried out by Storey in 1937 in East Africa (Nichols, 1947). Low levels of CMD resistance were observed in the cultivated species, *Manihot esculenta*, from East Africa and other cassava-growing countries. However, higher CMD resistance was obtained by crossing with ceara rubber (*Manihot glaziovii*) and continued backcrossing to cultivated cassava in the early 1940s (Nichols, 1947). None of the selections from these progenies were immune to CMD.

Seeds of clone 5318/34 bred by Storey et al. were introduced into Nigeria by Beck in 1956. He identified clone 58308 to be resistant to CMD in 1958 (Beck, 1960 and 1982; Ekandem, 1970). Although breeding was discontinued in 1961, the CMD-resistant clone 58308 was maintained and continued to show resistance for nearly 30 years, despite heavy CMD pressure. Yield from this clone, however, was poor, both in quantity and quality (Hahn et al., 1977). Crosses were further made at the International Institute of Tropical Agriculture (IITA) between 58308, local cultivars, and *M. glaziovii*. IITA-improved families exhibited superior resistance to CMD under IITA conditions, compared to those from Latin America, East Africa, and India (Table 1). As CMD has not been reported in Latin

Table 1. Comparison of cassava families (seedlings) from various regions for resistance to cassava mosaic disease (CMD) at IITA, Ibadan, Nigeria, 1974.

Region ^a	CMD score ^b					Families tested (no.)	Families scoring 1 or 2 (%)	Average score
	1	2	3	4	5			
IITA ^c	5	97	170	40	2	314	32	2.8
East Africa	0	2	12	19	36	69	3	4.3
CIAT ^d	0	7	66	50	82	205	3	4.0
India	0	0	0	0	6	6	0	4.8

a. Open-pollinated seeds from different cultivars were introduced from various regions. "IITA" refers to the open-pollinated seeds from IITA-improved clones.

b. Score: 1 = highly resistant; 5 = highly susceptible.

c. IITA = International Institute of Tropical Agriculture, Ibadan, Nigeria.

d. CIAT = Centro Internacional de Agricultura Tropical, Cali, Colombia.

America, the low frequency of resistant families is to be expected. IITA-improved clones such as TMS 30395 and TMS 30001 are nearly immune to CMD.

Clone 58308 produced about 50% of IITA's CBB-resistant progenies (Hahn, 1978; IITA, 1972). Resistance to CBB was tested at IITA via stem puncture inoculation methods on 583 IITA hybrid families (resulting primarily from crosses with 58308) and on other families from East Africa and the Centro Internacional de Agricultura Tropical (CIAT). The results are presented in Table 2 (Hahn, 1978; IITA, 1974). IITA-improved clones TMS 30211 and TMS 30555 showed higher levels of CBB resistance than 58308 (Maraité and Meyer, 1980; Perreaux, 1977).

Table 2. Comparison of three sources for resistance to cassava bacterial blight (CBB).

Source ^a	CBB score ^b					Families tested (no.)	Families scoring 1 or 2 (%)	Average score
	1	2	3	4	5			
IITA ^c	32	126	139	16	1	314	50.3	2.4
East Africa	0	5	37	20	2	64	7.8	3.3
CIAT ^d	0	30	31	144	0	205	14.6	3.6

- a. CBB scores from IITA were made after inoculation (high pressure) and those from East Africa and CIAT were made under natural infection (low pressure).
 b. Score: 1 = highly resistant; 5 = highly susceptible.
 c. IITA = International Institute of Tropical Agriculture, Ibadan, Nigeria.
 d. CIAT = Centro Internacional de Agricultura Tropical, Cali, Colombia.

Incorporation of disease resistance into breeding populations

The incorporation of genes responsible for disease resistance from other cultigens or related species into improved cultivars or populations has been given priority in cassava breeding at IITA.

Backcrossing, followed by selection, has been used extensively (Hahn et al., 1977) to introduce new sources of resistance from related *Manihot* species. Two or three backcrosses to adapted cultivars were made in order to incorporate the CMD resistance sources from *M. glaziovii*. Except for incorporation of resistance, no overall improvement in cassava was achieved. Therefore, the methodology for transferring genes associated

with disease resistance (which are frequently quantitative in nature) into adapted cultivars or breeding populations, while still retaining desirable genes, needs further investigation and improvement. This is particularly necessary for a breeder who wishes to: transfer disease resistance genes from exotic germplasm and other related species into breeding populations in a relatively short time; increase genetic variation of desirable genes and; improve the chances of recombination in the populations. At IITA a series of hand crosses were made between adapted and exotic material and the hybrids were grown out as a population, with natural random crossing in subsequent generations. The most promising selections were pollinated with bulk pollen from selected clones.

As cassava is normally cross-pollinated, adequate random pollination usually takes place in well-designed isolation plots with several selected clones. However, a certain degree of self-pollination cannot be avoided and complete parental representation might sometimes be difficult because of the lack of synchronization during flowering. Therefore, population improvement approaches which aim at a continuous genetic upgrading through new germplasm introduction, cyclic selection, and recombination procedures can be specifically adapted to cassava (Hahn, 1978; Hahn et al., 1977). The degree of success depends very much upon the selection of parents going into an isolation plot, based on their breeding values. Population improvement may take many forms. However, half-sib family selections have been most appropriate for cassava breeding at IITA (Hahn et al., 1977). With this scheme, breeding populations for the improvement of disease resistance, yield, quality characters, and other agronomic characters have been successfully upgraded, and a large number of promising individuals have been isolated. Resistance to CMD and/or CBB was improved in one cycle, taking 1-2 years (Hahn et al., 1980b).

Screening for disease resistance

Breeding for resistance to diseases aims at improving the cultivars resistance in a wide range of environmental conditions and for a long period. The final goal is stable productivity. Screening in the field is generally based on phenotypic expression of disease symptoms by plants that are naturally infected by disease. Screening is most reliable when done under environmental conditions that closely replicate cassava-growing areas, favor full symptom expression by genotypes, and have adequate disease inoculum. The optimal environment will enhance the differences

between genotypes in the manifestation of the symptoms. The environment should be as uniform as possible. The selection of the screening sites and seasons is very important for efficient field screening. The sites should, as much as possible, represent the major cassava-growing areas or regions in climate, soils, topography, biological organisms (diseases and vectors), and cultural methods. The genotypes to be screened should also be at the most appropriate stages of plant growth for good disease infection to occur and for better symptom expression.

Screening for disease resistance has normally been done at an early stage of breeding and the resistance confirmed at later stages. A heavy selection pressure has been applied for disease resistance at the early breeding stage.

Screening methods

Field screening for resistance to CMD should be done in an environment where inoculum from diseased cassava is present, whitefly populations are high, and the average temperature is relatively low (below 30 °C). Screening against CMD is also most effective in a locality where annual rainfall is 1000-1500 mm, elevation is lower than 500 m, average temperatures are about 20-25 °C, and soils have a pH of 4-6 and are rich in nitrogen and phosphorus but low in sodium. Seedlings to be screened need to be grown before the onset of the rainy season (or early into it) so that they are exposed to the high disease pressure that occurs in the middle of that season. During this period whitefly populations are high, temperatures are not very high, and plant growth is vigorous.

Detopping the seedlings also enhances CMD symptom expression. Selected seedlings should be replanted in the following year for resistance confirmation. Tests for CMD resistance for 2 years are sufficient in localities with high disease pressure, but at least 4-year tests are needed in localities where disease pressure is low, such as in high-altitude areas (Hahn et al., 1980b). Resistance to CMD has shown moderate to high heritability in plants tested under optimal environments. This finding suggests that selection for CMD resistance is effective and, in such environments, is possible at an early breeding stage.

CBB scores depend upon time of planting, age of plant, and time of observation (Hahn, 1978), and have shown variation from year to year. CBB screening should be done in the rainy season when the rate of CBB symptom development and severity are high and when plant tissues are succulent. Seedlings should, therefore, be raised before or early in the rainy season as is the case for CMD resistance screening. The correlation

between CMD and CBB is significant and implies that selection for resistance to one of the diseases will result in resistance to the other. If heritability can be manipulated by providing favorable testing conditions and better techniques for CBB screening, the gain in CMD resistance should parallel that in resistance to CBB. If CBB incidence is not high under natural field conditions, artificial inoculation with CBB provides a better test. In localities where both CMD and CBB are problems, screening of breeding material for resistance to both diseases at the same time should be done. This method increases efficiency in screening and reduces expenses. Resistance to CBB, like that to CMD, has been shown to be moderately to highly heritable under optimum environments for symptom expression.

To minimize possible screening errors or, in other words, to maximize the probability that the selected genotypes can be adapted over a wide range of environments, researchers should ensure that the genotype-environment interaction effect is small.

Since CAD incidence and severity are higher in the rainy season when relative humidity is high and temperature is relatively low (conditions which favor the growth and sporulation of the fungus), screening of breeding material for CAD resistance should be done during the rainy season and in areas where such environmental conditions prevail.

Durability of disease resistance

Since 1973, IITA-improved breeding material with resistance to CMD and CBB has been distributed in both seed and tissue culture form to 31 countries in Africa with a wide range of environmental conditions. Although both disease incidence and severity for the tested genotypes changed with environments, the trends in disease resistance have been consistently similar to results at IITA. The genotypes which have been grown in many countries throughout Africa have continuously shown resistance to the diseases for nearly 10 years. This absence of genotype-environment interaction, the continuous resistance of the genotypes to diseases for nearly 10 years, and the apparent polygenic nature of resistance to the diseases suggest that the resistance is durable and will continue to be so in many African countries. Whether it will prove to be race-nonspecific depends upon the pathogenic variation—the information on which is not yet available (Hahn et al., 1980a).

CAD showed protogenic variation among the 18 isolates from different

parts of Nigeria but no genotype-isolate interactions were observed, which suggested the absence of genotype-specific races among the races tested (Muimba and Terry, 1981). Results from the study, particularly on pathogenic variation and genotype-race interaction for CAD, warrant further investigation.

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Recent Advances in Resistance to Insect and Mite Pests of Cassava

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Introduction

Cassava (*Manihot esculenta*) is a perennial shrub of the Euphorbiaceae. It is grown throughout the tropical regions of the world and is a major energy source for 300 to 500 million people. Cassava originated in the Americas, was later taken to Africa, and more recently introduced into Asia (Beck, 1982; Leon, 1977). Cassava is cultivated mainly in developing countries on small farms with little modern technology. Depending on ecological conditions, the growing period is 8 to 24 months.

Cassava pests represent a wide range of arthropods—approximately 200 species have been recorded. Although many are minor pests, causing little or no economic losses, several must be classified as major pests. These include mites, thrips, mealybugs, and whiteflies. This complex has been extensively reviewed by Bellotti and van Schoonhoven (1978).

Since cassava is a long season crop, often grown by subsistence farmers with a low profit margin, the continual use of pesticides to control insects and mites is economically prohibitive as well as environmentally unsound. The most feasible alternative methods of control are host plant resistance, biological control, cultural practices, or any combination of these (Bellotti and Kawano, 1980).

Resistance to insects or mites attacking cassava is not extensively reported in the literature. Many of the reports deal only with field observations and, until recently, there was little systematic evaluation of germplasm. Because of recent increased interest in cassava several national and international institutions have assembled extensive germplasm banks which are available to researchers for evaluation for resistance to the numerous cassava pests (Byrne, 1984).

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At present, cassava is grown mostly on small plots by small farmers throughout the tropical growing regions of the world. The genetic variability in this system is enormous because each area or zone is often sown to a distinct variety. The genetic variability in this system constitutes, in essence, a geographic multiline which is a genetic safeguard against major epidemics of pests and diseases. This is especially true in the Americas where cassava evolved and has been cultivated for thousands of years, resulting in thousands of traditionally grown varieties. The CIAT germplasm bank, a collection of farmer-grown varieties, now exceeds 3800 accessions. Many of these accessions contain resistance to one or more of the major cassava pests (Byrne, 1984; CIAT, 1975, 1976, 1977, 1978, 1979, 1980a, 1981, 1982, 1983, and 1984).

In contrast, the cassava-growing regions of Africa and Asia do not contain this extensive genetic diversity. In Africa, in recent years, this lack of genetic diversity has contributed to the widespread outbreaks of mites and mealybugs, causing severe crop losses (Herren, 1981). These types of pest outbreaks have rarely occurred in the Americas. In Asia, where genetic uniformity is more common, such as in Thailand (Cock, 1985), there exists the potential danger for severe, widespread pest outbreaks.

As new, high-yielding hybrids are developed, released, and sown to extensive areas, genetic uniformity will increase and much genetic variability may eventually disappear. The new hybrids will be well suited to modern agronomic practices, but such genetic uniformity is an invitation to disaster from epidemics of pests and diseases. In subsistence agriculture, in which much of cassava is now grown, there is a reasonably stable equilibrium between pests and genotypes. Integrated control programs built around plant resistance are needed to maintain this equilibrium in modern agricultural systems, where extensive areas are planted to uniform genetic material (Bellotti and Kawano, 1980).

Importance of resistance in cassava pest management

Resistance of plants to insects is the property enabling them to avoid, tolerate, or recover from injury by insect and mite populations that cause greater damage to other plants of the same species under similar environmental conditions. This property usually derives from certain of the plants' biochemical and/or morphological characteristics which so affect the behavior and/or the metabolism of insects or mites as to influence the relative degree of damage caused by these pests (Kogan, 1975).

Stable host plant resistance offers the most advantageous and practical long-term solution for controlling cassava pests because it is economical, easy to use, and compatible with other control measures (Bellotti and Byrne, 1979). Kogan (1975) describes other desirable features of host plant resistances: specificity—plant resistance is usually specific to a pest or pest complex with no direct detrimental effect on beneficial insects; cumulative effect—immunity to the insect or mite is not needed because the effect on the pest population may be compounded in succeeding generations; persistence—most resistant varieties remain stable for a long time; and harmony with the environment—there is virtually no danger of contaminating the environment or endangering man or wildlife.

The compatibility of plant resistance with other tactics in pest management make it especially attractive to the cassava agroecosystem. Cassava, being a long-season, vegetatively-propagated crop, is often subjected to continual attacks of insects, mites, and diseases. This cassava pest complex is, in turn, attacked by numerous natural enemies, whether parasites, predators, or microorganisms, that help reduce and stabilize the pest population. Plant resistance and this biological control are compatible and complementary systems.

Normally, selected clones should have a balanced resistance to all the important problems in a given ecosystem. Selection for single resistance factors without considering other traits or pests and diseases may be a useful tool in specific pathological or entomological studies, but generally it is an inefficient means to accumulate resistance factors to a complex of diseases and pests (Lozano et al., 1983).

The cassava insect and mite complex

Most important species and their geographic distribution

There are 17 major pests of cassava (Bellotti and van Schoonhoven, 1978). The groups of pests described in Table 1 are all found in the Americas, 12 are reported from Africa, and 6 are found in Asia (Bellotti and van Schoonhoven, 1977). This is expected since, wherever there is great variation of the host plant, there is a great variability in the organisms that attack the plant or are in symbiotic relationship with it (Jennings and Cock, 1977).

Yield losses and type of damage

Cassava is often considered a rustic crop and therefore generally free of

Table 1. Cassava pests and their control.

Common name	Scientific name	Control ^a
Mites	<i>Mononychellus</i> spp.	R, BC, C
	<i>Tetranychus</i> spp.	
	<i>Oligonychus</i> spp.	
Thrips	<i>Frankliniella williamsi</i>	R, C
	<i>Corynothrips stenopterus</i>	
	<i>Caliothrips masculinus</i>	
Lace bugs	<i>Vatiga manihotae</i>	R
	<i>V. illudens</i>	
Whiteflies	<i>Aleurotrachelus socialis</i>	R, C
	<i>Bemisia tabaci</i>	
	<i>Aleurothrixus aepin</i>	
Mealybugs	<i>Phenacoccus herreni</i>	R, BC, CP
	<i>P. manihoti</i>	
Hornworms	<i>Erinnyis ello</i>	BC, C
	<i>E. alope</i>	
Scales	<i>Aonidomytilus albus</i>	BC, CP, C
	<i>Saissetia</i> spp.	
Subterranean sucking insects	<i>Cyrtomenus bergi</i>	CP, R
Shoot flies	<i>Silba pendula</i>	CP, C
	<i>Neosilba perezii</i>	
	<i>Carpolonchaea chalybea</i>	
Stemborers	<i>Coelosternus</i> spp.	CP, C
	<i>Chilomina clarkei</i>	
	<i>Lagochirus araneiformis</i>	
Fruit flies	<i>Anastrepha</i> spp.	C
Termites	<i>Coptotermes</i> spp. and others	C
Leafcutting ants	<i>Atta</i> spp.	C
Gall midges	<i>Jatrophobia brasiliensis</i>	C, BC
Variiegated grasshopper	<i>Zonocerus</i> spp.	C, R
Leaf beetles	<i>Colapsis</i> sp. and others	C
Cutworms	<i>Prodenia eridania</i>	C
	<i>Agrotis ipsilon</i>	

a. R = resistance; BC = biological control; C = chemical control; CP = cultural practices.

arthropod pests. Studies now show that cassava is not free from insect and mite attacks and that these pests are limiting factors in production.

Insects can damage the plant by attacking: the leaves and reducing the photosynthetic area and efficiency; the stems, weakening the plant, and inhibiting nutrient transport; and planting material, leading to microbial invasion that reduces germination and yield. Some pests, such as whiteflies and fruit flies, are vectors or disseminators of diseases while others attack the roots, leading to secondary rots.

Indications are that pests that attack the plant over a prolonged period, such as mites, thrips, lace bugs, mealybugs, whiteflies, and stemborers, reduce yield more than those that defoliate or damage plant parts for a brief period, that is, hornworms, fruit flies, shoot flies, and leafcutting ants. The cassava plant recuperates from this type of damage under favorable environmental conditions. Adequate rainfall and soil fertility are the critical factors. Cassava is often grown in regions with prolonged dry seasons because it tolerates water stress. However, populations of thrips, mites, lace bugs, and mealybugs increase during dry periods and compound the damage to the crop.

Yield losses have been recorded for several cassava pests (Bellotti et al., 1983b). These include mites (8% to 87%), whiteflies (4% to 79%, depending on length of attack), mealybugs (up to 88% on susceptible cultivars), thrips (6% to 28%, depending on varietal susceptibility), hornworms (18%, single attack), scales (4% to 19%), and stemborers (up to 56% when heavy stem breakage occurs) (Bellotti et al., 1983a and 1983b).

Priorities in a pest resistance program

The cassava pest complex represents a wide range of arthropod fauna (Bellotti and van Schoonhoven, 1978). It is unrealistic to consider breeding for resistance to all these pests, nor is it necessary to do so as there are alternative methods for controlling many pests. Cassava pests may be divided into several categories (Table 2):

Key pests—those that regularly limit crop production (Ortman and Peters, 1980). These include mites, mealybugs, and thrips;

Occasional pests—those that occur at infrequent intervals but cause severe damage when present. These include hornworms, lace bugs, whiteflies, grasshoppers, and leafcutting ants;

Incidental pests—those that are constantly present but infrequently

Table 2. Cassava pests in relation to their importance in a pest management program.

Pest category	Common name	Principal species	Area of importance
Key pests ^a	Mites	<i>Mononychellus</i> spp. <i>Tetranychus</i> spp.	Americas, Africa Asia
	Mealybugs	<i>Phenacoccus manihoti</i> <i>P. herreni</i>	Africa Americas
	Thrips	<i>Frankliniella williamsi</i>	Americas
Occasional pests ^b	Lace bugs	<i>Vatiga</i> spp.	Americas
	Whiteflies	<i>Aleurotrachelus socialis</i>	Americas
	Grasshoppers	<i>Zonocerus</i> spp.	Africa
	Leafcutting ants	<i>Atta</i> spp.	Americas
	Subterranean sucking insects	<i>Cyrtomenus bergi</i>	Americas
Incidental pests ^c	Scales	<i>Aonidomytilus albus</i> <i>Saissetia</i> spp.	Universal Universal
	Shoot flies	<i>Neosilba perezii</i>	Americas
	Fruit flies	<i>Anastrepha</i> spp.	Americas
	Stemborers	<i>Coelosternus</i> spp. <i>Chilomina clarkei</i> <i>Lagochirus</i> spp.	Americas Americas Americas
	Gall midges	<i>Jatrophia brasiliensis</i>	Americas

a. Pests that regularly limit crop production.

b. Pests that occur at infrequent intervals but cause severe damage when present.

c. Pests that are constantly present but infrequently damaging.

damaging, such as scales, shoot flies, fruit flies, stemborers, and gall midges;

Potential pests—those that may occur with a change in crop and cultural practices or may be introduced into regions where they do not presently exist. Several of the above-mentioned pests would fall into this group if they were to be introduced from the Americas into Africa

or Asia. The mite and mealybug problems in Africa are good examples of this; and

Persistent pests—those pests that attack the crop over a prolonged period of time. The cassava lace bugs, whiteflies, mites, mealybugs, and thrips are included in this group.

Obviously those considered key pests should be candidates for a host-plant resistance program—in fact, emphasis for resistance has been given more to mites, mealybugs, and thrips than to any of the other cassava pests (Bellotti and Kawano, 1980; Byrne, 1984).

Other pertinent considerations in establishing a program to utilize host plant resistance for specific cassava pests include the following (Bellotti and Kawano, 1980):

The level of economic damage being caused by a particular pest should be significant;

Resistance should be sought for those pests for which it is considered feasible to find resistance. For example, it is unlikely to find resistance to such pests as the cassava hornworm, cutworms, leafcutting ants, or grasshoppers and limited resources should not be used in this direction;

The availability of adequate and low-cost alternative methods could negate the need to enter into an extensive resistance breeding program. Biological control, cultural practices, or even an occasional pesticide application often will maintain pest populations below economic injury level; and

Low levels of resistance can be adequate if it is combined with other control methods, such as biological control or cultural practices. Under traditional cassava farming conditions, pest populations are maintained at reduced levels by a combination of resistance, natural enemies, and improved agronomic practices (Lozano and Bellotti, 1980).

Advances in breeding for insect and mite resistance in cassava

Resistance in cassava has been reported for mites (several species), thrips, mealybugs, whiteflies, scales, stemborers, shoot flies, lace bugs, and the subterranean sucking insect. Only those considered to be most important in terms of breeding for resistance will be discussed in detail. These include

mites, thrips, mealybugs, whiteflies, and lace bugs. Resistance studies can generally be divided into two groups:

Evaluation of existing germplasm for clones expressing resistance to one or more pests; and

Incorporation of resistant germplasm into a breeding program to produce hybrids expressing resistance to pests and containing acceptable agronomic qualities.

Examples of the former are common in national and international cassava improvement programs while examples of the latter are restricted to a limited number of institutions. To develop a resistant cassava cultivar, the following are required: genetically conditioned resistance; a reliable evaluation scheme; and breeding methods to incorporate this resistance into a commercially acceptable cultivar (Bellotti and Byrne, 1979).

Resistance is partitioned into three components: antibiosis; antixenosis (nonpreference); and tolerance. Antibiosis is the mechanism by which the resistant plant has a detrimental effect on the pest's developmental biology. Antixenosis denotes an adverse effect of the plant on the pest's behavior—the plant is avoided by the pest. Tolerance has no effect on the pest population but is rather the plant's ability to withstand and/or compensate for the damage caused by the pest. The results of resistance studies for cassava insects and mites have been reviewed previously (Bellotti and Kawano, 1980; Byrne, 1984; Byrne et al., 1983). Only the most recent studies will be examined in this paper.

Mites

Cassava has been screened for mite resistance in numerous countries in the Americas, Africa, and Asia and by numerous workers (Byrne et al., 1983). Most screening has involved species of the genera *Mononychellus*, *Tetranychus*, and *Oligonychus*. Although many of these evaluations were minimally replicated (over one site or in one year), it is evident that all cassava varieties are attacked by mites (that is, no immunity exists) and that genetically conditioned resistance exists. Most of the recent work with mite resistance deals with *Mononychellus* mite (Table 3), which was recently introduced into Africa from South America. Losses in root yield have varied from 8% to 87%, depending on the intensity, length, and timing of the attack, as well as the cultivar (Byrne et al., 1982b). High levels of resistance have been found for *Mononychellus* mites, possibly because these mites have few alternate hosts and the pest and cultigen have coevolved.

Table 3. Status of resistance in cassava to the *Mononychellus* and *Tetranychus* mites.

Mite	Institution ^a (country)	Accessions evaluated ^b (no.)	Present status	Resistance mechanisms	Source
<i>M. tanajoa</i>	CNPMF, Brazil	357 (F)	16 resistant	Unknown	Farias et al., 1981
<i>M. caribbeanae</i>	Univ. Puerto Rico	11 (F)	3 possibly resistant	Unknown	Cruz, 1981
<i>M. progressivus</i>	IITA, Nigeria	200,000 seedlings	No selection indicated	Pubescence	IITA, 1980
	IITA, Nigeria	60 clones (F)	10 resistant		Hahn, 1982a
<i>M. tanajoa</i>	Zaire	23,936 seeds (IITA) (F)	No selection indicated		Lutaladio, 1982
	Zaire	1,460 lines (F)	219 lines selected		Lutaladio, 1982
<i>M. progressivus</i> ; <i>M. tanajoa</i>	CIAT, Colombia	2,197 (G and F)	43 resistant	Antibiosis	CIAT, 1976-1984
<i>M. caribbeanae</i>			Mite-resistant hybrids available	Ovipositional nonpreference	Bellotti and Byrne, 1979
				Nonpreference	Byrne et al., 1982a and 1982b
<i>T. kanzawai</i>	Visayas State College of Agriculture, Philippines	295 (G)	50 selected	Tolerance	Bernardo and Esguerra, 1981a and b
		50 (F)	4 selected	Unknown	Bernardo and Esguerra, 1981a and b
<i>Tetranychus</i> spp.	CTCRI, India	12 (F)	5 (low mite population)	Unknown	Lal and Hrishu, 1981
<i>T. urticae</i>	CIAT, Colombia	2,120 (S)	17 selected as resistant	Ovipositional nonpreference; Antibiosis	CIAT, 1978, 1979, 1980a and 1980b

a. CNPMF = Centro Nacional de Pesquisa de Mandioca e Fruticultura; IITA = International Institute of Tropical Agriculture; CIAT = Centro Internacional de Agricultura Tropical; CTCRI = Central Tuber Crops Research Institute.

b. F = field evaluation; G = greenhouse evaluation; S = screenhouse evaluation.

1985

At present, resistance research with the *Mononychellus* mites is primarily confined to three institutions: Centro Internacional de Agricultura Tropical (CIAT) in Colombia; International Institute of Tropical Agriculture (IITA) in Nigeria; and Centro Nacional de Pesquisa de Mandioca e Fruticultura/Empresa Brasileira de Pesquisa Agropecuária (CNPMP/EMBRAPA) in Brazil. All three institutions have screened large amounts of germplasm and have identified mite-resistant cultivars (Table 3).

Mononychellus mite resistance appears to be based on four different mechanisms of resistance: two which alter mite biology; one that involves tolerance; and one that is associated with pubescence (Byrne et al., 1982a). Mites feeding on susceptible varieties (as evidenced by higher field population and foliar damage ratings) had greater fecundity, greater acceptability, shorter developmental time, longer adult life span, lower adult and nymphal mortality, and greater greenhouse reproduction than did mites on most of the resistant varieties (low field populations and foliar damage ratings).

There were two distinct patterns of mite reaction on different mite-resistant sources: the first, that of M Col 1434, resulted in negative effects on mite fecundity, acceptance, adult female life span, development time, larval and nymphal survival, and greenhouse reproduction. The second pattern was exhibited by the clone M Bra 12 and is characterized by intermediate acceptance, suppressed adult female life span, and a lowered greenhouse reproduction. When compared to the susceptible clones, M Bra 12 had no effect on mite fecundity, developmental time, or larval and nymphal mortality. Since M Col 1434 and M Bra 12 are similar with respect to field populations, foliar damage ratings, and mite reproduction in the greenhouse, it is suggested that two independent mechanisms exist, but the basis for these has not been clarified (Byrne et al., 1982a).

The association of leaf and shoot pubescence and mite resistance has been reported by several workers (Byrne et al., 1982a; CIAT, 1981; Hahn, 1982a; IITA, 1981 and 1982). Pubescence most likely works as a protective barrier for the young shoot and expanding leaves where the *Mononychellus* mites prefer to feed. A distance between the trichomes of 0.3 mm or less makes it difficult for the mites to rest and feed (IITA, 1981). Pubescence, therefore, acts to protect the most susceptible part of the plant from the *Mononychellus* mite. It is easy to visually select highly pubescent types and it would be difficult for the mites to genetically overcome this barrier. However, the wisdom of selecting for high pubescence as the major factor for mite resistance is questioned by Ayanru and Sharma (1983) since a

highly pubescent variety TMS/U 42046, when attacked by mites, showed considerable chlorophyll depletion which the authors linked to mite susceptibility. High pubescence may be effective at light or even moderate mite attacks, but appears to be overcome at very high mite levels.

It is therefore suggested that the goal of a resistance breeding program should be to combine the several mechanisms involved to ensure a resistance that will withstand high mite populations as well as genetic changes of the mite. This may be difficult to accomplish since some of the mechanisms are not readily identifiable and therefore not satisfactory for rapid field screening. More studies into the mechanisms of resistance to mites are needed to develop better screening techniques. Resistance to the *Mononychellus* mite in cassava appears to be controlled primarily by additive genetic effects as shown by the high narrow-sense heritability estimates of 50%-78% (Byrne et al., 1982b; CIAT, 1981; IITA, 1981).

Most of the germplasm accessions identified as resistant are agronomically inferior types. Consequently, a program is underway to combine resistance with good yield and quality. Clones such as M Bra 12, which already combine good yield potential and resistance are used heavily in hybridizations. Many first generation hybrids, now in the third year of yield trials, are superior to either parent in resistance and yield.

Resistance studies for the *Tetranychus* mites are not as advanced as those for the *Mononychellus* mites. At present research into cassava resistance for the *Tetranychus* mite is mainly being carried out by the Visayas State College of Agriculture (ViSCA) in the Philippines, the Central Tuber Crops Research Institute (CTCRI) in India, and CIAT in Colombia (Table 3). At CIAT, 2120 accessions from the germplasm bank were repeatedly evaluated in the screenhouse for resistance to *T. urticae* and 17 cultivars were eventually selected as resistant (CIAT, 1978). These selected cultivars lacked a field screening under heavy mite attack to verify screenhouse results. It should be noted that these 17 cultivars are also resistant to the *Mononychellus* mite. Evaluations of 295 cassava accessions at ViSCA resulted in four cultivars eventually being selected as resistant to *T. kanzawai* (Bernardo and Esguerra, 1981a).

The first workers to study the biological response of *Tetranychus* mites to different varieties of cassava found that differences occurred in developmental time, adult longevity, and mite fecundity (Saradamma and Das, 1974). However, this work was not followed up with field studies to confirm whether these differences were responsible for differences in field populations or damage. At CIAT, biological studies of *T. urticae* on three

cassava cultivars showed that developmental time was greater and female adult longevity was shorter on the resistant cultivars as compared to the susceptible control (CIAT, 1980a).

Screening for resistance to *Oligonychus peruvianus* was done in Colombia (CIAT, 1978 and 1979), to *O. gossypii* in Nigeria (IITA, 1979), and to *O. biharensis* in India (Lal and Hrisi, 1981). At CIAT, 250 accessions of 2231 screened were selected as promising for resistance.

Thrips

Several species of thrips are pests of cassava, especially in the Americas (Bellotti and van Schoonhoven, 1978). *Frankliniella williamsi* has received the most attention for resistance breeding. This species damages the terminal bud of the plant, leaves do not develop normally, and leaflets are deformed and show irregular chlorotic spots. Yield losses range from 6% to 28%, depending on varietal susceptibility (CIAT, 1976; van Schoonhoven and Peña, 1976). Field screening at CIAT showed 20% of the germplasm collection to be highly resistant and an additional 29% show only minor damage (Bellotti and Kawano, 1980). Resistance is related to the pubescence of leaf buds and unexpanded leaves (van Schoonhoven, 1974). This gross morphological character for resistance appears to be very stable and biotypes are not expected to develop. The heritability (narrow and broadsense) of thrips resistance is about 80%, which indicates that, for the most part, it is additively inherited (Byrne, 1984). Incorporating high thrips resistance into high-yielding genotypes, especially for the lowland tropics with a prolonged dry season, is a major component in the CIAT hybridization program, and rapid progress has been made in this field.

Mealybugs

There are two major species of mealybug attacking cassava in Africa and the Americas. *Phenacoccus manihoti* was introduced from the Americas into Zaire, Africa, during the early seventies (Hahn and Williams, 1973). It has subsequently spread throughout much of the cassava region of Africa, causing severe yield reductions (Herren, 1981). *P. herreni*, a very closely related species, is causing considerable damage in certain areas of the Americas, especially in the northeast of Brazil (Bellotti, 1983; Bellotti et al., 1983a). The feeding of these mealybugs causes leaf yellowing and curling, defoliation, and, with high infestations, green shoot death. Recent studies indicate that root losses can reach 87% (CIAT, 1985; Herren, 1981).

Resistance studies for these two species are in progress at IITA in Africa,

CIAT in the Americas, and IPA (Instituto Pernambucano de Pesquisa Agropecuária) in Brazil. The evaluation of germplasm is based mainly on damage scales, artificial and natural infestations, and under field conditions. It has been shown that resistance sources exist in both the cultivated species (CIAT, 1980a and 1984; Ezumah and Knight, 1980; Hahn, 1983; IITA, 1981) and in several related species (de Albuquerque, 1977; Hahn, 1982b). Several clones, within cultivated cassava, which exhibit decreased mealybug populations have been identified at IITA and are being used in the breeding program (Hahn, 1982a; IITA, 1981). A relationship between hair density on the leaf and resistance to the mealybug has been shown.

More than 2000 clones in the CIAT cassava germplasm bank were evaluated in the field during a natural infestation of the mealybug *P. herreni*. Over 500 clones, about 24%, showed no damage symptoms, although many of these undoubtedly simply escaped attack. Evaluation of these is being continued (CIAT, 1984).

Whiteflies

Whiteflies are important in cassava primarily because they are vectors of several virus diseases. However, it has also been shown that high whitefly populations can cause severe yield reductions through direct damage (CIAT, 1980a, 1981, and 1982; Vargas and Bellotti, 1981). Yield losses reached 79% during an 11-month attack by the whitefly, *Aleurotrachelus socialis*. Other important species in the Americas are *Aleurothrix aepin*, *Bemisia tuberculata*, and *Trialeurodes variabilis*. It is not certain which of these species is the most important in virus transmission. *Bemisia tabaci*, the most important species in Africa and India and the vector of the African cassava mosaic disease, has not been reported feeding on cassava in the Americas.

Screening for resistance to whiteflies at CIAT has been for *A. socialis*, the species causing greatest yield losses in the Americas. Approximately 1400 cultivars from the CIAT germplasm bank have been screened under high field populations of the whitefly. About 50 cultivars have been selected as promising for resistance and 5 have been identified as resistant. These have entered into a hybridization program and the progeny are being evaluated (CIAT, 1976, 1977, 1982, 1983, 1984, and 1985). Initial results of these crosses show high levels of whitefly populations for progeny of resistant x susceptible crosses but only a moderate level of damage symptoms. The resistant x resistant progeny show a moderate whitefly population but a very low level of damage symptoms (CIAT, 1982). Results of greenhouse studies on resistance mechanisms indicate

that ovipositional nonpreference as well as antibiosis may be responsible for whitefly resistance (CIAT, 1982).

Lace bugs

The cassava lace bugs, *Vatiga manihotae* and *V. illudens*, are reported feeding on cassava in several countries of the Americas. Lace bug attack manifests itself during the dry season when high populations can cause considerable defoliation. Leaves have yellow spots that eventually turn reddish brown, resembling *Tetranychus* mite damage. Yield losses are not known (Bellotti and van Schoonhoven, 1978).

Approximately 2000 lines of the CIAT germplasm bank have been evaluated during two seasons with natural infestations of *V. manihotae* in the field. These evaluations have resulted in 131 lines being selected as promising for resistance. Evaluations under high field infestations still need to be done to accurately determine resistance.

Screening for resistance to the lace bug species *V. illudens* is being done in Brazil (Cosenza et al., 1981; EMBRAPA-CPAC, 1982). Results indicate that lace bug resistance exists and several varieties have been selected. Greenhouse studies indicate that nonpreference and antibiosis may be the resistance mechanisms involved.

Other pests

A review of the literature shows that resistance has been reported for several additional cassava pests. These include scales, stemborers, shoot flies, grasshoppers, gall midges, and fruit flies (Bellotti and Kawano, 1980; Bellotti and van Schoonhoven, 1978). Most literature describes field observations under natural infestations. Some replicated trials are described but are not part of continuing research programs.

Although hydrogen cyanide (HCN) content has often been suggested as a resistance factor in cassava, little evidence exists to support this speculation. However, some observations indicate that certain insects prefer low-HCN cultivars to high-HCN ones. Recent studies at CIAT show that the subterranean sucking insect, *Cyrtomenus bergi*, the nymphs and adults of which feed on cassava roots, strongly prefers low-HCN or sweet varieties over the high ones in both laboratory and field studies. Only 0.3% of the roots of M Col 1684 (high HCN) were damaged while 27.3% of those of CMC 40 (low HCN) were damaged in field studies (CIAT, 1984 and 1985).

Techniques for evaluating cassava germplasm

A breeding program that involves host plant resistance to insects and mites must begin with an extensive, working germplasm collection. The CIAT cassava germplasm collection contains more than 3800 accessions, with considerable genetic variability available. This collection is mostly comprised of varieties grown by traditional cassava farmers throughout the Americas. The collection, therefore, should contain accessions that have been selected by farmers for many years to withstand the pests or diseases prevalent in a given ecosystem (Lozano et al., 1980). Germplasm collections suitable for screening for pest or disease resistance are available at several institutions but none are as extensive as the CIAT collection. Additional sizable collections are at CNPMF in Brazil (more than 700 vegetative accessions), IITA in Nigeria (2000 vegetative accessions + accessions in seed form), and CTCRI in India (1800 vegetative accessions). At present, there are at least 15 countries in the Americas, 1 in the South Pacific, 7 in Asia, and 5 in Africa that have local cassava collections that are actively maintained for breeding or agronomic studies (Gulick et al., 1983).

The evaluation of cassava germplasm for insect and mite resistance involves an interaction between the plant and the pest. Thus cassava resistance to pests can be studied in two dimensions: the variation that takes place in the cassava plant because of pest attack; and the variations expressed in pest populations as a result of their feeding on the host. The design of an evaluation scheme or research method should, therefore, make it possible to measure or quantify these variations, especially those that occur in the cassava plant. If the resistance is to be incorporated into a breeding program, then it is additionally important to be able to estimate the source of the variance, or the mechanism involved, as well as the heritability of the trait or traits identified. An intimate knowledge of the biology and feeding habits of the insect is, therefore, necessary.

A review of the literature indicates that numerous criteria (Ortman and Peters, 1980) have been used to evaluate insect resistance in cassava. These include:

Visual evaluation of infested cultivars, such as leaf speckling, discoloration and distortion, retarded plant growth, stem distortion, and length of internodes (mites, thrips, mealybugs, lace bugs, whiteflies, shoot flies, fruit flies);

Determination of the difference in yield between infested and non-infested plots (thrips, mites, mealybugs, whiteflies);

Determination of the number of insects, larvae, or nymphs attracted to a cultivar when given a free choice (whiteflies, stemborers, mites, mealybugs, lace bugs);

Measurement of amounts of root surface discolored as a result of insect feeding (subterranean sucking insect);

Observation of the comparative effects of forced insect feeding (in confinement) on plants by measuring length of insect life cycle, mortality, or reproductive rate (mites, mealybugs, whiteflies, stemborers and lace bugs);

Weight of insects after definitive feeding period on different cultivars (mealybugs);

Determination of number of eggs laid (mites, hornworms, lace bugs, fruit flies, whiteflies);

Determination of number of surviving insects and progeny produced (mites, mealybugs, whiteflies, lace bugs);

Correlation of morphological factors with injury (thrips, mites, mealybugs); and

Measurement of amount of food utilized (mites, hornworms, grasshoppers).

In the initial studies of cassava germplasm it is important to examine large quantities of diverse material. In general, if there is an adequate infestation, reliable evaluation for resistance can be done in small plots (five plants to one plot) and often with seedling plants. Single plant seedlings or small plot selection for resistance (or to determine susceptibility) is routinely done for mites (Bernardo and Esguerra, 1981b; CIAT, 1979; IITA, 1980), thrips (Bellotti and Kawano, 1980; CIAT, 1978), lace bugs (CIAT, 1979 and 1981), mealybugs (CIAT, 1984; IITA, 1981), and others. In these initial studies the essential goal is to eliminate the bulk of susceptible material. Additional cycles of evaluations are used to confirm the preliminary evaluations which have selected promising materials. This procedure has been used in cassava with mites, thrips, mealybugs, lace bugs, and whiteflies. It reduces the number of genotypes that must be evaluated for yield depression in large, replicated, plots.

There are several important aspects and techniques involved in a resistance evaluation and breeding program for cassava pests. These are discussed in detail by Bellotti and Kawano (1980) and will, therefore, only be summarized here:

The critical aspect of resistance evaluations is to have sufficiently high levels of the pest present to be able to distinguish between resistant and susceptible genotypes. It is important to select a site where the pest, for ecological reasons, is epidemic on an annual basis;

Cultivars should be planted so that the appropriate stage of evaluation coincides with maximum pest pressure;

Field populations of pests can be augmented by artificial inoculations from pest colonies;

The planting of susceptible border rows will aid in an even and high pest population;

A reliable rating scheme with various levels of damage discrimination is needed to distinguish resistant and susceptible material. In initial studies this is usually a 0 to 5 scale that describes progressively worse foliage and plant damage;

Later evaluation studies should permit a more precise definition of the level and expression of resistance;

Greenhouse or screenhouse evaluation procedures have been used for certain pests. They have been successful in mite screening because these evaluations have been comparable to field results (Byrne, 1980). However, preliminary results indicate that greenhouse screening for mealybug resistance at CIAT has not been successful; and

Rating schemes can also measure insect populations when damage symptoms are not sufficiently pronounced to evaluate accurately. They are useful if the insect is easily detected so that rapid field evaluations can be made.

Screening cassava germplasm for resistance to insects and mites

The procedures used for screening cassava germplasm for resistance to mites (*Mononychellus* spp.), thrips, whiteflies, mealybugs, and lace bugs will be briefly described (Bellotti and Kawano, 1980). Damage rating schemes, such as a 0 to 5 scale, which describe progressively worse plant

damage are usually employed (Bellotti and Kawano, 1980; Bernardo and Esguerra, 1981b; Cosenza et al., 1981; Cruz, 1981; Farias et al., 1981; IITA, 1981).

Mites (*Mononychellus* spp.)

In the initial screening phase the main objective is to eliminate about 80% of the cultivars and reevaluate the remainder. *Mononychellus* spp. primarily feed on the upper leaves of the plant, especially on leaves emerging from the bud. They cause yellow to white speckling and deformation of leaves.

For evaluation of the CIAT germplasm collection, stem cuttings 2 inches long are planted in 4-inch diameter plastic pots. Approximately 1 month after germinating they are removed to the greenhouse (30 to 34 °C) and placed in large (1 x 2 m) mesh cages, 60 plants to a cage. Two weeks later, they are infested with mites. Each pot represents one variety and the variety may be repeated several times in one cage or different cages (CIAT, 1976).

Infestation is done by placing one or two lobes of a mite-infested cassava leaf (50 to 100 mites) on the upper leaves of each test plant. Mites from the field are regularly reintroduced into the colony. Damage evaluations start the second week after infestation and are made each week thereafter for four consecutive weeks. Second and third inoculations are made if the initial one is not successful. A damage scale based on these symptoms is used during this initial phase:

- 0 = No mites or symptoms;
- 1 = Mites on bud leaves, some yellow to white speckling of leaves;
- 2 = Many mites on leaves, moderate speckling of bud leaves and adjacent leaves;
- 3 = Heavy speckling of terminal leaves, slight deformation of bud leaves;
- 4 = Severe deformation of bud leaves, reduction of bud, mites on nearly all leaves, with whitish appearance and some defoliation;
- 5 = Bud greatly reduced or dead, defoliation of upper leaves.

Those cultivars selected as promising for resistance are planted in areas where mite attacks are endemic (for example, Guajira in Colombia), using replicated blocks with susceptible border rows.

Byrne (1980) found that correlations between blocks within experiments and between experiments were similar, as was the correlation between greenhouse and field screening. This indicates that the effects of variety-site interaction are less important than the varietal effects. Thus, resistance to *Mononychellus* sp. is relatively stable across environments (CIAT, 1979). In addition, yield trials were carried out to determine the differential effect of mites on susceptible and resistant cultivars. Yield reduction in resistant clones (protected vs. unprotected plots) was not significant, averaging 15%, while reduction in susceptible varieties averaged 70% (CIAT, 1979).

Thrips (*Frankliniella willamsi*)

The symptoms of thrips damage are much more pronounced during the dry season, although the insects are present throughout the year. The procedure for evaluating resistance to thrips in cassava was developed by van Schoonhoven (1974). The CIAT germplasm collection was evaluated under natural infestation during three dry seasons (CIAT, 1977). Plants were evaluated at 4 and 8 months, and an average of these two assessments was used as a resistance classification. Symptoms of thrips damage were classified into six reaction classes:

- 0 = No symptoms;
- 1 = Yellow irregular leaf spots only;
- 2 = Leaf spots, light leaf deformation, parts of leaf lobes missing, brown wound tissue in spots on stems and petioles;
- 3 = Severe leaf deformation and distortion, poorly expanded leaves, internodes stunted and covered with brown wound tissue;
- 4 = As above, but with growing points dead, sprouting of lateral buds;
- 5 = Lateral buds also killed, plants greatly stunted, with "witches' broom" appearance.

The nature of thrips resistance was studied on 8-month-old nonflowering clones representing each of the resistance levels. Thrips populations were determined by collecting three terminal buds from single plants in a plastic bag, immersing them in 30% alcohol, and counting the insects under a microscope. Plant pubescence was determined by counting the number of hairs on the undersurface of one side of an unexpanded leaf lobe. Two leaves per plant were sampled when leaves measured about 1 cm

in length. It was found that the leaves of susceptible clones had few or no hairs whereas the leaves of resistant clones had many. Thrips were found on all clones regardless of resistance, but fewer were found on resistant ones. No correlation was found between thrips resistance and plant cyanide content, thus showing that thrips resistance and low cyanide content are not mutually exclusive.

Whiteflies (*Aleurotrachelus socialis*)

The pupal stage of *Aleurotrachelus* sp. is oblong and black, with a white waxy excretion around the outer edge, and is easily seen on the leaf underside. Cassava lines are screened in an area having heavy natural infestations. Ten plants of each line are sown in two replicates of five plants each and rows of susceptible varieties are dispersed throughout the field. Evaluations are made every 2 months beginning when the plants are 2 months old.

Resistance evaluations are made by using three scales: one for the number of pupae per leaf (three leaves sampled per plant); one for the percentage of leaves infested with pupae (several leaves sampled per plant at various levels); and one for damage symptoms caused by whitefly feeding.

Pupal scale:

- 0 = No pupae;
- 1 = Less than 50 pupae per leaf;
- 2 = 51 to 100 pupae per leaf;
- 3 = 101 to 250 pupae per leaf;
- 4 = 251 to 500 pupae per leaf;
- 5 = More than 500 pupae per leaf.

Population scale:

- 0 = No infestation;
- 1 = Less than 20% infested;
- 2 = 21% to 40% infested;
- 3 = 41% to 60% infested;
- 4 = 61% to 80% infested;
- 5 = 81% to 100% infested.

Damage symptom scale:

- 0 = No damage;
- 1 = Slight speckling of lower leaves;
- 2 = Heavy speckling of lower leaves;
- 3 = Mosaic-like symptoms on leaves but little wrinkling, sooty mold on lower and central leaves;
- 4 = Wrinkling and yellowish mottling of lower and apical leaves, some leaf necrosis, considerable sooty mold;
- 5 = Severe wrinkling of apical leaves and leaf necrosis.

These three scales permit correlation of damage symptoms with whitefly numbers. Large whitefly populations with few damage symptoms could indicate that a tolerance mechanism is involved. In this case a damage symptom evaluation alone would not necessarily indicate the whitefly population. Tolerant varieties would not reduce whitefly populations, which would be the main goal of a resistance program aimed at reducing virus transmission.

Lace bugs (*Vatiga manihotae*)

Evaluations for lace bug resistance was done in the cassava germplasm bank for two successive years, using natural infestation. The following damage scale was used:

- 0 = No lace bugs present;
- 1 = A few yellow spots on lower leaves;
- 2 = Many spots on lower leaves, leaves turn yellowish;
- 3 = Many yellowish red spots on leaves, lower leaves curl;
- 4 = Lower leaves curl and dry up, intermediate leaves curl;
- 5 = Defoliation of basal and intermediate leaves, apical leaves turn yellow.

Mealybugs (*Phenacoccus herreni*)

Initial screening for mealybug resistance was done in the greenhouse

(average temperature 24 °C and 70% relative humidity). Two 4- to 5-week-old plants of each accession grown from stem cuttings were inoculated by placing two mealybug ovisacs on the growing point. Evaluations were made 2 and 4 weeks later and mealybug counts, as well as damage symptoms, were recorded. Eight hundred varieties were evaluated using this methodology. Results were disappointing as some varieties expressing resistance under greenhouse screening proved very susceptible under field screening (CIAT, 1985). New methodology for field screening is now being developed. One drawback to field screening is that mealybug populations are often not high enough nor evenly distributed. Artificial infestation from a greenhouse mealybug colony to field cultivars has had mixed success. Initially egg masses were placed in the growing shoot at the onset of the dry season. These egg masses suffered heavy predation by the ample complex of natural enemies that exists at CIAT. Adequate field populations, therefore, often did not develop. A system utilizing small leaf cages to protect the egg masses and infesting the lower leaves has proved more successful.

More than 2000 varieties in the CIAT cassava germplasm bank were evaluated in the field during a natural infestation (CIAT, 1984). The following damage rating was used:

- 0 = No symptoms;
- 1 = Apical leaf margins undulate;
- 2 = Slight curling of new leaves, stem development normal;
- 3 = Deformation and yellowing in most newly attacked leaves, appearing cabbage-like, with a slight shortening of internodes;
- 4 = Death of some leaves, drastic shortening of internodes, terminal stems spiral shaped, flower petiole reduced, presence of sooty mold;
- 5 = Death of buds, defoliation, abundant sooty mold, plant development stunted.

Approximately 60% of the accessions had a damage rating of 3 or above and were described as susceptible. Those accessions with a lower rating will be reevaluated in the field under both natural and innoculated conditions.

Edaphoclimatic zones and insect complexes

Cassava is grown under a wide range of environmental conditions in the tropical and semitropical regions of the world. In recent years both CIAT and IITA have tried to describe the climatic and edaphic characteristics that define these regions. CIAT has delineated six combinations of edaphoclimatic characteristics which appear to constitute a necessity for basically different genotypes (Hershey, 1984; Lozano et al., 1980). Edaphoclimatic zones (ECZs) are defined on the basis of temperature, rainfall distribution, and soil characteristics. The potential importance of pests and diseases in cassava is largely dependent upon the climatic and soil conditions of a region, along with the presence of a susceptible host and cultural practices.

Each ECZ, therefore, can be identified with a unique combination of disease and insect pest problems (Lozano et al., 1984). For example, low to moderate rainfall with prolonged dry periods (3-6 months) and high temperatures are characteristic of ECZ I. The pest complex that corresponds to these conditions includes mites, thrips, mealybugs, and lace bugs. Combinations of these pests in sufficiently high populations to cause severe yield reductions can be found in several areas of the Americas (the north coast of Colombia, the northeast of Brazil, and northern Venezuela). Ideally, selected clones for these regions should have a balanced resistance to all of the important pests and disease problems of ECZ I.

The overall cassava breeding strategy at CIAT in relation to pest and disease complexes consists of: evaluation of germplasm accessions in diverse ECZs in Colombia; parental selection and formation of gene pools for each ECZ based on performance of germplasm accessions; hybrid evaluation and selection primarily within, but also across, ECZs; continual improvement of a broad range of traits, including insect and mite resistance, through recurrent selection methods; and recommendations to national programs for testing of selected clones and/or progeny of specific crosses (Hershey, 1984).

The principal evaluation and selection sites should include as many of the potential stress factors as possible for the particular edaphoclimatic zone in order to make the final selected products as broadly relevant as possible within similar regions. In terms of insect and mite resistance evaluation, emphasis is given to selection for a broad, combined tolerance/resistance to the yield-limiting pests within each ECZ, as well as disease tolerance, high-yield potential, and good root quality. The desired end

results are clones with a broad adaptability within each ECZ. Clones have been developed with combined tolerance or resistance to mites and thrips and potentially will also include mealybugs and lace bugs.

Breeding methodology

Under traditional farming systems in which cassava has evolved, isolation and cultural practices aided in keeping pest pressure at relatively low levels. In these systems only low or intermediate host resistance levels were necessary. For intensified cultural practices and extensive cassava-growing areas, higher resistance levels are often required.

Cassava is a monoecious species, with both male and female flowers on the same plant. This, along with the fact that female flowers open about two weeks before male flowers, results in high levels of natural outcrossing. Nevertheless, when an individual clone is planted in large plots, the possibility increases for intercrossing among plants of the same clone, which is genetically the same as selfing.

All cultivars appear to be highly heterozygous, based on wide segregation of progeny and on high levels of inbreeding depression. Cassava is generally considered to be an allotetraploid, but seems to behave as a functional diploid for most characters. Vegetative propagation allows fixation of genes in heterozygous plants at any stage of a breeding program. Thus, any character identified in an individual plant can be indefinitely propagated.

Little information exists on the genetics of resistance to insect and mite pests in cassava. Heritability studies for the *Mononychellus* sp. of mites, and thrips have shown predominantly additive variance on the basis of parent-progeny regression analysis (Byrne, 1980; CIAT, 1981; IITA, 1981). On the basis of segregation patterns, resistance appears to be multigenic for all pests so far studied, although definitive genetic studies have not been done. These preliminary studies suggest that a population improvement scheme will be most effective in breeding for insect and mite resistance. Crosses between genotypes with resistance genes at different loci, each having additive effects should result in higher resistance levels in some proportion of the progeny. A recurrent selection scheme which allows accumulation of these additive effects appears to be the most effective strategy.

A critical aspect of breeding for resistance is to begin with an adequate germplasm base. First, locally available clones should be evaluated for the

existing pests. If adequate resistance exists, there may be no need to introduce new germplasm. However, many programs will benefit from well-selected introductions from national or international germplasm collections. These introductions can take various forms, such as: clones with identified resistance; progeny (true seed) from clones with identified resistance; and/or progeny (true seed) which have been evaluated on a family basis for resistance. Generally, clonal introductions can best be utilized in crosses with locally adapted material, while seed introductions, if large enough in number, can often be directly selected for resistance and local adaptation because of the large variability represented.

In many regions more than one insect or mite problem exists and multiple resistance must be sought. For each additional character a breeder wants to improve, the rate of progress which can be achieved decreases rapidly. This again emphasizes the importance of carefully identifying the priority of problems for breeding. For most programs, breeding for resistance to the key pests will be a sufficient challenge. As for most multiple breeding objectives, it is generally more efficient to select simultaneously for the different resistances within the same population rather than to breed for high resistance to individual pests in separate populations with later recombination.

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Breeding Cassava for Adaptation to Environmental Stress

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Introduction

Cassava (*Manihot esculenta* Crantz) originated in South and Central America where its widest morphological diversity exists (Leon, 1977; Lozano, 1977). The crop was introduced to the west coast of Africa in the Congo River delta basin in the latter part of the 16th century, and to the east coast via Madagascar and Zanzibar in the latter part of the 18th century. Cultivation then spread inland from each side. Although its adoption was initially slow, cassava's ability to withstand locust attack and tolerate drought and low soil fertility favored its adoption as a vegetable and famine crop (Jones, 1959). Its introduction to Asia from South America and Africa is more recent (Jennings, 1959).

Cassava is grown in a wide range of environments between latitudes 30° N and 30° S, although the bulk of it is grown between 20° N and 20° S (Jones, 1959). Within these latitudes, cassava is cultivated in soils varying from rich loam to poor sand, at altitudes between sea level and 2000 m, where average annual temperatures are 15-35 °C, and annual rainfall varies from 500-5000 mm. It can survive dry periods of about 6 months or more (Hahn et al., 1979).

Propagation is generally from stem cuttings with the initial regeneration phase dependent on the reserves in the cutting. Contribution from photosynthesis starts about 3 weeks after planting. Rooting starts from the soil-covered nodes, with calluses formed at the base of cuttings (Cours, 1951) and of new shoots (Cock, 1980). The number of basal roots formed is dependent on the genotype, bud development, and nutritional and hormonal factors (Indira and Sinha, 1970). The shoot consists of nodal units, each of which has an internode, a node, an axillary bud, and a

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palmate leaf on a petiole (Cock, 1980). Two types of branching are observed on a normal cassava plant (Hunt et al., 1977). They are: forking branches which occur at the apex of the stem when the apical meristem changes to the reproductive state; and, lateral branches which arise from axillary buds some distance from the apex. The forking type branching is synchronized with all branching occurring at about the same time (Cock, 1980). The number and size of shoots developed from the initial cutting is influenced by its length, size, moisture content, number of buds, orientation during planting, and environmental factors.

Growth, development, and yield

Crops are required to accumulate biomass at different stages of their life cycles, using whatever the environment offers (Bunting, 1975). As such, critical portions of their lives are tailored to fit within certain times of the year to maximize the use of favorable conditions for yield-forming activities. The duration in which environmental conditions are favorable is determined by external limitations of climate, soil, pests, and diseases.

The regions of assimilate production (source) and consumption (sink) are separated by the transport system of the plant (Wareing and Patrick, 1975). Bunting (1975) classifies crops into three broad phenological groups, depending on the proportion of their life span used to form yield. Because its storage organ is vegetative, cassava belongs to the class in which yield is produced throughout much or all of the possible growing period. Thus, dry weight accumulation and distribution among the different plant organs change markedly during the growth cycle. An annual range of 40-47 tons/ha of total dry matter production has been reported for cassava (Cock et al., 1977; Enyi, 1973; Holmes and Wilson, 1977; Loomis and Gerakis, 1975). However, partitioning of dry matter tends to be more important in determining how different factors control growth of the plant as a whole, translocation of the photosynthetic products, and their storage in the roots.

A detailed study of cassava growth by Cours (1951) showed that changes in the weight of the whole plant, of the starch in storage roots, and of the supporting tissue (wood and fibrous root material) followed a sigmoid curve with time. The rate of increase in leaf surface area, however, followed a cyclic semiwave pattern with diminishing amplitude during subsequent yearly cycles because of the environment and factors inherent in the crop (Cock, 1977; Cours, 1951; Enyi, 1973). Boerboom (1978), in determining

dry weight partitioning patterns among the major organs of cassava during growth, showed that the distribution was constant after bulking began. These linear relationships were under both genetic and environmental control. Thus, during the initial growth period, the yield-forming organs are initiated, their number and size predetermined, and located in a particular stage of the season for starch accumulation under appropriate environmental conditions. Five components work together to determine the weight of dry matter laid down in the yield organs during the yield-forming period: source size, photosynthetic and crop growth rate, sink size, partitioning of photosynthates, and duration of yield-forming activities during which these processes occur.

Leaf area index

The determining functions of leaf area index (LAI) include the number of active apices resulting from branching, rate of leaf formation per apex, leaf size, and leaf life (Irikura et al., 1979). LAI has been found to increase rapidly to a maximum during the first few months of growth (2-6 months, depending on the variety and environmental conditions) before declining. The maximum LAIs recorded vary between 6 and 12 (Cock, 1976; Cock et al., 1979; Cours, 1951; Enyi, 1972a, 1972b, 1972c, and 1973; Keating et al., 1982a, 1982b, and 1982c; Tan and Cock, 1979; Williams, 1972). These high LAIs can be maintained for a while, but only with very high leaf fall and very high leaf production rates, resulting in the shading of leaves and reducing leaf life (Rosas et al., 1976).

Leaf photosynthetic rate

Cassava shows light saturation response of C-3 plants with a relatively small increase above 1200-1500 einsteins/m²/sec (1200-1500 mol photons/m²/sec in SI units) (Mahon et al., 1977b), a net efflux of CO₂ at 45 vpm CO₂, and an estimated CO₂ compensation point of 68 vpm at 25 °C (Mahon et al., 1977a). In measuring the photosynthetic rates of attached leaves of cassava and nine wild species of *Manihot* grown in growth chambers, Mahon et al. (1977b) recorded maximum rates ranging from 15 to 29 mg CO₂/dm²/hr for *M. quinquepartita* and *M. dichotoma*, respectively, with all the cassava clones within this range.

Crop growth rate

Reported crop growth rates (CGRs) vary between 80 and 150 g/m²/wk (Cock, 1976; Cock et al., 1979; Enyi, 1973; Holmes and Wilson, 1977; Keating et al., 1982b; Williams, 1972), depending on whether or not

adjustments were made for fallen leaves during growth. These rates are maintained over long periods (Cock 1976; Holmes and Wilson, 1977) even though they are low compared with other crops. CGR increases with LAI up to values of 3-4 and then remains nearly constant with further increases in LAI (Cock, 1980; Cock et al., 1979).

Sink size

The root crops have a great potential in the tropics (de Vries et al., 1967; Nestel, 1973) with cassava having a suggested yield potential of 30 t/ha of dry storage roots per year (Cock, 1974). This high yield potential is based on its long root filling period rather than on a rapid growth rate. Growth rates vary between 40 and 50 g of dry storage roots/m²/wk (Cock et al., 1979). However, higher growth rates on the order of 60-70 g/m²/wk among the cassava breeding lines of CIAT have been obtained (Cock, 1980).

Yield of cassava has three components: the number of storage roots per unit area (X), the average storage root weight (Y), and the percentage of dry matter (Z). Storage root weight can be further subdivided into cell number and size (Hahn and Hozyo, 1980). These yield components are determined at different stages in the ontogeny of the plant and are differentially affected by variation in the environment (Tai, 1975). The formation of yield components in sequence results in a different relationship between a component trait and the environmental resources. The development of the first component trait, that is, the number of storage roots per unit area, is solely determined by genetics and the environmental resources available during the early stages of growth. A component trait which develops subsequent to others is not only influenced by the resources available during its formation, but also by the development and characteristics of its predecessor (Figure 1).

Root bulking starts with the occurrence of certain anatomical changes. The polarity of root growth changes from longitudinal to radial (Indira and Kurain, 1977) through secondary vascular growth (formation of secondary xylem) which ensures thickening (Indira and Sinha, 1970). This initiation of secondary growth in the root starts about 21 days after planting and is dependent in part on assimilate supply (Indira and Sinha, 1970). Storage root numbers are determined as early as 12 weeks (Wholey and Cock, 1974), while the storage root development depends on the increase in number of cells and on starch accumulation in the cells (Kasiele, 1983).

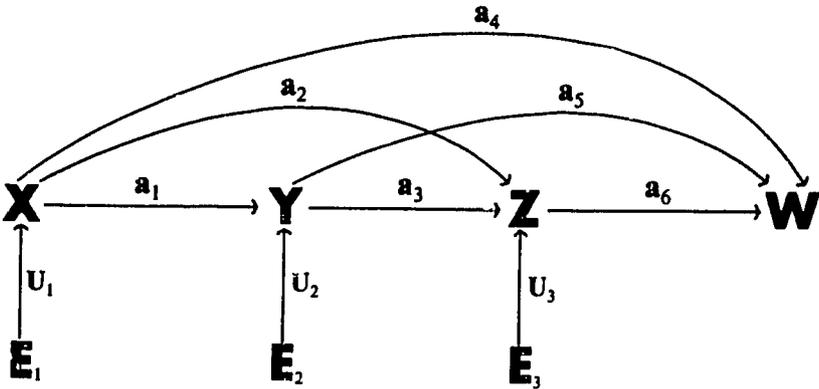


Figure 1. A causation diagram showing the developmental relationships between yield and the yield components: yield (W), number of roots per unit area (X), root size (Y), and percent dry matter (Z). The lower case letters on the various single-arrow paths are path coefficients. E_1 , E_2 , and E_3 indicate the independent groups of environmental resources.

Cock et al. (1979) hypothesized that as leaf area increases, CGR increases more slowly, and that the dry matter required for stem and leaf production increases linearly with LAI. The difference between CGR and top growth rate, that is, root growth rate, increases up to a certain level of LAI and then decreases. Thus, an optimal LAI exists for maximum yield and manipulation of the various components of LAI leads to a maximum yield. Top growth, therefore, has priority over root growth.

Factors affecting productivity

The factors affecting the productivity of cassava can be classified into three broad classes: physical (climatic and edaphic); biological; and physiological. The major physical factors include temperature, light (photoperiod and intensity), soil moisture availability, nutrients, pH, and relative humidity. The pests and diseases constitute the biological factors, while the physiological factors are inherent in the developmental processes necessary for the attainment of characteristic form and function. This depends on a chain of interrelated events which are sequential in time, gene-regulated at critical sites and times, and modified by environmental influences.

Temperature

Sprouting is impaired when soil temperatures are below 17 °C. However, time to emergence decreases with increasing temperature up to 30 °C,

depending on the variety. Higher soil temperatures also reduce germination (Keating and Evenson, 1979).

Irikura et al. (1979) tested four varieties with differing vigor in three locations with minimal seasonal temperature changes. They found that increasing the temperature from 20 to 24 °C increased leaf size (maximum obtained earlier) and leaf formation rate, that is, increased LAI, but decreased leaf life, while branching occurred earlier. Further temperature increases (from 24 to 28 °C) tended to reduce LAI in two varieties because of reduction in branch number and leaf life as against a still further increase in leaf formation rate. The change in leaf life and leaf formation rate was more marked with changes in temperature from 20 to 24 °C than from 24 to 28 °C. However, some varieties produced most branches at each temperature. Yields were greatest with the more vigorous varieties at the lowest temperature, a trend which was reversed at the high temperature. Root dry weight increased from 8-16 months after planting, with an optimal LAI between 2.5-3.5. Concerning variety x temperature interaction for yield, the authors concluded that special genotypes might be adapted to temperatures below 24 °C even though phenotypically, they need not necessarily be different.

Temperature differentially affects the different phases of root bulking. Where a temperature may favor storage root initiation, it can reduce root growth and/or maturity, which tends to be complicated by day and night temperatures. Low night temperatures favor tuberous root initiation while high day temperatures (29 °C) slightly increase photosynthesis with high rates of respiration (CIAT, 1976). A greater portion of assimilates is used in respiration with a small portion accumulated in tuberous roots (Gupta, 1978). Higher numbers of storage roots are produced at low night temperatures while larger roots are formed at higher temperatures (Bodlaender, 1960). Root yields are also influenced by soil temperatures, especially during temperature regimes unfavorable to root growth. Low temperatures tend to diminish the dependence of root bulking initiation (number of storage roots) on short days, while moderate temperatures favor root growth. Root to shoot ratio thus diminishes at higher temperatures and longer daylengths (Posthusmus, 1977).

Lig'it

Any increase or decrease in solar radiation will affect the size of the plant and hence yield. Owing to the minimal differences in day length in the tropics, photoperiod may not play a major role in the productivity of cassava. Short-day conditions, however, promote root bulking (Bolhius,

1966), possibly because a tuber-inducing substance is formed under this photoperiod.

The optimal day length for root bulking in cassava seems to be 12 hours (Bolhius, 1966; Otoo, 1983). Lowe et al. (1976) reported that long days promote stem growth and as such limit the supply of assimilates to the storage roots, resulting in reduced storage root yields. Even though this observation holds generally under conditions which bring about a reduction in rate of utilization of assimilates in shoot growth, Otoo (1983) showed that varietal differences occur for optimal day length (Table 1).

Higher light intensities favor root bulking (Bodlaender, 1960). Shading has been found to markedly affect root growth rate with little effect on top growth rate (Cock et al., 1979; Kumar and Hrishi, 1979). Up to 36% yield reduction was observed in trials at IITA with 60% shading in comparison to the control, with no reduction in root number (Table 2). Cock et al. (1979) found that shading to 95% had little effect on the life of leaves older than 30 days, while a higher shading caused rapid leaf abscission. The

Table 1. Effect of day length on cassava root formation^a.

Treatment	No. of thickened roots	Fresh root weight (g/plant)	Dry root weight (g/plant)
58308 and TMS 30395 (early flowering)			
8-hr day length	5.7	150.4	40.0
12-hr	1.8	47.8	14.9
16-hr	0.2	1.7	0.4
LSD (5%)	2.2	61.9	18.1
TMS 30001 and TMS 30572 (intermediate flowering)			
8-hr day length	4.8	191.3	47.3
12-hr	4.8	201.1	54.4
16-hr	2.7	154.6	44.2
LSD (5%)	ns	ns	ns
TMS 50395 and Isunikankiyan (late flowering)			
8-hr day length	3.3	110.2	25.0
12-hr	3.0	194.4	47.0
16-hr	0.7	37.9	8.5
LSD (5%)	1.9	84.5	20.4

a. Harvest at 6 months.

SOURCE: Otoo, 1983.

Table 2. Effect of shade on fresh weight and number of storage roots of cassava at 17 and 25 weeks after planting.

Shade (%)	Root weight (kg/plant)		No. storage roots	
	17 weeks	25 weeks	17 weeks	25 weeks
0	1.44	2.38	11	12
20	1.26	2.28	11	12
40	0.91	2.15	11	9
60	0.82	1.62	10	10
LSD (5%)	0.33	0.66	3	3

SOURCE: IITA, 1981.

decline in photosynthetic rates with leaf age under high light intensity seem to be clone specific, since different rates of reductions were observed among the clones tested by Aslam *et al.* (1977).

Relative humidity

Cassava responds to changes in vapor pressure deficits by closing its stomata and consequently reducing photosynthetic rate (CIAT, 1981). Varietal differences exist in response to vapor pressure deficit but whether or not they affect the ultimate yield is not yet known, because the environmental growing conditions have variable ambient relative humidities at different times of the year.

Soil moisture

Although cassava is tolerant to drought (Onwueme, 1978), higher yield levels are obtained with a longer moisture cycle or with conservation by mulching (IITA, 1982). Connor *et al.* (1981) compared the growth of two clones (M Mex 59 and M Col 22), differing in vigor, during and after a period of water stress. The water stress was accomplished by covering the ground with plastic to prevent rainfall penetration. They found that biomass production was reduced by water stress and, as a result, changed the pattern of substrate allocation to different parts of the plant—a process which persisted throughout the rest of the growing season even after the removal of stress. This effect was more pronounced in the biomass above ground, where the rate of leaf formation per apex, branching, and leaf size were reduced. Leaf life was, however, increased by the stress. Root development was least affected, with the more vigorous clone (M Mex 59) having an increased assimilate accumulation. Removal of the water stress tended to influence rapid canopy redevelopment.

M Mex 59 had a higher yield from the stressed plot than from the control plots. It must, however, be pointed out that the stress was not applied during a specific stage during the ontogeny of the crop, but rather chronologically. M Col 22, an early maturing variety, suffered considerably since the stress period coincided with its period of major storage root bulking. By contrast, the bulking period of M Mex 59 coincided with the recuperation phase. The sparse root system penetrated as deep as 250 cm. All these processes suggest a strategy of water conservation. On encountering stress, cassava reduces its water uptake and conserves carbon and nitrogen in the leaves so that when water becomes available it can begin rapid growth again.

Ghuman and Lal (1983) found that irrigation significantly increases root yields and diameter, with these effects being more pronounced in unmulched than in mulched treatments.

The fresh weight of storage roots is reduced practically to zero when the air-filled pore space in the soil is below 9%-10%. This decrease in air-filled pore space affects yield by affecting total plant weight, even though the marginal distribution of dry weight to storage roots is not changed (Vine, 1979).

Although indications exist for a genotype x drought stress interaction, the available data are insufficient, covering too narrow a range of genotypes for a generalization.

Soil nutrients

Although cassava has the reputation of yielding relatively well on poor soils in comparison with many other crops, large supplies of nutrients are necessary for its production. Conflicting results have been obtained on the response of cassava to fertilization, presupposing the existence of genotype x fertilizer interaction (Williams, 1975). Increasing fertilizer application increases the crop growth rate, resulting from increased LAI (San Jose and Mayobre, 1982). Thus, fertilization can improve the production of the photosynthetic apparatus needed for gross assimilate production and storage root development. However, care must be taken not to induce excessive shoot growth at the expense of root growth.

Nitrogen. Cassava requires a considerable amount of nitrogen (Forno et al., 1977; Obigbesan and Fayemi, 1976; Samuels, 1970). However, abundant nitrogen favors the vegetative top growth at the expense of storage root development. Chew (1970) obtained a linear response to

nitrogen (N) between 0 and 160 kg/ha of N at a rate of 25% yield increase per 60 kg/ha of N.

Potassium. Cassava removes large quantities of potassium (K) from the soil. Howeler (1978) estimates that about 70 kg/ha is required by the crop to produce a 30 t/ha harvest. If the tops are removed during harvest, then the K removed is more than double (Asher and Howeler, 1980). Potassium plays an important role in the synthesis and translocation of starch which in turn increases the storage root yield (Kumar and Hrisi, 1977 and 1979). Potassium application induced the production of large storage roots without having any significant effect on the number of storage roots (Ngongi et al., 1977). On newly cleared land, no positive yield responses were observed either to N or K applications. Instead, root yields decreased with increasing rates of N application, particularly without K applications (Table 3), and these decreases varied among varieties.

Table 3. Effect of different levels of nitrogen and potassium on cassava yields (t/ha).

Level of nitrogen (kg/ha)	Levels of potassium (kg/ha)				Mean
	0	50	100	150	
0	26.7	24.8	26.7	27.1	26.3
50	23.8	24.6	25.7	26.5	25.2
100	23.5	26.0	26.2	25.3	25.3
150	22.1	22.6	24.7	24.1	23.4
Mean	24.0	24.5	25.8	25.8	

SOURCE: IITA, 1981.

Phosphorus. The amount of phosphorus (P) absorbed by cassava is relatively small even though it has an important role in the phosphorylation of starch reserves. Starch content was reduced from 32%-25% in the absence of P (Malavolta et al., 1955), and increased P fertilization increased yield in Sierra Leone (Godfrey-Sam-Aggrey and Garber, 1978). Zaag (1979), however, showed that root yield was less dependent on P in comparison with shoot yield. He therefore concluded that root yields decrease with increasing levels of P.

Soil acidity

The major soils used for cassava production are strongly acid (Tan and Bertrand, 1972) and varietal responses to lime application range from low to very high (Spain et al., 1975). Thus, considerable variation in tolerance

to high soil acidity exists among cassava cultivars. Rogers (1965) indicated that cultivars are capable of growing on soils ranging in pH from about 5.0 to 8.0, while Chew (1970) reported the adaptation of cassava to acid peaty soils limed from an initial pH of 3.7 to around 4.7. Edwards and Kang (1978) obtained small nonsignificant responses to low lime rates while drastic yield reductions were observed at higher lime rates. This suppression in root production occurred independently of any changes in leaf weight. Thus, the major limitation to root development was not dependent on leaf production. Lime-induced zinc deficiency may not necessarily have been the cause of the yield reduction as proposed by Spain et al. (1975), since zinc concentrations in the leaves were higher than those at which zinc deficiency symptoms usually occur.

Diseases and pests

Diseases and pests cause severe yield losses in cassava, the extent of which could be as high as total crop failure, depending on the type of disease or pest and time of attack.

Viruses reported to attack cassava have a very sharp geographical distribution. The brown streak virus and African mosaic virus are generally found in Africa, while the common mosaic virus, leaf vein mosaic virus, and the latent virus are restricted to tropical America. The economically important bacterial diseases include *Xanthomonas campestris* pv. *manihotis* (cassava bacterial blight), *Erwinia carotovora* (bacterial stem rot), and *Aglrobacterium* spp. (bacterial stem gall).

About 30 fungal diseases have been reported affecting the leaves, stems, and roots of cassava: the *Cercospora* leaf spots (*C. vicosae*, *C. henningsii*, and *C. caribaea*), concentric leaf spots (*Phyllosticta* spp.), superelongation disease (*Elsinoe brasiliensis*), and anthracnose (*Colletotrichum* spp.) affect the leaves; *Glomerella* and *Botryodiplodia* spp. affect stems; and *Phytophthora*, *Pythium*, *Sclerotium*, and *Rhizoctonia* spp. affect the roots (Hahn et al., 1979; Lozano, 1977).

The greatest diversity of pests attacking cassava are present in the Americas. These include green mite (*Mononychellus tanajoa*), shoot fly (*Silba pendula*), lace bug (*Vatiga manihotae*), mealybug (*Phenacoccus manihoti* and *P. herreni*), and white scale (*Aonidomytilus albus*) to mention but a few. The green mite and mealybug are the most devastating pests to cassava production in Africa, after their accidental introduction to Uganda and Zaire, respectively (Bellotti, 1977; Hahn et al., 1979).

Diseases and pests can damage cassava plants by attacking leaves and buds, thus reducing growth, photosynthetic area, and efficiency. Root growth is totally curtailed with complete defoliation. Cassava mosaic disease (CMD) reduces leaf area drastically, while *Cercospora* spp. produce toxins that cause leaf yellowing, leaf spots, and premature leaf fall. Cassava bacterial blight (CBB), however, reduces leaf area in addition to inducing leaf fall. Even though mites do not reduce leaf number they tend to impair photosynthetic rates of individual leaves, in addition to causing leaf reduction through distortion. Growth may cease with mealybug infestation while the green mite reduces rate of crop growth. The active transportation system of nutrients and photosynthates between source and sink is blocked by CBB and anthracnose, causing wilting of leaves and dieback, which is later manifested in yield reduction.

All these pests and diseases will reduce yields more drastically if the attack is over a long period, because cassava is able to recover from short periods of attack under favorable environmental conditions such as water and nutrient availability.

Vegetative propagation encourages the perpetuation of the diseases and pests, and breeding for resistance provides the most effective means of control. Resistance to cassava mosaic is under quantitative genetic control (Hahn and Howland, 1972; Jennings, 1970) and is controlled by recessive genes with about 60% heritability (Hahn et al., 1977). Hahn et al. (1980) have noted a significant genotypic correlation between cassava bacterial blight and mosaic disease ($r = 0.90$), apparently due to linkage. Msaba (1981) has reported that resistance to CMD and CBB is controlled by recessive polygenes with additive effects. Negative correlation between CBB intensity versus storage root yield ($r = -0.70$) and root starch content ($r = -0.59$) have been obtained (Obigbesan and Matuluko, 1977).

Pubescence of young leaves seems to confer some level of resistance to the cassava mealybug (CMB) and cassava green spider mite (CGM). This character is regulated by more than one gene, with a partial recessive effect (IITA, 1982). A highly significant correlation ($r = 0.69$) between CMB and CGM tolerance levels indicates the possible improvement of resistance to CGM through selection of CMB-resistant clones.

Physiological factors

Improvement of crop productivity through plant breeding has been mainly achieved through the manipulation of plant characteristics to

utilize environmental factors with improved efficiency. Physiological and biochemical means of improvement are a recent objective.

All plants follow a developmental rhythm. The physiological and biochemical processes occurring during the development of a plant are integrated so that an equilibrium state is established at all times during growth, differentiation, and development. Changing the internal equilibrium alters the final product and the extent of this alteration in relationship to yield is dependent on the degree of association between the two. As a result, a ceiling of yield is created. Relaxation of these negative correlations can result in great yield increases of some crop plants. The short-statured hexaploid wheats, derivatives of the Norin 10 cultivar, outyield the standard wheats as a result of the relaxation of the negative correlations between the yield components.

The relationships among plant characteristics appear to be more allometric than genetic. Allometric relationships among number of roots (X), mean root weight (Y) and dry matter (Z) may result from competition to bring about structural balances (Tables 4 and 5).

A clone which performs well over a wide area must either resist environmental changes or adjust favorably through physiological changes,

Table 4. Correlation coefficients among yield components of cassava.

	Root yield (W)	Number of roots (X)	Mean root weight (Y)
Number of roots (X)	0.12		
Mean root weight (Y)	0.41	-0.74**	
Dry matter content (Z)	-0.51*	0.01	-0.61*

Table 5. Path coefficients among yield components in cassava.

	Root yield (W)	Number of roots (X)	Mean root weight (Y)
Number of roots (X)	1.87		
Mean root weight (Y)	2.36	-0.74	
Dry matter content (Z)	0.93	-1.00	-1.35

which are ultimately expressed in the physical components of yield. Representing yield as the volume of a rectangular parallelepiped with the components as edges and assuming there is equal probability of changes along axes, then the volume of the cube will be least changed by random changes in the X, Y, and Z axes. However, if changes are not random or if a particular edge is more resistant to change than the other two, then some other configuration may be more resistant to changes in volume. The greatest change is obtained with a change in its shortest edge (Grafius, 1956 and 1964). With the geometric presentation, no component is more important than the other. A unit change in any edge may contribute to a change in another edge, depending on the shape of the parallelepiped, and certain configurations may be advantageous in certain environments.

Case study: Cameroon

Cameroon has a large variation in agroecological zones varying from evergreen rainforest to steppe, altitudes from 0 to 4000 m, and rainfall of 400-5000 mm. Soil fertility varies from very poor, sandy, sedimentary soils to very rich volcanic soils. Five broad classifications of agroecological zones are recognized: highland savanna; coastal lowland; south continental land; Adamawa; and north Cameroon. South continental land and north Cameroon have each been subdivided into two parts (Table 6). This subdivision is based principally on total rainfall and distribution, altitude, and vegetation, which in turn determine the disease and pest complexes which are thought to be of potential economic concern. Each zone has its own variation in soil type. However, most of the very fertile land is occupied by parastatal farms, leaving only the marginal land for food crop production. Most of the agroecological zones of the world's major cassava-growing areas can be found in Cameroon, making it a good site for genotype-by-environment studies.

The Cameroon National Root Crops Improvement Program (CNRICIP) is one of the three outreach programs of the Root and Tuber Improvement Program of the International Institute of Tropical Agriculture (IITA). It is charged with the development of production systems suitable and acceptable for use by small farmers which increase the yields of the major root and tuber crops: cassava, cocoyam, yam, and sweet potato. This involves the development of high-yielding varieties with multiple resistance to the major diseases (cassava mosaic disease, cassava bacterial blight, and cassava anthracnose disease), wide adaptation, high nutritive value, and consumer acceptability.

Table 6. Characteristics of the agroecological zones of Cameroon.

Agroecological zone	Vegetation	Altitude (m)	Annual rainfall (mm)	No. of rainy days/year	Mean annual temperature (°C)
I Western highland	Savanna	1000-2000	2000 (Unimodal)	150-220	22.0
II Coastal lowland	Evergreen forest	0-500	2000 (Unimodal)	180-240	27.0
IIIa South continental land	Semideciduous forest	500-900	1500 (Bimodal)	120-165	23.7
IIIb South continental land	Derived savanna	500-900	1500 (Bimodal)	120-165	24.2
iV Adamawa	Sudan-Guinea savanna	1000-1400	1200 (Unimodal)	110-120	23.3
Va North Cameroon	Sudan savanna	200-700	900-1200	70-120	—
Vb North Cameroon	Steppe	200-1000	600-900 (Unimodal)	30-70	—

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During the dry season of 1980-1981, the cassava green spider mite (CGM) was found with a low incidence around Garoua-Boulaï, near the Central Africa Republic border. It is now distributed all over the country. The cassava mealybug (CMB) has been recently identified within 15 km of the Cameroon-Nigeria border town of Ekok. Thus, the major biological constraints to increasing cassava production are present, even though their levels vary within each agroecological zone.

Cultural practices are also being developed to maximize yields of the improved varieties. With the division of the agroecology in Cameroon, emphasis is placed on breeding for variation within rather than across the agroecological zones.

IITA's breeding program involves crossing and selection against the major diseases (CBB, CMD) and pests (CGM, CMB). Improved true seeds from interpollinated superior clones with sources of resistance to diseases (Figure 2) and pests and with good agronomic traits are sent to national programs in different locations in Africa for selection under their local conditions. CNRCIP has benefited from this scheme. Decentralized selections were made at three major locations which are representative of the major agroecological zones: Muyuka in the high-rainfall lowland zone on poor sandy soils (Zone II); Nkolbisson in the south continental forest zone with medium rainfall on red lateritic soils (Zone IIIa); and Meiganga in the highland savanna with moderate rainfall (Zone IV). Secondary selection sites are used in the high-rainfall highland savanna (Babungo, Zone I), south continental savanna (Bertoua, Zone IIIb), and the drier lowland savanna zones (Mbéré, Zone Va).

Seedling nurseries are established with over 10,000 seeds and seedlings screened for resistance to CMD and CBB under natural epiphytotic conditions. This is done during the rainy season when conditions are favorable for the development of the diseases. Tolerant or resistant plants are marked and further screened against pests during the dry season.

The selected seedlings (about 1000-1500) are cloned and planted in single-row plots of 10 m² with 10 plants. A local cultivar is planted after every 10 clones for comparison. This serves as a reconfirmation of the first year's evaluation. Poorly performing clones are rejected.

About 100-150 clones, selected from the previous year's clonal evaluation, are placed in a preliminary yield trial with plot sizes of 30 m² (3 x 10 m), replicated three times. Yields are determined, using only the middle row, while other agronomic evaluations are done on a whole-plot basis.

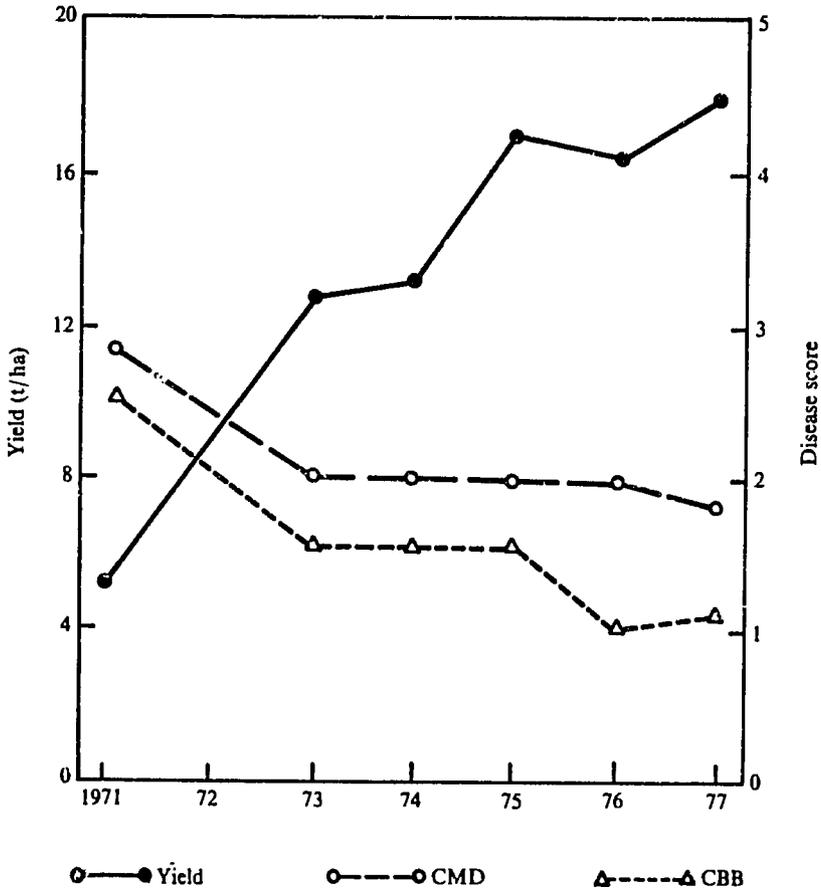


Figure 2. Mean yield and disease resistance scores of improved varieties since the beginning of IITA's cassava improvement program. (Adapted from IITA, 1982.)

Selected clones are evaluated for their dry matter content and root cyanide content using the enzymatic assay (Cooke et al., 1978).

In the fourth year, the most promising 50-70 clones are moved into an advanced yield trial, using 4-row plots which are 10 m long and replicated four times. The central two rows are harvested for yield. Multilocational yield testing is performed on the 20 best clones at four or five different locations using a design similar to that of the advanced yield trial. The best performing three to five clones are tested at farm level and those most appreciated are multiplied for distribution.

The present yield trials show clones performing better with respect to yield potential (Table 7) and disease resistance compared to local cultivars from the respective agroecological zones (CNRCIP, 1981, 1982, and 1983). Promising selections or improved lines have given variable results when grown in areas other than those from where they were selected (IITA, 1982 and 1983). Varieties selected at IITA (in the region of moderate rainfall and soil fertility) and tested at Mokwa (in the dry savanna) and Onne (in the high-rainfall zone on poor soils) show variable yields (Table 8).

Similarly, varieties selected in the rich valley soils in the Bandundu region of Zaire show a reduction in yield when tested in the plateau region (Table 9). Different times of planting also affect yield (Table 10). A combined analysis of variance for yield trials in which 10 varieties were

Table 7. Yields of improved and local check clones at different evaluation stages.

Agroecological zone (site of selection)	Yield of local check clone (t/ha)	Average yield of five best clones (t/ha)	
		Preliminary yield trial	Advanced yield trial
II Muyuka	17.0	39.8	32.2
IIIa Nkolbisson	19.8	37.0	31.6
IV Meiganga	2.9	10.2	14.0

Table 8. Performance of promising cassava clones at various locations in Nigeria, 1982-1983.

Clone	Fresh root yield (t/ha)				Dry matter (%)	Pest and disease scores ^a			
	IITA	Mokwa	Onne	Mean		CMD	CBB	CGM	CMB
TMS 50395	23.8	11.1	12.5	15.8	24	2.0	1.1	3.1	2.5
TMS 4(2)1425	21.5	8.3	16.3	15.4	26	2.0	1.0	2.3	2.5
TMS 30572	20.9	12.6	11.1	14.9	27	2.1	1.0	3.1	3.0
TMS 63397	20.3	9.4	9.4	13.0	28	1.9	1.0	3.6	2.8
60506 (check)	13.5	7.0	8.3	9.6	23	2.9	2.0	3.5	3.0
LSD (5%)	6.0	5.5	4.0						

a. CMD = cassava mosaic disease; CBB = cassava bacterial blight; CGM = cassava green spider mite; CMB = cassava mealybug.

SOURCE: IITA, 1983.

Table 9. Performance of cassava varieties in multilocation yield trials, Bandundu Region, Zaire, 1982-1983.

Variety	Fresh root yield (t/ha)	
	Five plateau sites	Two valley sites
F100	12.0	17.8
F150	9.4	13.7
F156	9.1	13.3
Local	4.0	13.0

SOURCE: IITA, 1983.

Table 10. Performance of promising cassava varieties tested at the International Institute of Tropical Agriculture, Nigeria, 1980-1981, first and second seasons.

Clone	Fresh root yield (t/ha)		Dry matter (%)		CMD ^a score		CGM ^b score	
	1st	2nd	1st	2nd	1st	2nd	1st	2nd
	TMS 4(2)1425	21.6	12.1	34.8	28.9	2.1	2.0	1.3
TMS 30572	19.6	9.3	31.3	34.5	2.0	2.0	2.4	4.0
TMS 30555	19.0	9.6	27.5	33.1	2.0	2.0	2.3	4.3
TMS 30001	17.2	—	29.1	—	1.9	—	3.3	—
60444	7.0	0.7	22.7	26.3	3.0	3.0	2.6	3.7
LSD (5%)	1.3	3.9						

a. CMD = Cassava mosaic disease.

b. CGM = Cassava green mite

SOURCE: IITA, 1981.

tested at 3 locations in Nigeria for 2 years showed significant interaction between variety and location (Table 11). Poor correlation coefficients between locations were obtained for two sets of yield data on the 10 varieties tested: 0.37 for IITA and Mokwa, 0.21 for IITA and Onne, and 0.12 for Mokwa and Onne. Using yield values for two locations and predicting for the third location also showed low correlation coefficients (Table 12). A correlation coefficient of 0.22 was obtained when yields at IITA and Mokwa were used in predicting yields at Onne, and 0.38 when IITA and Onne yields were used for predicting Mokwa yields.

An attempt was made to determine some agronomic factors inherent within the clones selected at one location which cause a variation in yield when tested at another place. A reciprocal yield evaluation was performed

Table 11. Combined analysis of variance for yields of 10 cassava varieties tested in uniform trials at locations in Nigeria, 1981-1983.

Source of variation	Degrees of freedom	Mean square
Variety	(V-1)	22.7 ^a
Variety x year	(V-1)(Y-1)	51.3
Variety x location	(V-1)(L-1)	111.7 ^a
Variety x location x year	(V-1)(L-1)(Y-1)	41.6
Error	LY(V-1)(R-1)	36.0

SOURCE: IITA, 1983.

Table 12. Correlation coefficients between observed and estimated yields of 10 cassava varieties^a.

Test sites	Site for which yield was predicted		Mean of three sites
	Mokwa	Onne	
IITA ^b	0.37	0.21	0.75
IITA and Mokwa		0.22	0.85
IITA and Onne	0.38		0.79

a. Figures were calculated for single test sites based on yields at one or two other sites.

b. IITA = International Institute of Tropical Agriculture, Nigeria.

SOURCE: IITA, 1983.

with clones selected at Muyuka (80 m elevation) and Babungo (1130 m elevation). The characteristics of soil at the selection sites (Table 13) show a wide variation even though they all fall under the high-rainfall zones, but with different temperature regimes. Relative humidity is higher at Muyuka than Babungo.

Higher yields were obtained at locations from which the clones were initially selected. Clone 7839 produced 31.3 t/ha of fresh storage roots at Muyuka while clones 79307-8 and 7746 each produced 27.2 t/ha at Babungo. Yield and number of storage roots of Babungo-selected material were halved when evaluated at Muyuka (Table 14). Yields were also halved when Muyuka-selected material was evaluated at Babungo. However, storage root numbers remained the same. The incidence of disease in Babungo-selected cassava was very high at Muyuka since the initial selection had been made under low cassava mosaic disease pressure at Babungo.

Table 13. Analysis of soils of two selection sites in Cameroon.

Soil characteristics	Selection site	
	Muyuka	Babungo
Texture (topsoil)	Sandy loam	Clay loam
(subsoil)	Sandy clay loam	Clay
Organic C (%)	0.81	2.39
Total N (%)	0.06	0.28
Average P	3.10	9.00
pH (H ₂ O) 1:2.5	4.7	5.6
(KCl) 1:1	3.9	4.4
CEC meq/100 g (NH ₄ OAc)	1.89	15.33
K ⁺ (NH ₄ OAc) meq	0.04	1.29
Na ⁺	0.01	0.02
Ca ⁺⁺	0.28	7.76
Mg ⁺⁺	0.00	2.73
% Base sat.	17.46	76.97
Al ³⁺ + H ⁺ (%)	90	0.24

Table 14. Average performances of cassava clones selected and evaluated reciprocally at two locations with different elevations in Cameroon.

Selection site	Evaluation site							
	Yield (t/ha)		Root no. per 10 m ²		Mean disease scores ^a			
	M	B	M	B	CMD ^b		CBB ^b	
				M	B	M	B	
Muyuka (M) (elevation 80 m)	23.1	12.1	64	59	1.0	0.6	1.0	0.7
Babungo (B) (elevation 1130 m)	15.4	24.5	51	100	3.0	0.1	2.0	0.7

a. Scores rated on a 0 to 4 scale: 0 = no damage; 4 = severe damage.

b. CMD = cassava mosaic disease; CBB = cassava bacterial blight.

The yield component which was more prone to change varied among the different selections. Size and number of storage roots were more prone to change among the Muyuka- and Babungo-selected clones, respectively. This is implied from the relative decrease in value of the path coefficient between number of roots and yield (1.01 to 0.78) among the Muyuka-selected material (Table 15). The Babungo-selected material had a higher increase in direct effect of tuber size on yield (0.51 to 2.32) than in direct effect of tuber number on yield (0.57 to 1.68) (Table 15).

Table 15. Path coefficients among fresh storage root yield (W), number of storage roots per 10 m² (X), and average storage root weight (Y) of cassava selected and reciprocally evaluated at two locations in Cameroon.

Selection site	Evaluation site	Path coefficient		
		X→Y	Y→W	X→W
Muyuka	Muyuka	-.37	.73	1.01
Muyuka	Babungo	-.14	.73	.78
Babungo	Muyuka	.71	.51	.57
Babungo	Babungo	-.93	2.32	1.68

Thus, in addition to selecting against the physical and biological constraints of the agroecological zones, certain physiological processes are selected which are later expressed as yield components. Changing the environment changes these physiological processes, which in turn change the yield components. However, certain components are more prone to change than others. This signifies the importance of allometric relationships during the development of yield components in yield determination. CNRCIP places more emphasis within than across the different agroecological zones, since each zone has its own disease and pest complexes interacting with their physical constraints.

Recommendations

To initiate a national breeding program for cassava, the country should first be divided into agroecological zones based on physical and biological constraints that affect productivity. Within these zones, representative sites should be chosen where decentralized selection processes can be

undertaken. Parent material and their progenies should be evaluated for resistance to diseases and pests and other agronomic characteristics. Hybridization need not be carried out on a decentralized basis, since disease-free cuttings of high-yielding, stable varieties can be sent to a centralized place for hybridization. Resulting true seeds should then be sent to the original zone of selection of their parents for evaluation.

Local germplasm should be collected from the different ecological zones for evaluation. If pests and diseases cannot be adequately evaluated under field conditions, evaluation should be under controlled conditions. Some of these local cultivars can be used as parents, depending on the type of improvement to be done. A high-yielding, disease-susceptible local cultivar can be improved by incorporating resistance through crossing with resistant varieties and then selecting for resistance and favorable characteristics. Source populations with large genetic variation could be developed using population improvement schemes with cyclic recombination and selection procedures. A continuous upgrading of the population is thus assured.

The decentralized selection procedure would produce varieties with the necessary resistance for adaptation to specific ecological zones, in addition to stable yields. The progress in the improvement program will depend on the genetics of the desired traits, selection of parents with high breeding values, the number of traits to be incorporated, and the number of progeny evaluated yearly (Lozano et al., 1980).

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Stability of Performance of Cassava Genotypes

*James H. Cock**

Introduction

The more variable the conditions under which a crop is grown, the more variation there will be in its growth and yield. Generally, more intense management of an agricultural system leads to less variable growth conditions. For example, under intense management, rice cultivated in Japan is exposed to low variation—fluctuations in water availability, fertility, and disease and pest attack are minimized by irrigation and applications of fertilizers and pesticides. Cassava, on the other hand, is generally grown under low levels of management and is subject to the uncertainty of natural rainfall patterns, to variations in soil fertility, and to the attack of diseases and pests during its long growth cycle. This suggests a much greater yield variation under low levels of management. However, the farmer with a small resource base, who generally is unable to utilize management that eliminates the causes of variability, is the least able to tolerate large fluctuations in yield or quality of his product.

It is probable that the traditional farmer has developed his agricultural system and selected his varieties with a very high priority placed on stability of yield over seasons. The farmer is mainly worried about stability over time (temporal stability)—he is not generally concerned with stability of yield across geographic regions (spatial stability), although he may be interested in stability across different production systems (system stability). This latter is particularly true in cassava-growing areas where different planting dates and harvesting times occur, in which case the farmer may use different varieties and agronomic practices for each planting season, or he may look for a stable system that gives good yields and quality, irrespective of planting date.

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A research institute is, unlike the farmer, very interested in spatial stability because the technology it develops must be applicable over large areas if a reasonable return on investment in research is to be obtained. Thus, to satisfy farmers' needs and its own requirements, a research center must aim to produce technology that has, in terms of yield and quality, temporal, spatial, and system stability. While attention must be given to these aspects of stability, it should be recognized that not only is it extremely difficult, if not impossible, to obtain one variety or production system that has stability over all the different conditions under which cassava is grown, but also, it is not necessary. The strategy of the cassava-breeding programs must be to obtain stable production systems within defined limits of variability in growing conditions and management. In this context the major concern, in the case of spatial stability, is not stability over vastly different growing conditions or geographical areas (macrospatial stability), but rather spatial stability within a relatively narrow range of growing conditions which have to be defined (Table 1).

Table 1. Cassava edaphoclimatic production zones and their main characteristics.

Edapho-climatic zone	General description	Mean temperature (°C)	Dry season duration (mo.)	Annual rainfall (mm)
1	Lowland tropics with intermediate to long dry season; low to moderate annual rainfall; high year-round temperature.	Above 22	3-5	700-2000 (unimodal distribution)
2	Acid soil savannas; moderate to long dry season; low relative humidity during dry season.	Above 22	3-5	Above 1200 (unimodal distribution)
3	Lowland tropics with no pronounced dry season; high rainfall; constant high relative humidity.	Above 22	Absent or very short	Above 2000
4	Medium-altitude tropics; moderate dry season and temperature.	21-24	3-4	1000-2000 (bimodal distribution)
5	Cool highland areas; moderate to high rainfall.	17-20	Variable	Above 2000
6	Subtropical areas; cool winters; fluctuating daylengths.	Minimum 0	Variable	Above 1000 (summer rainfall)

The classification of these growing conditions by edaphic and climatic parameters alone is obviously not realistic—it is well known that the major elements determining differences in growing conditions are biotic factors. These biotic factors are, however, not only dependent on the climatic and edaphic conditions and the geographical location of a site, but also on the cassava genotype, its management, and the area planted in the particular area under consideration. The classification into edaphoclimatic zones is useful in determining the gross physical environment and also in predicting which biotic factors are likely to be, or become, important when different genotypes are grown.

In this paper the major causes of variability or instability are discussed with particular reference to the development of stable genotypes. Most examples are taken from data obtained by the Cassava Program at the Centro Internacional de Agricultura Tropical (CIAT) whose major testing sites and their characteristics are described in Table 2.

Table 2. Selected characteristics of major testing sites in Colombia.

Site	Average temperature (°C)	Rainfall		Soil fertility level	pH
		mm/yr	Distribution		
Media Luna	27	1600	Unimodal	Low	6.5
Caribia	28	1400	Unimodal	Medium	6.3
CIAT-Palmira	24	1000	Bimodal	High	6.8
CIAT-Quilichao	25	1800	Bimodal	Very low	4.5
Carimagua	26	2000	Unimodal	Very low	4.4
Papayan	18	2100	Bimodal	Very low	5.5
Rio Negro	27	1700	Unimodal	Low	4.2
Nataima	28	1500	Bimodal	Medium	6.1
Chigorodo	28	1800	Short dry season	High	6.6
Florencia	25	2900	Short dry season	Medium	3.8
San Martin	25	2200	Unimodal	Medium	4.2

Factors causing instability

Temperature

There is a very strong genotype by temperature interaction (Irikura et al., 1979) in areas where temperature fluctuates little from month to month. The data available suggest that for temperatures of less than 22 °C the genotypes required are different to those for higher temperatures. Little data exist on the interaction between genotype and temperature when the latter shows seasonal fluctuation. The CIAT international trials data obtained in the late seventies suggest that certain clones (for example, CMC 40) are well adapted to moderate temperatures with little fluctuation (for example, 24 °C throughout the year) and also do well in areas where temperatures may be below 10 °C for 1-3 months of the year. Few other clones have shown this adaptability, growing well only at higher constant temperatures (for example, M Ven 218) or growing well only at lower constant temperatures (for example, M Col 1522). Spatial stability for temperature effects will be difficult to obtain and lines will need to be bred for the following specific temperature conditions: warm areas with nearly constant temperatures; cool areas with nearly constant temperatures; and areas with fluctuating temperatures.

Although cassava is not grown over the wide range of latitudes as are other crops such as rice, potatoes, and beans, it does in fact face a wider range of temperatures during its long growth cycle than these crops. In the case of beans and potatoes in the subtropics, the planting season is adjusted so that the crop is grown in the cooler part of the year, while rice grown at higher latitudes is grown only at the warmest time of the year. The long growth cycle of cassava in areas where temperature fluctuates markedly throughout the year leads to a potential problem with stability across systems. If planted at different times of the year the crop will experience different temperatures at different growth periods. From a physiological point of view, it is likely there will be a strong genotype by planting date interaction, that is, a potential lack of system stability.

Temporal stability with respect to temperature may be easier to achieve. Temperatures within the tropics are very similar over the same period from year to year, and hence temperature effects are of less concern in causing temporal instability.

Photoperiod

In the tropics, seasonal changes in photoperiod are not large. Nevertheless, they are of sufficient magnitude to affect cassava yields, particularly at

higher latitudes. Some varieties are more sensitive than others (CIAT, 1981; Keating et al., 1982a and 1982b; Veltkamp, 1986). Long days only affect cassava in the first 3 months after planting. Hence, change of photoperiod will only affect stability in areas where the planting season is during or immediately preceding the long-day period. Thus, system and spatial stability will both be important with respect to photoperiod. It should be noted that all varieties tested so far are photoperiod-sensitive in terms of such parameters as branching and dry matter distribution, although some varieties show relatively stable yields in different photoperiods (Table 3). To date, only a narrow range of clones have been tested for photoperiod response.

Table 3. Effect of long days on yield, 9 months after planting.

Variety	Dry matter yield (t/ha)		Reduction (%)
	Long days	Short days	
M Col 22	8.3	9.5	13
M Col 1684	4.6	8.7	47
M PTR 26	4.9	8.1	40

SOURCE: CIAT, 1981.

Water

The cassava plant is extremely tolerant of water stress, but a long dry period can seriously decrease yields (Connor et al., 1981). Rainfall patterns differ markedly from region to region and will undoubtedly result in yield differences. Nevertheless, it does seem possible to find varieties with a stable yield response to different water availability patterns. In a trial at Carimagua, several varieties yielded the same with or without irrigation and only one yielded significantly more with irrigation (CIAT, 1978 and 1979). In Quilichao, exclusion of rain from plots of M Mex 59 actually increased yields, while decreasing yields of M Col 22. In both these trials, those clones with highest yield and high harvest index were also the most sensitive to drought stress (Figure 1). More recent trials suggest that certain varieties that have stability above optimal leaf area index (LAI) under well-watered conditions reduce the LAI to only slightly less than the optimum when a dry period occurs, and that these varieties have both high-yield potential and good yield stability under varying conditions of water availability (Figure 2).

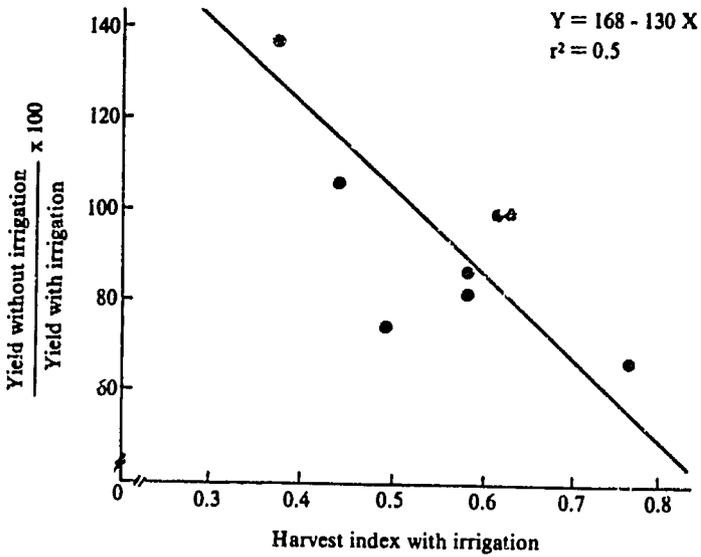


Figure 1. Relative yield with and without irrigation during the dry season in Curimagua, Colombia, as related to harvest index. (Adapted from CIAT, 1979.)

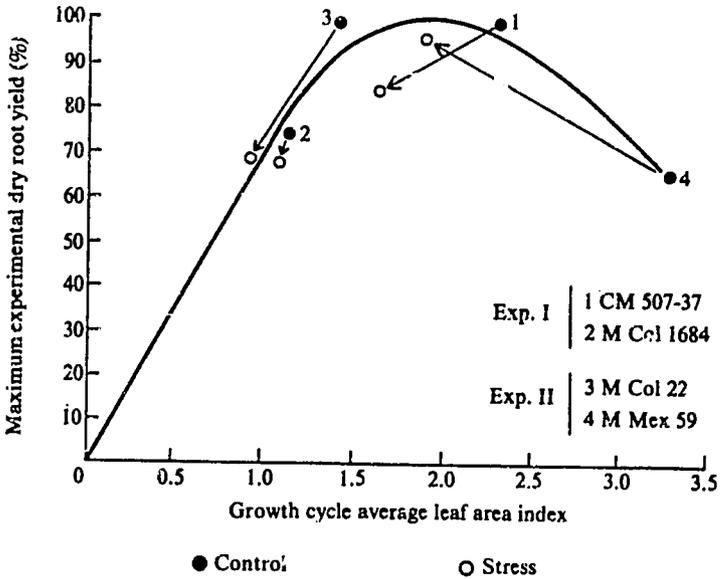


Figure 2. Dry root yield as a function of growth cycle average leaf area index under nonstress and midterm water stress conditions for four cultivars with different vigors. (Adapted from CIAT, 1984.)

The intensity of water stress is highly variable from region to region and from year to year. Hence, temporal and spatial stability are of great importance. System stability is also important as different planting dates may subject the plant to stress at different growth stages. It is not yet clear whether high-yielding clones are obtainable that can be planted either at the beginning or end of the rainy season. However, certain clones (for example, CM 342-170), yielded well in Caribia and Media Luna irrespective of planting season (Table 4) and others have stable starch content (for example, Secundina), irrespective of harvest date, although the yield of the latter is relatively low as compared to new selections (CIAT, 1981).

Table 4. Effect on yield of planting early or late in the rainy season for CM 342-170 at 11-12 months after planting in Media Luna, Colombia.

Planting time in rainy season	Dry matter yield (t/ha)	
	With fertilizer	Without fertilizer
Early	6.0	5.4
Late	5.9	5.8

SOURCE: CIAT, 1981.

Soil

Cassava is grown on a very wide range of soils. However, it is most commonly found on those that tend to be acid and of low fertility. Cassava is extremely stable in its response to pH *per se* in the range 4-7.5. Low pH in mineral soils is frequently associated with high levels of aluminum (Al) which is toxic to many plants. Cassava is remarkably adapted to high levels of Al saturation and most genotypes show a stable reaction if Al saturation is below 80% (Figure 3). In highly alkaline soils, where salts are often a problem, cassava is very sensitive to small changes in pH and salt concentrations, with large differences among genotypes. These areas, however, are of little or no importance for cassava production. The remarkably high yields of M Col 1684 in several locations (Figure 4) suggest that genotypes do exist that have a stable reaction to different soil types.

While cassava shows a very stable response to different soil conditions such as pH and Al saturation, it is responsive to changes in fertility (Asher et al., 1980). Fertility differences affect spatial stability (because soils vary from area to area), system stability (because farmers may either fertilize

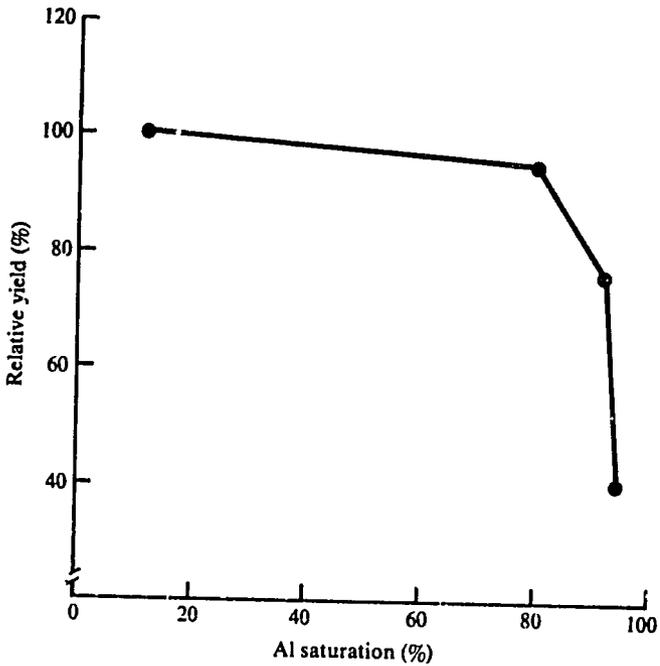


Figure 3. Response of cassava to different levels of aluminum (Al) saturation. (Adapted from CIAT, 1978.)

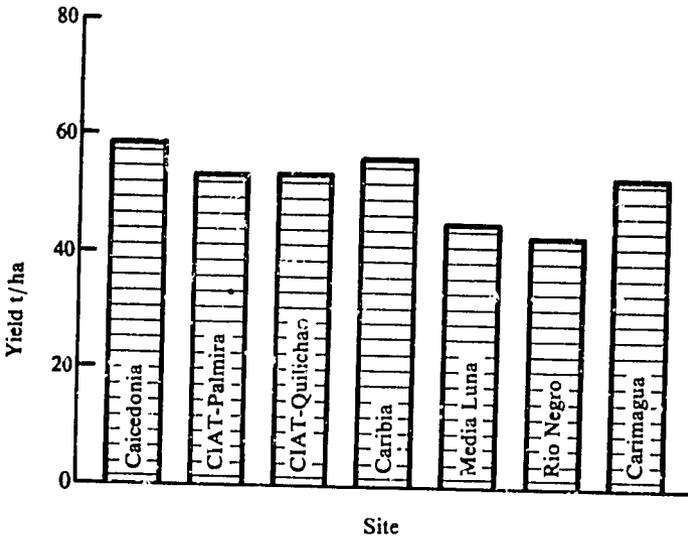


Figure 4. Maximum yield obtained with M Col 1684 at various sites with different soil characteristics. (Adapted from CIAT, 1976 to 1984. Annual reports.)

crops or use management practices that alter fertility), and temporal stability (because soil fertility declines with continuous cassava cropping). Cassava has certain inherent characteristics that make it less sensitive to fertility changes than other crops (Cock and Howeler, 1978; Edwards et al., 1977). In addition, the use of chemical fertilizers and the association with mycorrhiza reduce differences in yield or quality related to fertility differences.

Several clones have now been selected that show both high yield potential and relatively stable yield at different levels of phosphorus (Table 5). Thus, although yields will be higher at higher fertility levels, varieties can be selected that show less yield decline at low fertility levels.

Table 5. Effect of phosphorus application on yield in varieties tolerant of low soil phosphorus levels in Quilichao, Colombia.

Variety	Fresh root yield (t/ha)	
	No applied phosphorus	Phosphorus applied at 75 kg/ha
M Bra 30	52	50
M Era 3	41	51
CM 489-1	35	52
M Col 1514	38	48
CM 430-37	36	47

SOURCE: CIAT, 1984.

Diseases and pests

The effects of diseases and pests on stability are much more complex than the abiotic factors already described. The major reason for this is that the abiotic factors, in broad terms, influence the growth of the plant but the plant itself has little effect on the abiotic factors (a decline in soil fertility with continuous cropping of cassava is an obvious exception to this generalization). On the other hand, most of the biotic factors not only influence the growth of the plant but are also influenced themselves by the growth of the plant and the genotype of that plant.

In addition, fluctuations in abiotic factors that affect temporal stability tend to be random (for example, changes in temperature or rainfall) or to follow relatively predictable trends (for example, decline in soil fertility).

Experience can help us assess the probability of fluctuations of different magnitudes in the case of random type variation and, with a few genotypes, the probable effects on growth can be determined. Similarly, controlled experiments in a small number of sites with few genotypes can enable us to predict the likely decreases in soil fertility over time. The situation with the biotic factors is entirely different—there will be random fluctuations influenced by random changes in the environment. There will also be long-term trends that are partially dependent on the genotypes and on changes in the pathogen that are extremely difficult to predict.

Diseases and pests show great variability from area to area, although certain disease and pest complexes are common to different sites within each of the major ecological zones. *Phoma* leaf spots are a major problem in cooler areas. In dry areas thrips and spider mites may cause severe losses in yield and quality, and cassava bacterial blight (*Xanthomonas manihotis*), anthracnose (*Colletotrichum* spp.), and superelongation disease (*Elsinöe brasiliensis*) are major problems in the acid soils of savanna areas. Our experience suggests that by adequate selection of resistant clones for each edaphoclimatic zone, germplasm with microspatial stability in terms of disease and pest reaction may be obtained and, eventually, as a greater number of resistances are combined, macrospatial stability may also be obtained.

Variability in disease and pest severity across systems may be extremely large. For example, pesticide treatment and use of “clean” planting material may delay the buildup of disease and pest problems. Different dates of planting may reduce the disease or pest incidence, while poor pest management may increase pest damage. All these factors point to a potentially large system instability in cassava, especially when pest control is mainly through management.

A further complication in the case of disease and pest damage is that vigorous clones are able to tolerate higher levels of damage than higher yielding but less vigorous ones, with little change in yield or quality (Figure 5). Hence, stability based on the ability of the plant to tolerate damage with little effect on yield may be directly related to low yield potential. To achieve the same stability levels of lower yielding varieties, it will be necessary to increase resistance levels in higher yielding genotypes.

Present situation in stability

Most breeding programs attempt to produce varieties with temporal stability within a considerable (but not all-inclusive) spatial and system

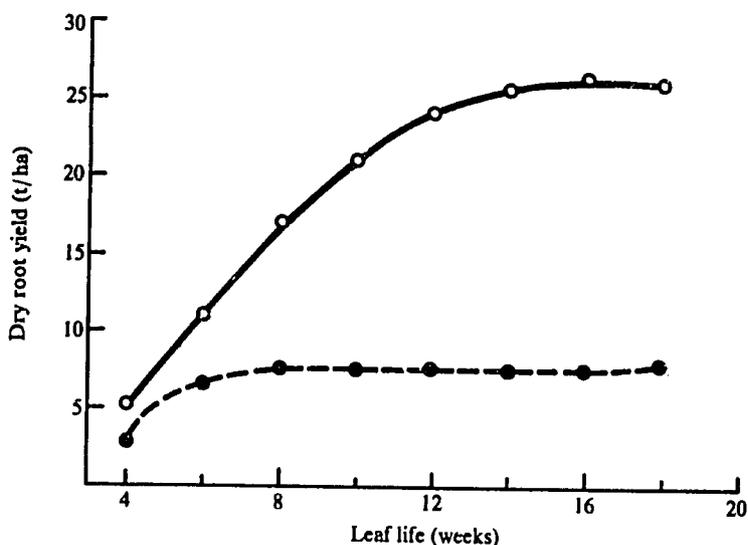


Figure 5. Simulated effects of reduced leaf life (caused by diseases and pests) on yield of a near ideal (○) and a vigorous plant type (●). (Adapted from Cock, 1978.)

variability. When varieties are needed for widely different ecosystems or production systems, different genotypes will be required because no one variety will serve for all purposes.

System stability

The major factors affecting system stability are genotype, fertility, stake selection and treatment, stake storage, planting systems, planting and harvesting date, weed control, cropping systems, and pest management. The reality of cassava production systems results in the use of limited input technology which minimizes the use of irrigation, high fertilizer applications, and continued use of pesticides. Yet all of these could contribute to greater stability.

Fertility levels. Fertility levels can readily be modified by use of chemical fertilizers which are, however, expensive and probably will not be used to the extent that all differences in fertility effects on yield and quality are eliminated. Hence, it is desirable to have genotypes and concomitant technology that are relatively stable over different fertility levels. Mycorrhiza may also play an important role in increasing stability in soils of low phosphorus (P) content.

Stake selection and treatment. Stake selection and treatment are recommended practices, but are not always followed. In low-stress areas such as CIAT-Palmira, high stable yields have been obtained with selected but untreated stakes. However, in areas such as Carimagua, or in those areas where stakes are stored before planting, lack of treatment and selection will certainly decrease stability. Genotypic variation exists in the ability to produce well without treatment (Table 6) and genetic tolerance to suboptimal conditions of planting material may be sought.

Planting and harvesting date. Cassava is generally planted in the rainy season, but the planting time may be either at the beginning or the end of the rainy season. Under Carimagua conditions, planting at the end of the rainy season has given greater yields (Figure 6) because the disease pressure is less severe during the early growth stage. From a physiological point of view it is highly probable that stress at different periods will affect different genotypes differently. However, it would also appear possible to obtain genotypes that give moderate yields at either planting date (Table 4).

Starch content may also be affected by planting and harvesting dates. When plants of certain genotypes are harvested at the beginning of the rainy season or after a cold season, starch content is low. This effect is so great that, in Thailand, many starch plants close for two months of the year when starch content is at a minimum.

The high root starch content required for the fresh market is only applicable to about one-third or less of the total cassava produced. In other

Table 6. Percentage germination of selected clones with and without stake treatment in Media Luna, Colombia.

Clone	Not treated	Treated
M Ven 25	93	95
CM 681-2	92	94
M Col 113	83	94
M Col 1684	63	94
M Col 72	41	96

SOURCE: J. C. Lozano, personal communication.

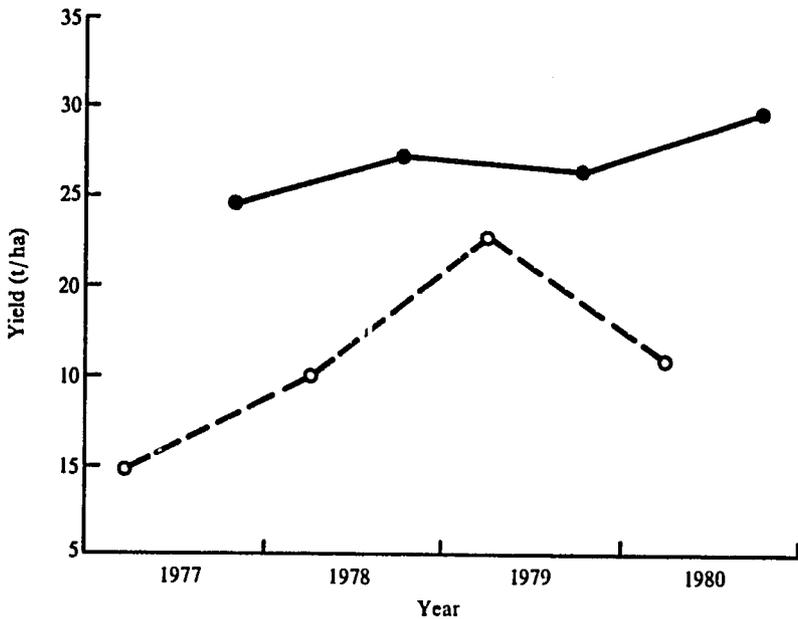


Figure 6. Maximum yield obtained in Carimagua with late (●) and early (○) planting in advance yield trials.

markets, the most important factor is starch yield per hectare, although a high starch content is an advantage. Varieties that have high starch content regardless of harvesting time (for example, M Ven 156, CM 523-7, Venezolana, and Secundina) do not, however, have great yield potential. The difficulty in obtaining lines with high stable starch content as well as high starch yield per hectare is not known. It certainly seems likely that starch content declines as reserves from the roots are used to produce new foliage after the dry or cold season and that this should later result in higher yields. Hence, high yield and stability of starch content may not be compatible.

Starch content tends to be greater when the temperature is lower, and vice versa. Thus, in subtropical areas starch content tends to be greater in winter (G. Hammer, personal communication). It is not clear whether lines exist with a stable reaction to temperature changes. In some subtropical areas cassava is planted at the beginning of winter (for example, Cuba) and in others in the spring (for example, Rio Grande do Sul in Brazil). It is not known whether the same varieties will be effective under these very different systems, that is, show system stability. It is known, however, that

certain photoperiod-sensitive lines perform poorly when planted at the beginning of summer, since they are affected by long days during the first 3 months after planting. Other lines are less photoperiod-sensitive and should have a more stable response.

Planting systems. There is considerable information on cassava planting systems. Most data show little yield difference between horizontal, inclined, and vertical planting. However, there is no doubt that lodging, which can drastically reduce both yield and starch content, is less likely with vertical and inclined planting.

In areas with heavy rainfall, root rots may become a severe problem and planting on ridges or mounds (Lozano et al., 1980) was found to reduce root rots and increase stability of yield and quality.

Cropping systems and management. Much of the world's cassava, up to 40%, is grown in intercropping systems. Leihner (1983) and Moreno and Hart (1979) showed that a greater yield stability results under these systems, particularly at low management levels. In the case of intercropping with short-season grain legumes, the same cassava genotypes yield well when intercropped or in monoculture, suggesting that the cropping system in these cases will have no detrimental effect on yield stability. The starch content of intercropped cassava is generally less than that grown in monoculture.

Differences in weed control can cause enormous differences in yield, particularly in less vigorous cassava varieties. Thus, on the north coast of Colombia M Mex 59 showed remarkable yield stability over a wide range of different weed control management levels, whereas M Col 22 was extremely unstable. However, the highest yield was obtained with M Col 22 under good weed control (Figure 7). This situation, which also occurs with respect to other factors such as disease and pest resistance, suggests that stability in some cases can only be obtained as a trade-off with yield potential. Nevertheless, results from technology validation trials show that moderately stable yields may be possible over a range of different management systems (Table 7).

Pest management. Certain diseases and pests can be controlled by management practices other than host plant resistance. The hornworm (*Erinnyis ello*) is a good example. Simulated damage by leaf removal shows that the vigorous but low-yielding clone M Col 113 showed greater yield stability than the higher-yielding M Col 22 (Cock, 1978). These data indicate that system stability may be conferred by low-yielding but

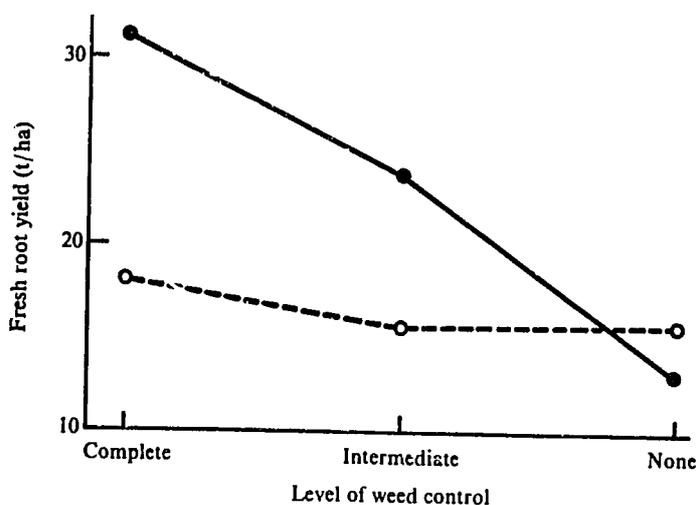


Figure 7. Effect of different levels of weed control on a vigorous (*M Mex 59*, O) and less vigorous (*M Col 22*, ●) cassava clone. (Adapted from CIAT, 1978.)

Table 7. Comparison of yields obtained in trials managed by scientists in regional trial and managed by farmers with different management skills, Colombia.

Technology type and variety	Yield (t/ha) obtained by		
	Scientists	Skilled farmer	Unskilled farmer
Traditional technology			
Secundina	—	10.0	6.1
CM 342-170	—	20.5	9.6
Improved technology but no fertilizer			
Secundina	12.6	16.5	10.5
CM 342-170	20.8	21.4	19.7

SOURCE: Lynam, J. K.; Toro, J. C.; Celis, E.; and Díaz, R. O. Unpublished data.

vigorous genotypes. While this may be generally true it is not the case for pests that reduce germination or plant population in the early stages. The very vigorous clones tend to have a narrow optimum plant population and, hence, plant loss causes yield instability. On the other hand, less vigorous types can be planted at high plant populations, so that plant loss will have little effect on yield (Cock, 1978).

Microspatial stability

The interaction between genotype and site has made it necessary to look for specific genotypes adapted to each of the different edaphoclimatic zones defined in Table 1. There is still considerable variability between sites within the same edaphoclimatic zone, but the genotypes produced should have relatively stable performance across different growing conditions within the same zone (microspatial stability).

A considerable amount of information on microspatial stability has been obtained in the CIAT regional trials. High correlation coefficients (as well as similar yield levels) have been obtained between dry matter yields of varieties in different sites within the same ecological region. In the earlier trials, where the yield range was greater because of less rigorous selection of lines that entered the trials, the correlation coefficients were high, for example, 0.94 between Popayan and Darien (zone 5), using 15 varieties, and 0.88 between Media Luna and Rio Negro (zone 1), using 13 varieties. Later results continue to show high correlations between sites within each major edaphoclimatic zone, although coefficients are lower when sites are more different (Table 8). A large trial established on the north coast of Colombia (in Caribia and Media Luna), with a much wider range of varieties, showed that varieties performed similarly in both sites. These sites differ quite markedly in soil characteristics and intensity of the dry season. The results suggest that, at least in the north coast area, microspatial stability can be obtained. The yield level, however, will be greater in areas with more uniform rainfall and higher soil fertility, as indicated by the consistently greater yields in Caribia than in Media Luna.

Macrosatial stability

Since pronounced genotype by environment interactions are common, it cannot be expected that the same genotype will perform well in all ecological regions. Many trials show that different genotypes are required for colder regions. However, they also indicate that broad adaptability may exist in the warmer, lower-altitude areas because a small number of clones do well in several regions. This view is supported by the stable yield of M Col 1684, M Col 1468, and M Mex 59 over a very wide range of edaphoclimatic conditions, the remarkably stable yield of CM 507-37, and the stable starch content of CM 523-7 (Figure 8). Most clones, however, do not possess such broad adaptability. Hence, breeding objectives should not aim at macrosatial stability, although when it is obtained it is obviously a useful character.

Table 8. Correlation coefficients^a for dry matter yield between sites in the 1980-1981 regional trials and within each site between years 1980-1981 and 1979-1980 (includes data only where seven or more common varieties were used).

Edaphoclimatic zone ^b		Media Luna	Rio Negro	Nataima	Chigorodó	Florencia	San Martín	Carimagua
1	Media Luna	0.80	0.29 ^c	0.91	0.35	0.48	0.03	0.14
1	Rio Negro		0.68	0.88	0.75	0.89	0.58	0.80
1	Nataima			0.69	—	0.89	—	—
1, 3	Chigorodó				—	0.07	0.33	0.46
3	Florencia					—	0.38	0.61
2	San Martín						0.65	0.45
2	Carimagua							0.68

a. Based on fresh root yields.

b. See Table 1 for general descriptions.

c. In other years correlation coefficients between Rio Negro and Media Luna were 0.88, 0.82, 0.70, 0.83.

SOURCE: CIAT, 1980 and 1981.

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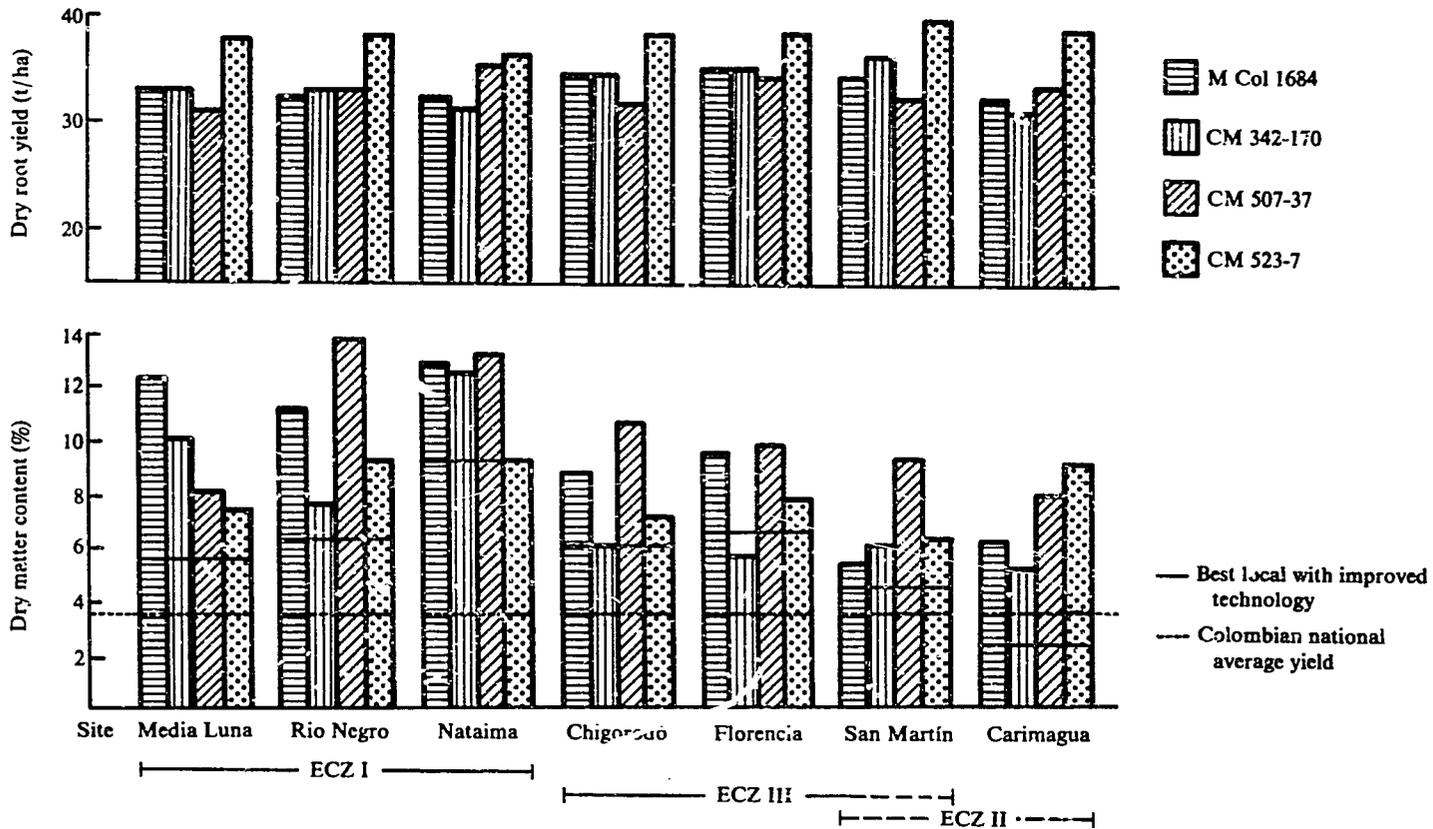


Figure 8. Yield of dry roots and starch content of several clones over a wide range of growing conditions. (See table 1 for general descriptions of ECZ.) (Adapted from CIAT, 1977 to 1984. Annual Reports.)

Temporal stability

Temporal stability is perhaps the most difficult to obtain. It has been suggested that the use of a large number of testing sites may give an idea of spatial stability and that this may be related to temporal stability. With the abiotic factors that affect stability there is a good possibility that temporal stability may be related to spatial stability, for example, it seems a priori that the effect of different rainfall patterns across sites is similar to that within sites across time. In the case of biotic factors, which may have a slow buildup of intensity, depending on the cassava genotypes present and on the evolution of new races of pathogens, it appears unlikely that spatial stability would be closely related to temporal stability. While a variety grown from clean seed may yield well under stress conditions in the first year, as it becomes infested with diseases and pests and debilitated by low nutrient status, its performance declines. These observations indicate, that in the case of cassava, a large number of trials in different sites can in no way replace long-term trials to determine temporal stability.

Yields of the same clone may show large fluctuations in a particular site because of changes in climatic factors. Thus, in Media Luna the yield of Secundina shows marked year-to-year variation (Table 9). The variability of the clone M Ven 156 was considerably less, suggesting that there are differences in the response to climatic variation and that variability did not increase as yield level increased. These differences may be a result of a direct physiological response of the plant or of secondary factors.

In Popayan the clone CMC 39 showed great yield instability, producing high yields in drier years and low yields in wetter years when it was severely attacked by *Phoma* leaf spots (Lozano et al., 1980). In the year following a wet year this variety yielded well and there was no long-term decline in

Table 9. Standard deviation (SD) as a percentage of mean yield of dry roots of several cassava lines in Media Luna, Colombia.

Variety	No. of cycles	Mean yield (t/ha)	SD	SD as % of mean yield
M Col 1684	5	9.3	2.9	32
M Ven 156	5	5.5	1.3	23
M Col 22	7	5.2	2.0	39
Secundina	7	3.4	1.4	40

yield (Figure 9). On the other hand, in Carimagua yields of M Ven 218 declined in a year when it was attacked by cassava bacterial blight (CBB), and even though clean planting material was used in subsequent years, yields never recovered (Figure 10). This yield decline occurred at a time when the total area of cassava in Carimagua increased, causing a marked change in the ecosystem. A similar example on a large commercial scale occurred in the Campo Cerrado of Brazil with the opening of a new cassava alcohol plant in Curvelo, Minas Gerais. In the first plantings, local clones yielded over 20 t/ha, but yields rapidly declined to 5-6 t/ha as the disease and pest pressure increased.

The decline in yield as a result of change in the ecosystem is complicated by a decline in the stake quality of diseased plants. In susceptible cultivars

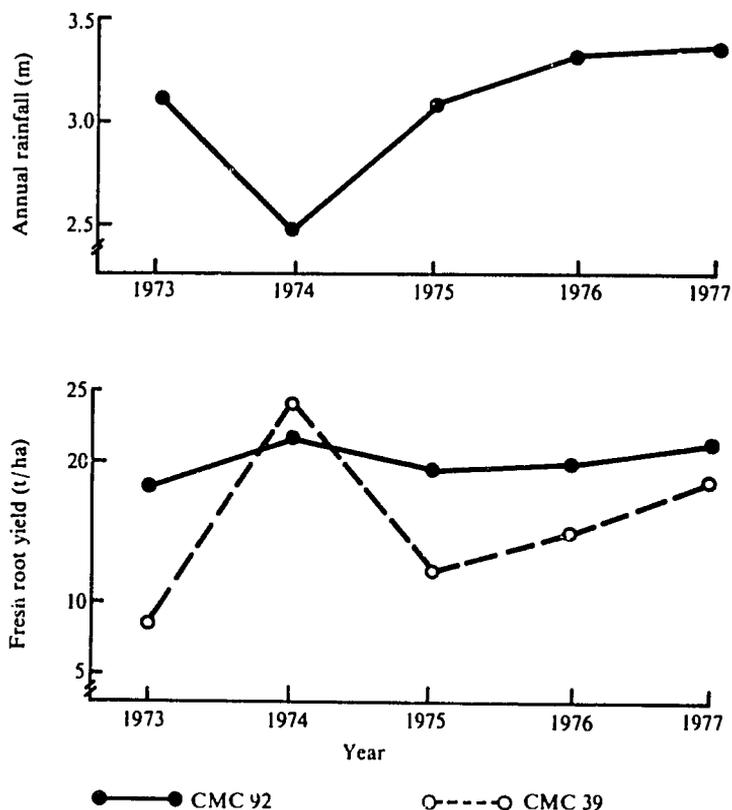


Figure 9. Yield of two cassava clones over several seasons, and rainfall during the growth cycle. (Adapted from Lozano *et al.*, 1978.)

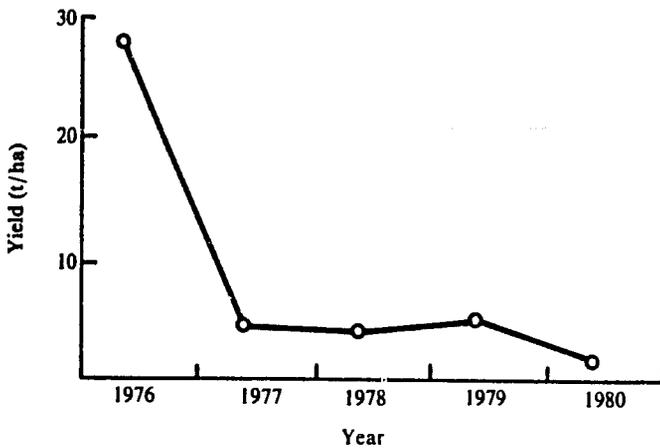


Figure 10. Yield of highly CBB-susceptible clone M Ven 218 over several years in Carimagua. (CBB = cassava bacterial blight.) (Adapted from CIAT, 1977 to 1984. Annual reports.)

this effect is so great that they cannot survive in areas like the Llanos (Figure 1i). Nevertheless, several clones that are tolerant to the prevailing conditions are able to maintain a steady stake production over time. In Carimagua, there is good evidence that stakes from well-adapted plants produced in Carimagua are as good as those produced in the relatively disease-free environment of CIAT-Palmira (Table 10).

These data suggest that stake production is not a major problem if clones are tolerant to the local stresses. The major problem is determining quickly if a variety is well adapted to a given area. For example, M Col 1684 was initially high yielding at CIAT. However, yields decreased over time because of its susceptibility to thrips. A major challenge facing breeders at present is to ensure that varieties that show this type of decline are eliminated in the selection process before release.

In many crops another significant problem with temporal stability is the breakdown of resistance, particularly vertical or major gene resistance. Robinson (1976) suggests that in a perennial crop such as cassava, breakdown in resistance as a result of new pathogenic races is uncommon. This view is supported by Lozano et al. (1980) in spite of indications that races may exist in the case of superelongation disease (CIAT, 1977 and 1980). Even in this latter case, where there is still the possibility of race specificity, there also appear to be other nonrace-specific resistance mechanisms that can be exploited.

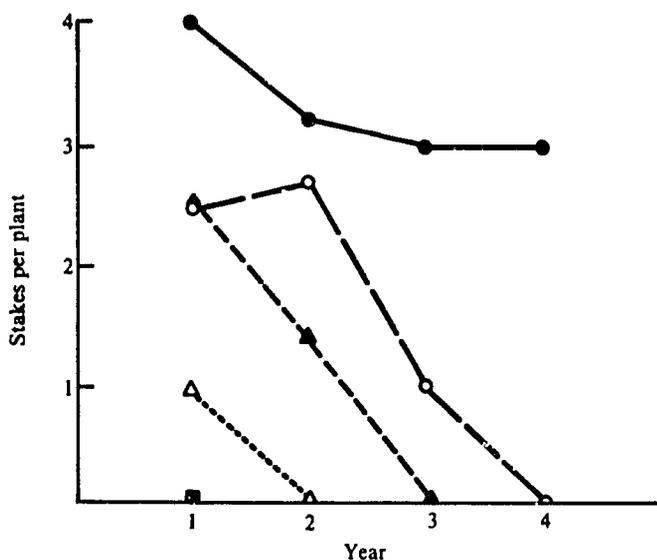


Figure 11. Number of stakes per plant from resistant (●), moderately resistant (○), slightly resistant (▲), susceptible (△), and very susceptible (■) clones over several years of continuous production in Carimagua, Colombia.

Table 10. Yield from Carimagua-produced and CIAT-produced planting material (stakes) of resistant and susceptible clones, Colombia.

Level of resistance	Fresh root yield in Carimagua (t/ha)	
	Stakes from Carimagua	Stakes from CIAT
Highly susceptible	No stakes available	7.3
Susceptible	4.0	6.1
Moderately resistant	15.9	18.4
Resistant	17.2	12.3

SOURCE: CIAT, 1981.

In vegetatively reproduced crops, “degeneration” of seed stock with time is a common occurrence. This appears to be the case with Secundina, planted in the Media Luna area, which has become progressively infected with the “Caribbean virus” and other systemic factors that reduce stake

quality. However, this progressive trend could change in relation to genotype resistance to these systemic factors. Apparently in many clones, clean plants produced from meristem culture are much more vigorous than either infected plants or plants that show no symptoms but have not been cleaned by tissue culture.

The possibility of latent causal agents causing degeneration is reinforced by the fact that yields of unselected F_1 progeny are generally greater than parental means. This increase, however, may be related to hybrid vigor in the progeny and not manifested in the parents because of a certain degree of inbreeding depression. Nevertheless, there is good reason to suspect that degeneration of planting material may occur with time in many clones. However, other clones have been repeatedly reproduced and still show good yield potential and in some cases F_1 progeny means showed no superiority over the parental mean. These data indicate that it may be possible to find genotypes that do not show degeneration. For example, clone CM 342-170, in contrast to Secundina, shows no decline in yield with time in Media Luna (Table 11).

Table 11. Yield of two clones with successive generations of planting material. (Clones were initially cleaned by tissue culture techniques.)

Generations since cleaning	Yield (t/ha) of clone	
	Secundina	CM 342-170
1	30	24
2	26	24
3	21	22
4	18	23

SOURCE: CIAT, 1984.

Development of stable genotypes

The primary center of diversity of cassava is in South America in areas with acid, infertile soils, particularly low in P and with high levels of Al saturation. Cassava has since been introduced to a more diverse range of climatic and edaphic conditions. However, until very recently, it was grown mainly as a backyard subsistence crop or as a crop in shifting

cultivation. The movement of cassava into rotational cropping systems on a commercial basis over large areas has occurred relatively recently. For example, in the acid savanna areas of Brazil cassava has only been grown as a backyard crop until the last 7 or 8 years and in northeast Thailand cassava has become an important crop only in the last 10 years. Rotational cropping in areas such as Media Luna in Colombia, has only occurred in the last 20 or 30 years to satisfy the large, recently-formed urban centres. In West Africa cassava became important this century as soil fertility declined and shifting cultivation changed to more stationary patterns because of land scarcity.

Hence, although cassava clones have evolved over millenia for use in shifting and backyard culture there is considerable room for adaptation to stationary agriculture, producing stable high yields of good quality product.

Farmers and research agencies have undoubtedly made progress in selection. For example, M Col 1468 (CMC 40) yields well over a wide range of conditions but is highly susceptible to thrips and low in starch content; Secundina and Venezolana on the north coast of Colombia have obviously been selected on the basis of eating quality because, until very recently, their products were unsalable unless they were of good quality; and Rayong 1, grown on more than a million hectares in Thailand, was selected for yield although it is relatively low in starch and susceptible to various diseases. The world germplasm collection at CIAT reflects the high level of selection. In the Llanos Orientales of Colombia local clones are successfully grown at the backyard level with no or low incidence of CBB and superelongation disease. Yet the germplasm collection from the Llanos Orientales shows an extremely low percentage of highly resistant clones suitable for more extensive cultivation (Table 12).

Table 12. Percentage of the germplasm accessions collected in the Llanos of Colombia which demonstrated combined resistance to endemic pathogens and pests.

Resistance character evaluated	Level of expression ^a	Percent
Cassava bacterial blight (CBB)	3	36
CBB + superelongation (SE)	3	29
CBB + SE + <i>Mononychellus</i> mite (MM)	3	16
CBB + SE + MM + <i>Vatiga</i> lace bug	3	14

a. 1 = highly resistant; 5 = highly susceptible.

SOURCE: C. H. Hershey, personal communication.

The basis for the development of genotypes with a stable reaction to different growing conditions over systems, space, and time is the available germplasm. In the case of CIAT this is based on some 3700 clones collected from farmers' fields throughout Latin America. This basic germplasm is then evaluated in the different edaphoclimatic zones. Germplasm with useful characters is then either used directly for crosses aimed at producing new cultivars, or placed in crossing blocks with the objective of producing elite germplasm that has even higher levels of resistance or tolerance than the initial germplasm selections. These elite clones with useful characters are crossed to produce large numbers of hybrid seeds. The selection of parents is made in the different edaphoclimatic zones but the crosses are made centrally at a site with a favorable environment for flowering and seed production.

The initial selection from seedling plants aims to eliminate obviously unsuitable material—this is done at CIAT. The good correlation between yield and harvest index at all sites and the good correlation between harvest index at CIAT and Caribia, Carimagua, and Media Luna in the absence of heavy disease pressure suggests that this system is valid, at least for removing lines of low yield potential. (Popayan, the highland testing site used by CIAT, is distinct and seedling plants are selected at that site.) Attempts to grow seedling plants directly in the higher stress sites has not been as successful because the seedlings are so weak, compared to stake-produced plants, that they may be killed off before they have a chance to prove themselves.

After initial, not rigorous selection, stakes are planted in the zone for which the cross was made for evaluation. At this stage plants are grown with a level of management that the "average" farmer should be able to emulate. While this may not necessarily ensure system stability, it does mean that if the cultivar finally produced is system-unstable, the farmer can readily modify his system in such a manner that the particular genotype is of value. The low management level used by CIAT also means that selection is done at low levels of fertilizer applications with no post-planting use of pesticides.

After the first year, selected material is replanted using locally produced planting material in each edaphoclimatic zone. After three years in the same site, advanced lines, which must by now have shown a certain degree of temporal stability, pass to the regional trials network and continue in the advanced yield trials for further evaluation of performance.

Varietal release

Cassava has a low rate of propagation and a long growth cycle. This means that it will not be possible, as in crops such as rice, to rapidly introduce new varieties to traditional growing areas and then replace them with improved ones, if and when they prove unsatisfactory. Cognizance of this has resulted in extreme caution on the part of CIAT's Cassava Program in promoting new materials without an extended testing period in the field. However, there are several reasons why it may not be necessary to exercise such extreme caution in the future.

One of the main fears of introducing a variety without a long period of testing in the field is that problems will arise with temporal stability, mainly because of diseases and pests that cannot be prognosticated in short-term testing. This fear would be well-founded if massive increases in planting material were envisaged in order to open up a new area for cassava cultivation. The area would probably be relatively free of diseases and pests initially and hence problems would take time to appear. Secondly, a new variety would be introduced without farmers having an extended time period to evaluate it.

In areas where cassava is presently grown, for example, the north coast of Colombia, the situation is different. Farmers have a long tradition of changing to new lines. Thus, the Blanca Mona line was almost entirely replaced by Secundina in the late seventies which itself is now being replaced by Venezolana and, recently, CMC 76. The replacement rate is slow and farmers evaluate the new lines while they are multiplying them. Even if they become enthusiastic about a new line, the slow rate of propagation prevents them from making a precipitate change to the new material.

This suggests that in an area of small farmers where cassava is a traditional crop, distribution to each farmer of a small amount of planting material in a fairly early selection stage carries little danger of causing problems, even if the variety later fails. Perhaps the only real danger is loss of credibility with the farmer. However, if the new line is given "as something to try" and new agronomic practices constitute the main recommendation, loss of credibility can be minimized.

If the farmers accept such arguments, promising materials with good yield and starch content should then be actively distributed to farmers. If at each regional trial 1000 stakes of the most promising material were given to 10 farmers (100 stakes each), then each farmer can be expected to reach a maximum of 1 ha after 3 years, assuming the variety was well accepted. By

observing the performance on the farms for three years, information can be obtained to help decide whether to formally release the new variety and instigate more intensive propagation.

When new varieties are to be introduced to a nontraditional cassava-growing area, the situation is completely different. Thus, in Mexico where cassava is being rapidly propagated on a massive scale to open up new areas, there is a real danger of severe problems with varieties after a few years. In such cases, two approaches are of paramount importance: first, to maintain a broad germplasm base with several different lines under multiplication; and, second, to carefully study the changing disease and pest populations during the multiplication phase.

Conclusions

Stability of yield over time (temporal stability) and across management practices (system stability) are important to the farmer, while to the researcher, stability within edaphoclimatic zones (microspatial stability) is essential and across edaphoclimatic zones (macrospatial stability) is desirable to maximize the applicability of research results.

Temporal stability

The generally high correlations between yield of the same genotypes across years within sites (Table 8) suggest that the same genotypes that are superior in one year will continue to show superiority relative to others over time, even though absolute yield levels may fluctuate.

Major problems resulting in temporal instability are the slow buildup of disease or pest pressure and degeneration of planting material with time. Certain clones with a broad resistance to diseases and pests appear to be capable of producing good-quality planting material and maintaining yields over long periods. Breakdown of genetic resistance as a factor in reducing stability does not appear to be a major problem in cassava. Little is known about the problems of degeneration of planting material. Nevertheless, certain clones have been reproduced over hundreds of cycles and are still highly productive, so stability can obviously be obtained.

System stability

Most cassava is produced and will be produced with low input technology. The philosophy adopted to obtain system stability is to fix a set of management practices readily achievable by farmers and select

clones for these practices. Selected clones are then evaluated under farmers' management practices and their stability assessed. The data collected so far suggest that relatively system-stable cultivars can be obtained. Nevertheless, in cassava production with extremely poor agronomy, additional yield stability may be conferred only by physiological redundancy, which requires a sacrifice of yield potential under good agronomy. Different genotypes may not be necessary for monoculture and intercropping when the intercrop has a short growth cycle (less than 100 days).

Microspatial stability

In general there are good correlations between yield performance of lines between sites within the same edaphoclimatic zones using similar management (Table 8). Microspatial stability is unlikely to be a major problem so long as clones have been selected under the range of conditions of a given zone.

Macrosatial stability

Areas with maximum mean monthly temperatures below 22°C will need specific genotypes. The adaptability of tropical clones to areas with a cool winter is not well established. However, the extremely stable yield performance of certain lines and the high starch content of others across edaphoclimatic zones I, II, and III suggest that stability across macrozones may be found in a limited number of lines.

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Inherent and Environmental Factors Related to Cassava Varietal Selection

*Kazuo Kawano**

Biological nature

Cassava is a monoecious species with the stigma and anther usually separated in different flowers on the same plant. The male and female flowers seldom open simultaneously on the same branch. However, it is common that female and male flowers on different branches of the same plant open at the same time. There seems to be no physiological or genetic mechanism to prevent self-pollination and cross-incompatibility has not been observed. Strong inbreeding depression is observed in characters such as root yield and total biological yield (Kawano, 1978). This strong inbreeding depression, in addition to the vegetatively propagated nature of the crop, is the biological mechanism through which high heterozygosity of the species is maintained (Kawano et al., 1978).

Vegetative propagation is of great advantage to breeders. Once a favorable genotype is obtained, it can be multiplied indefinitely. Character expression at the seedling stage is well correlated with that at the later clonal generations (Kawano, 1978). Early studies on cassava breeding (Arraudeau, 1962; Bolhuis, 1949; Chandraratna and Nanayakkara, 1948; Kost., 1947; Magoon, 1967) presented occasional difficulties such as scarce or no flowering of some clones, low seed setting on some female parents, and low germination. However, they, by and large, agreed with our experiences that cassava is one of the easiest among the major crops in which to create and handle recombinant genotypes.

Physiological nature

A food crop is genetically improved through an increase in either total dry matter production, harvest index, or both. Harvest index is the proportion

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of economic yield to the total biological yield of a plant. In cassava, it is the proportion of root weight to the total plant weight. Total biological yield represents the crop's photosynthetic efficiency, while harvest index represents the efficiency of the crop to convert photosynthesized products into an economically valuable form.

Kawano and Jennings (1983) evaluated the relative importance of harvest index and total plant weight to yield at different levels of environmental productivity in various major food crops. They found that, while the relative importance of total plant weight tends to be greater in low-yielding than in high-yielding environments, the harvest index is important across all the yield levels in cassava (Figure 1). This contrasts with rice, wheat, barley, oats, or peanut in which total plant weight is more important than harvest index under low-yielding environments (Table 1).

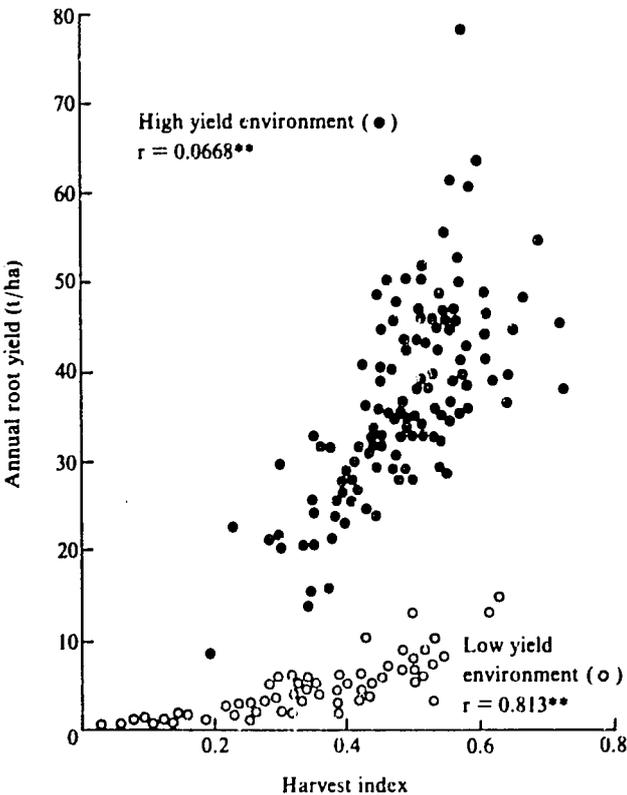


Figure 1. Relationship between harvest index and annual root yield of cassava under high (at CIAT-Palmira) and low (at Carimagua) yield environment.

Table 1. Relative importance of harvest index and total biological yield in major food crops under low- and high-yielding environments.

Crop	Yield-limiting factor ^a	
	Low-yielding environment	High-yielding environment
Cassava	HI, TY	HI
Rice, wheat, barley, oat, peanut	TY	HI
Maize	TY	TY, HI
Field bean	TY	TY

a. HI = harvest index; TY = total biological yield.

SOURCE: Adapted from Kawano and Jennings, 1983.

In maize, total plant weight is important throughout all the yielding levels while harvest index is important only under high-yielding levels. In field beans, total plant weight is important throughout all the yielding levels while harvest index is not important to the yielding level. Thus, manipulation of harvest index in cassava is a key to breeding and selection not only in high-yielding but also in low-yielding environments.

Selection for higher harvest index has been the main strategy of the cassava varietal improvement program at the Centro Internacional de Agricultura Tropical (CIAT). However, it was recognized that overemphasis on harvest index may lead to the neglect of total plant weight. The balance between total plant weight and harvest index may be highly important, especially in low-yielding environments.

Harvest index may not necessarily be correlated negatively to stem and leaf weight and there may even be a possibility of manipulating harvest index without changing stem and leaf weight (Table 2).

If this were possible, 33% improvement in harvest index (for example from .59 to .67) would result in 100% increase in root yield. This is probably too optimistic and yet the indication that harvest index is not automatically negatively correlated with stem and leaf weight—which represents canopy density or photosynthetic capacity—is encouraging. Looking simultaneously at harvest index and canopy, the breeder may arrive at a good balance between photosynthetic capacity and harvest index, avoiding the pitfall of selecting very high harvest index genotypes with low assimilation power.

Table 2. Comparison of yield parameters in two cassava varietal trials.

Trial	Fresh root yield (t/ha)	Fresh biological yield (t/ha)	Fresh leaf and stem wt (t/ha)	Harvest index
Trial 1^a				
Five best clones	41.6	61.5	20.0	.68
Control (local cultivar: Rayong 1)	28.9	49.8	20.9	.58
Advantage over control (%)	44	23	4	17
Trial 2^b				
Five best clones	59.3	86.5	27.2	.69
Control (local cultivars: Golden Yellow and Kadaoao)	32.0	60.8	28.7	.52
Advantage over control (%)	85	42	-5	33

- a. Conducted at Rayong Field Crop Research Center, Thailand, in 1983-1984, using 16 clones. (Data source: K. Kawano and C. Tiraporn, Dept. Agric., Thailand.)
- b. Conducted at Philippine Root Crop Research and Training Center (PRCRTC), Baybay, Leyte, Philippines, in 1983-1984, using 74 clones. (Data source: E. Apilar and K. Kawano, PRCRTC.)

Several good studies on physiological factors related to canopy formation and harvest index are available (Cock, 1976; Cock et al., 1979; Tan and Cock, 1979). One factor which seems to have been overlooked is the leaf area ratio as a function of leaf size and internode weight. There appear to be plants with compact canopies with short internodes and high leaf area index as opposed to tall canopies having long internodes and low leaf area index. The former may lead to the improvement of harvest index without losing photosynthetic power. These factors merit further attention from physiologists.

Competition and evolution of cultivars

Studies of intergenotypic competition in cultivated species lead to a better understanding of the evolutionary background of a crop and the physiological basis of plant yield. Of practical interest is the behavior of different genotypes in mixed populations in plant breeding and selection programs. Competitive ability is defined as the ability to perform better

when planted in association with other genotypes. The essential part of intergenotypic competition is the competition for light interception. Hence, the genotypes with a high harvest index are weak competitors because of the relatively fewer resources allocated to stem and leaf expansion and those with large stem and leaf weight are strong competitors. These principles are well demonstrated in rice (Jennings and Aquino, 1968; Kawano and Tanaka, 1967; Kawano et al., 1974) and also in cassava (Kawano and Jennings, 1983; Kawano and Thung, 1982).

In cassava, competitive ability is highly correlated with stem and leaf weight (Figure 2) and negatively correlated with harvest index (Figure 3).

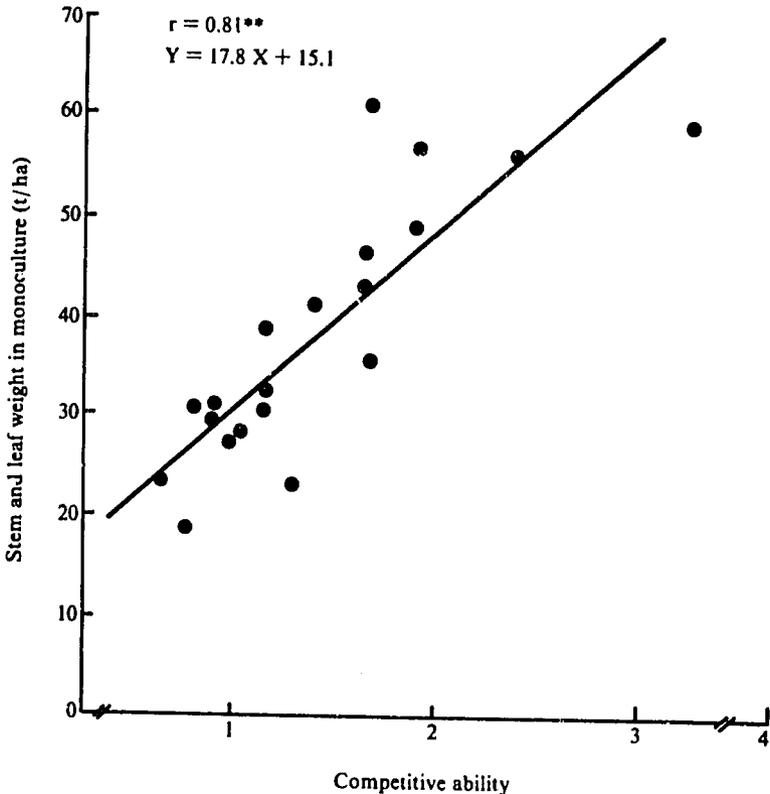


Figure 2. Relationship between competitive ability and stem and leaf weight of the same genotype. (Scale: 1 = low competitive ability; 4 = high competitive ability.) (Adapted from Kawano and Thung, 1982.)

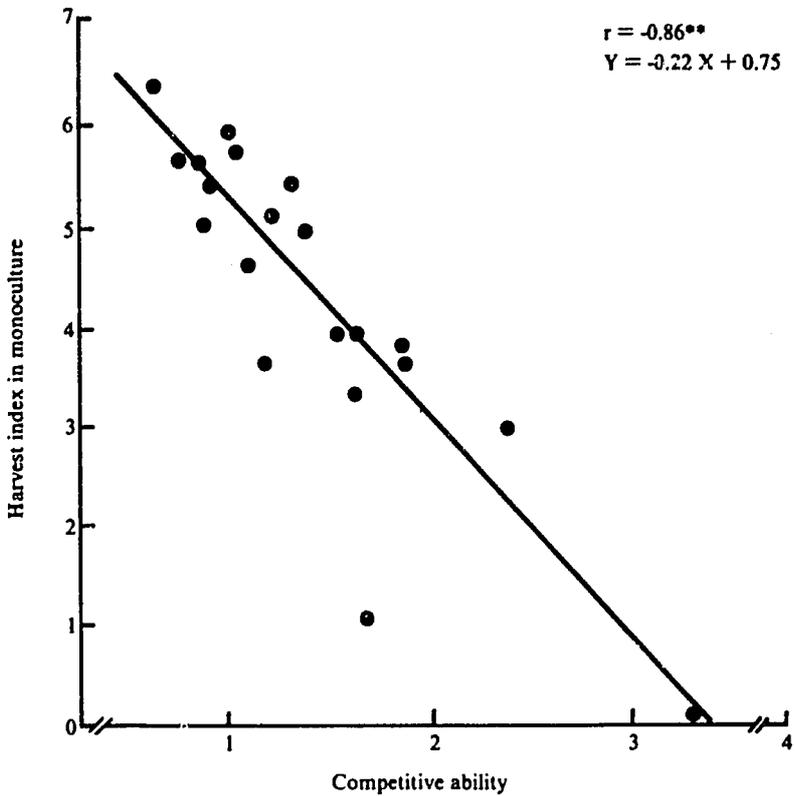


Figure 3. Relationship between competitive ability and harvest index of the same genotype. (Scale: 1 = low competitive ability; 4 = high competitive ability.) (Adapted from Kawano and Thung, 1982.)

Because harvest index is highly correlated with root yield in monoculture (Figure 1), competitive ability is negatively correlated with root yield in monoculture (Figure 4), while, by definition, it is less negatively correlated with root yield in mixed culture. Harvest index is relatively stable between monoculture and mixed populations, while root weight of the same genotype can change dramatically between the two populations because of the competition effect. As a result, harvest index in mixed culture is more highly positively correlated with root yield in monoculture than root yield in mixed culture is with root yield in monoculture (Figure 5). It can be concluded that at early stages of selection trials, in which genotype evaluation is based on individual plants or clones planted in mixture with other genotypes, harvest index is a better selection criterion for root yield in monoculture than root weight itself (Kawano et al., 1982).

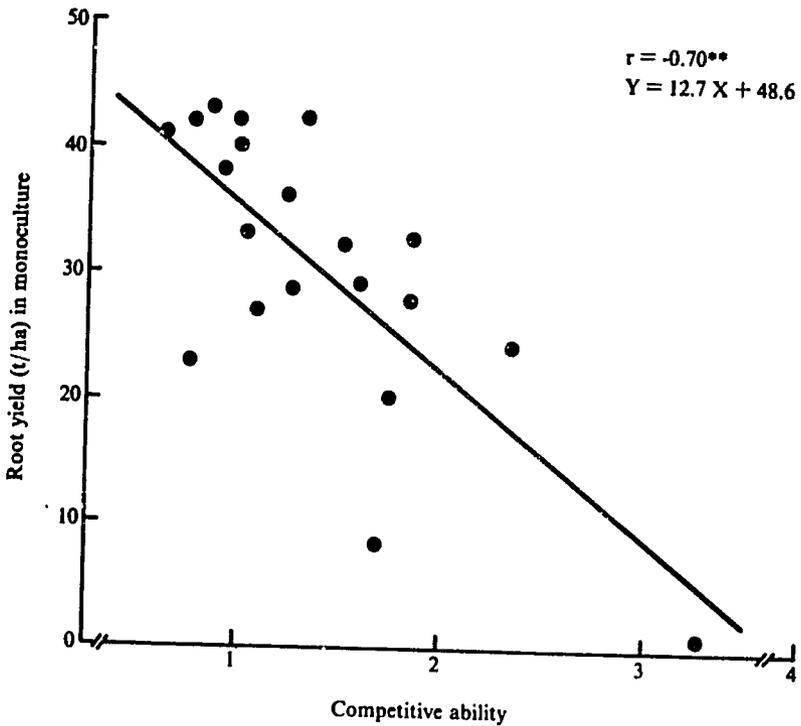


Figure 4. Relationship between competitive ability and root yield of the same genotype in monoculture. (Scale: 1 = low competitive ability; 4 = high competitive ability.) (Adapted from Kawano and Thung, 1982.)

Landraces or traditional cultivars, which often show respectable performance within their adapted environments with their accustomed cultural practices, are the results of natural selection and farmers' selections for thousands of years. If the competitive ability of the crop is positively correlated with economic yield in the production field, such as in the case of field beans (CIAT, 1977), the present-day breeder of the crop would have to work basically in the same path of natural and farmer selection. Hence, modern efforts to improve yield may represent only a fraction of what has been achieved during thousands of years. Consequently, a quantum jump in yielding ability of such crops is not likely.

In cassava and its wild relatives, however, the situation is different. Roots are not an organ for reproduction because seeds and stems are the means of propagation. Natural selection favors genotypes with large stem bulks and modern efforts to improve yielding ability in monoculture through higher harvest index are contrary to the general direction of

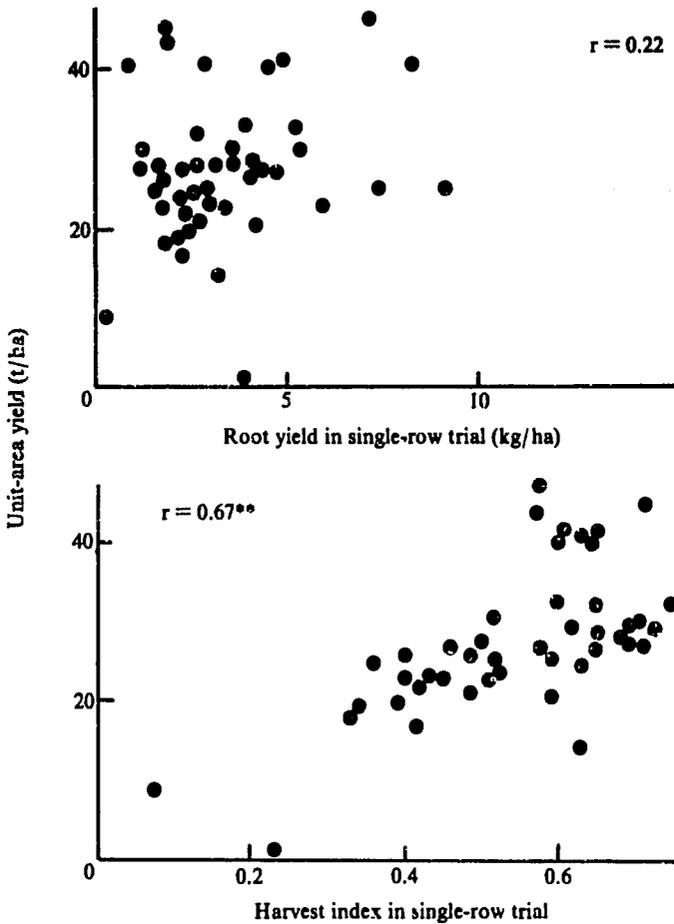


Figure 5. Correlation between root yield or harvest index in single-row trial (1-m row width) and unit area root yield in large plot trial of the same genotype. (Adapted from Kawano *et al.*, 1982).

natural selection. This suggests that the potential of cassava germplasm to respond to modern breeders' efforts is largely untapped. Consequently, a quantum jump in yielding ability of cassava is expected.

Diseases and pests

Biological constraints, especially diseases and pests, are among the factors that contribute to low productivity. In a review of numerous cases of crop

disease interaction, Robinson (1976) distinguished between vertical and horizontal pathosystems. He concluded that vertical (nonrate-reducing, monogenic) resistance, frequently present in sexually propagated annual species, often results from plant breeders disturbing evolutionally balanced systems. Nature, and less meddling by man, favored the development of horizontal (rate-reducing, polygenic) resistance in vegetatively-propagated perennials. This suggests that vegetatively-propagated perennial crops such as cassava are more easily bred for durable disease resistance.

Our experience coincides with this general view. Cassava bacterial blight (CBB), caused by *Xanthomonas campestris* pv. *manihotis*, is one of the most devastating diseases of cassava. CBB on infected leaves of resistant clones spreads slowly, while on susceptible clones it spreads rapidly, causing defoliation and stem death (Figure 6). Resistance is a quantitative trait and the relative order of resistance among cultivars is stable over many years and locations (Umemura and Kawano, 1983). Cassava resistance to superelongation disease, caused by the fungus *Elsinöe brasiliensis*, another serious disease of cassava, is characterized by a slow

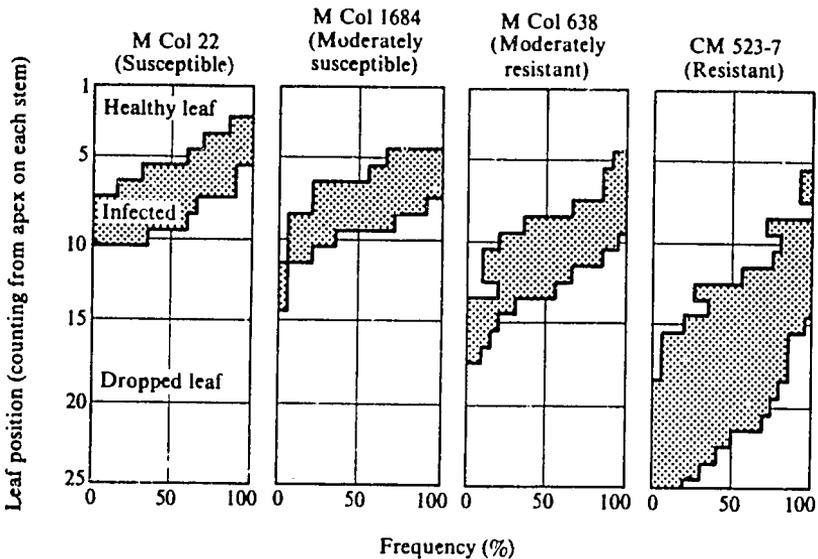


Figure 6. Frequency of healthy, infected, and dropped leaves at different leaf positions in cassava genotypes of different cassava bacterial blight (CBB) resistance (October, Carimagua, Colombia, average of 20 stems). (Adapted from Umemura and Kawano, 1983.)

rate of disease spreading (Kawano et al., 1983). Inheritance of cassava resistance to this disease is also quantitative (Figure 7). Aside from CBB and superelongation, there are many diseases and pests that can cause serious damage to cassava production. We are optimistic that cassava resistance to most of these are similar to resistance to CBB or superelongation, thus adding relatively little complication to the breeders' work.

The International Institute of Tropical Agriculture (IITA) and CIAT have been successful in identifying sources of resistances to most of the major diseases and some of the major insects. Some national programs, such as the one at the Central Tuber Crops Research Institute (CTCRI) in India, have identified resistance sources to their major diseases and are in an advanced stage of utilizing them. The ways to incorporate disease and pest resistance into yielding ability and adaptation are well indicated except for some pest problems in which genetic resistance is weak or yet to be found.

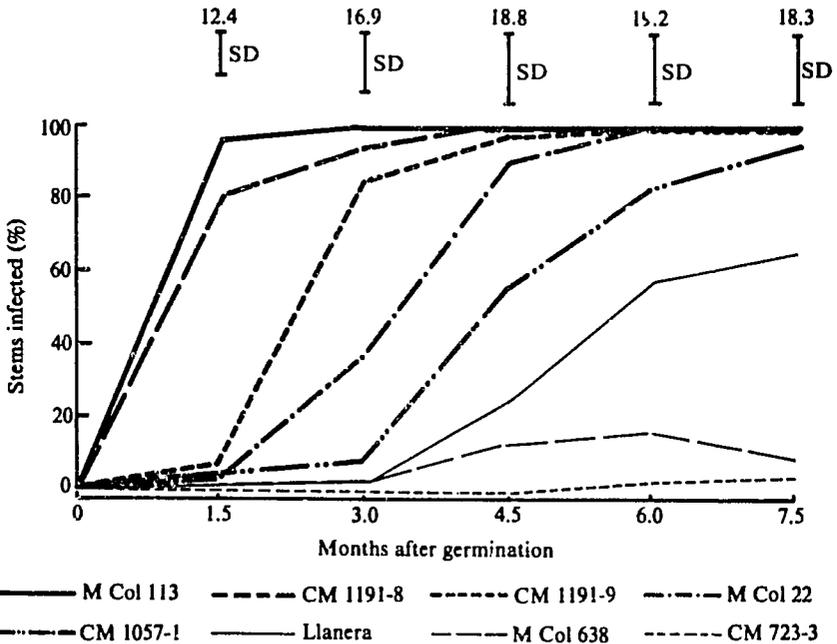


Figure 7. Superelongation disease development on different cassava genotypes at Carimagua. Statistical deviation (SD) ranges at 5% level for multiple comparison are given at each sampling month. (Adapted from Kawano et al., 1983.)

Inheritance of major agronomic characters

Our analyses in the past 10 years suggest that virtually all the important agronomic characters are controlled by a polygene system. Additive gene effects are predominant and narrow-sense heritability is high in the majority of these characters (Table 3), such as harvest index (Figure 8), root dry matter content (Figure 9), and CBB resistance (Figure 10). This suggests that a straightforward hybridization scheme, no matter whether it uses controlled or open pollination, followed by simple phenotypic selection is effective in creating desirable recombinants.

Table 3. Narrow-sense heritability of major characters of cassava^a.

Character	Range of heritability	Data source
Root yield	0.08-0.40	CIAT, 1974 and 1975
Harvest index	0.68-0.72	CIAT, 1974 and 1975
Total plant weight	0.19-0.73	CIAT, 1974 and 1975
Root dry matter content	0.51-0.67	Kawano 1978; Kawano, Gonçalves, and Cenpukdee, unpublished data
Root cyanide content	0.87-1.07	Kawano, de la Cuesta, and Gómez, unpublished data
Postharvest root deterioration	0.44-0.62	Kawano and Rojanaridpiched, 1983
Cassava bacterial blight resistance	0.63	Umemura and Kawano, 1983
Superelongation resistance	0.60-0.79	Kawano et al., 1983
Mite (<i>Mononychellus tanajoa</i>) resistance	0.78	CIAT, 1981

a. Given as regression coefficient of F_1 population averages on mid-parent values.

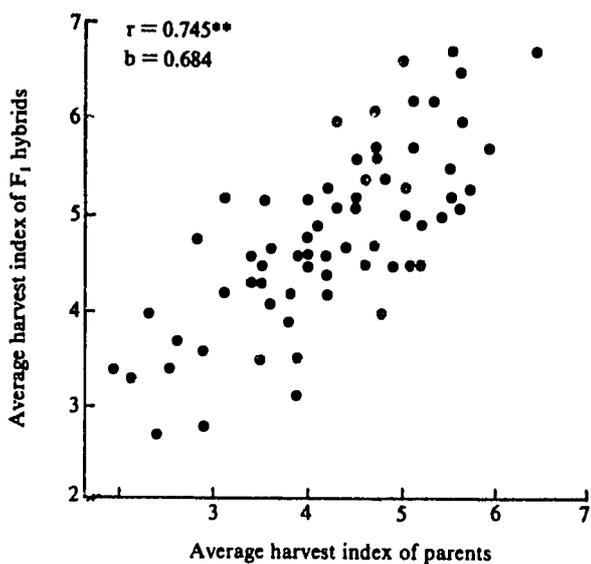


Figure 8. Relationship between average harvest indexes of parents and the respective F₁ hybrids. (Adapted from CIAT, 1975.)

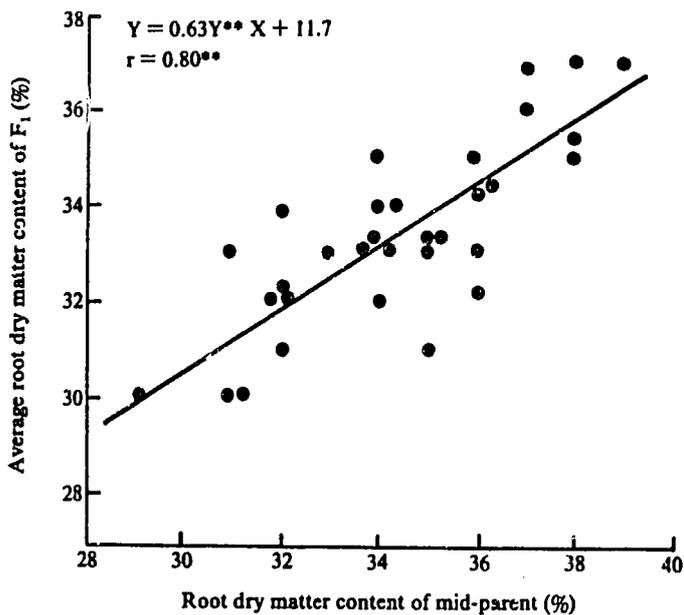


Figure 9. Regression of F₁ average against mid-parent value for root dry matter content. (Adapted from Kawano, Gonçalves, and Cenpukdæ. Unpublished data.)

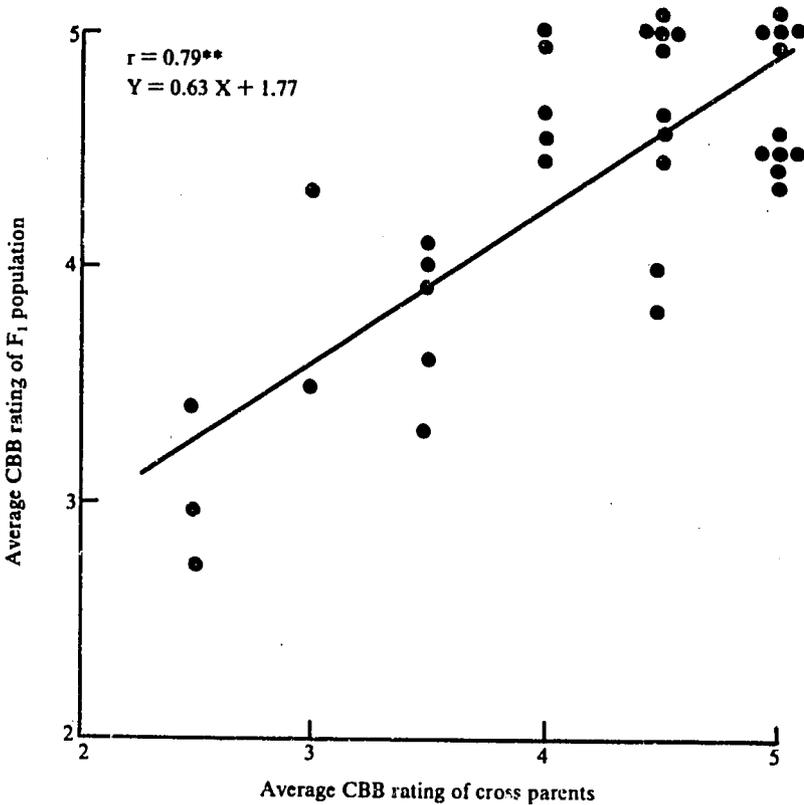


Figure 10. Relationship between parents and offspring in cassava bacterial blight (CBB) rating. (Adapted from Umemura and Kawano, 1983.)

Germplasm center and decentralized breeding program

Cassava originated and completed the major part of its evolution in Latin America. Although it was widely distributed throughout the lowland tropics of Latin America before the arrival of Europeans in the 15th century, it did not exist outside the Americas. However, in the post-Columbian era, the crop spread rapidly, first to Africa and later to Asia.

Germplasm variation of crop species is richest in the center of origin and diversification of the species. Evolution of disease and pest species that thrive on a crop is parallel to the evolution of the crop species. The number

of biological yield constraints is, therefore, highest in the center of crop origin and diversification (Jennings and Cock, 1977).

True to theory, nearly the entire germplasm variation of cassava exists in Latin America while the African and Asian germplasm consists of a part of the Latin American germplasm and its local recombinants. In Latin America there is a broad spectrum of diseases and pests, whereas in Africa the spectrum is narrower and even more so in Asia. The cassava mosaic disease in Africa and India appears to be the only major disease of cassava that does not exist in Latin America.

This background made Latin America a logical location for an international center of cassava germplasm development and consequently the Cassava Program of CIAT was established at Cali, Colombia, in the early 1970s. The specificity of African mosaic disease and the overwhelming importance of cassava to the African diet led to the establishment, in the late 1960s, of the Cassava Program at IITA, Ibadan, Nigeria, with regional responsibility in Africa.

Edaphoclimatic conditions of cassava-growing areas vary from country to country and from one area to another within a country. Quality requirements also vary depending upon utilization and location. Any new material for varietal selection must be thoroughly screened for local adaptation and other requirements.

Local germplasm is a result of generations of farmers' selections and an excellent source of adaptation to traditional cultural environments and requirements of the locality. Yet great progress, either in yield or resistance factors, is not expected as long as breeding programs use only local germplasm because, by nature, it possesses limited genetic variability. Thus, incorporating Latin American germplasm into local Asian breeding populations is desirable and inevitable.

Latin American germplasm, on the whole, offers much wider genetic variation but contains genes for local adaptation in much lower frequencies than local germplasm. Consequently, obtaining a recommendable cultivar selected from a small number of clones introduced from CIAT is unlikely. For Asian cassava-breeding programs, local selection from massively introduced CIAT seed populations, selection from local x CIAT crosses, or a combination of both becomes the most logical alternative.

Our observations on the germination of CIAT and Thai clones in the Rayong station seems to support this general tendency. CIAT clones, crossed at CIAT, germinated reasonably well with irrigation or under the

normal rainfall of 1984. However, the germination of CIAT clones was extremely low without irrigation under the very scanty rainfall of 1983, while that of the local clones, crossed at Rayong between locally selected cross parents, was acceptable. Rayong 1, a well-proven local cultivar, germinated very well under any situation (Table 4). The results support not only localized selections but also hybridization programs by national programs.

Table 4. Comparison in germination between CIAT and local clones at Rayong, Thailand.

Year	Treatment	Clone	Genotypes (no.)	Average germination (%)
1983	No irrigation	CIAT crosses	234	42.7
	No irrigation	Local crosses	135	60.4
	No irrigation	Rayong 1 (local cultivar)	1	86.6
1983	Irrigated	CIAT crosses	165	68.4
	Irrigated	Local crosses	1323	75.8
	Irrigated	Rayong 1 (local cultivar)	1	89.2
1984	No irrigation	CIAT crosses	1237	63.0
	No irrigation	Local crosses	1321	75.9
	No irrigation	Rayong 1 (local cultivar)	1	96.1

SOURCE: Field Crop Research Institute, Thailand, and Centro Internacional de Agricultura Tropical (CIAT), Colombia.

Selection environment

One of the greatest difficulties in tropical agricultural research is the transfer of experiment station results to farm production. This difficulty is even greater with cassava, which has its main areas of commercial cultivation in marginal agricultural areas.

The 12-year history of the CIAT cassava breeding program is also a history of defining selection sites. CIAT headquarters are located in the Cauca Valley of Colombia, characterized by fertile soils, a favorable rainfall pattern, and modest temperature schemes, where very little cassava is commercially grown. After a couple of years of breeding and selection at the headquarters, spectacular yield increases were demonstrat-

ed. However, it was soon evident that the elite materials were useless in more representative cassava-growing areas of the Colombian north coast, where soil fertility was low and the dry-season pressure was high. A different set of genotypes was selected which showed significant yield improvement on an experiment station located in the north coast. However, even these new elites were not as readily useful in farmers' fields as originally expected. The cultural environment at the experiment station was far better than that of the farmers so that the selection environment was not correctly representing the farmers' conditions. The CIAT cassava-breeding program suffered from a typical "experiment station vs. farmers' fields" syndrome (Kawano and Jennings, 1983).

It was only after the major selection sites were moved to a more typical cassava field on the north coast and to one of the most difficult (that is, characterized by extremely poor soil, a long dry season, and a broad spectrum of diseases and pests) cassava-growing areas in the Colombian Llanos that truly useful genotypes for difficult cassava-growing conditions were identified. One such example is CM 507-37, selected from the Llanos site, which has shown yield superiority both under low- and high-yielding environments (Figure 11). This group of genotypes, as well as selections from the cassava fields in the north coast, compose the mainstream of the CIAT cassava hybridization program.

The Thai cassava research program has its breeding headquarters in the Rayong Field Crop Research Center, where the soil fertility is generally low, the dry season is long, and rainfall is erratic—well representing the vast cassava areas managed mostly by small, poor farmers. Hybrid clones selected in Rayong seem to perform equally well or even better in less difficult cassava-growing environments outside the Rayong station (Table 5).

We can conclude that selection sites must be located in the most representative cassava production areas and the cultural practices of the selection plots must be adjusted to be within reach of the average farmers. If breeders are given a choice between easily manageable growing conditions and difficult growing conditions for the selection site, they are advised to take the greater challenge of the two.

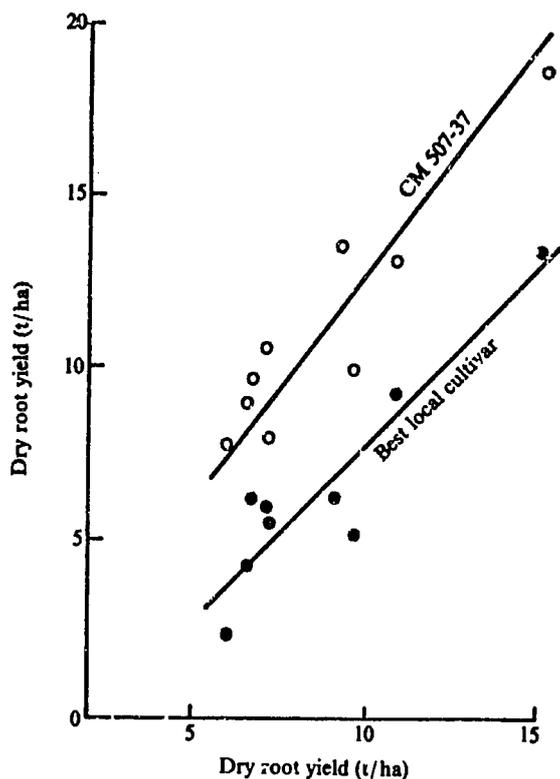


Figure 11. Regression of yields of CM 507-37 and best local cultivars on productivity level of the trial site. Productivity (dry root yield) of trial site is expressed as the mean of all varietal entries at each location. (Adapted from CIAT, 1981.)

Table 5. Yields of some promising clones grown in different environments in Thailand.

Clone ^a	Root dry yield (t/ha)			Average
	Low-yielding environment (Rayong)	Intermediate-yielding environment (Ban Mae Samrong)	High-yielding environment (Khon Kaen)	
CMR 23-29-15	9.2	11.6	15.1	12.0
CMR 23-128-141	6.6	8.9	13.8	9.8
CMR 23-149-128	7.6	8.6	11.5	9.2
CMR 23-17-251	8.7	5.7	10.6	8.3
Rayong 1 (local)	5.5	6.7	10.1	7.4

a. Crossed in 1980 and selected in 1980-1983 at Rayong station.

SOURCE: Field Crop Research Institute, Thailand.

Summary

The relatively uncomplicated flowering and pollination habit of cassava leads to easy creation of hybrids. Vegetative propagation greatly facilitates handling of genetic material of this crop. In segregating populations for single-row trials, harvest index can be used as the most important selection criterion for the final yield although effort has to be made to maintain good balance between harvest index and canopy density. Cassava and most, if not all, of its major diseases constitute horizontal pathosystems in which the resistance is characterized by slow disease development and controlled by additive polygenes. Thus, durable resistance may be obtained with relative ease. The great majority of important agronomic characters are controlled by additive polygenes, making a straightforward hybridization scheme followed by simple phenotypic selection effective in creating desirable recombinants.

While creation and manipulation of genetic materials in experiment stations are relatively easy, incorporation of exotic germplasm into hybridization and selection schemes is recommended. Special care must be taken in defining selection sites and accompanying cultural practices. Selection sites must be located in the most representative cassava production areas and the cultural practices of the selection plots must be adjusted to within the reach of the average farmer.

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Cassava Varietal Improvement in Thailand

*Sophon Sinthuprama and Charn Tiraporn**

Introduction

Cassava is considered as one of the most important economic crops in Thailand, although it is not a staple food of the Thai people. It is a cash crop produced by numerous small farmers and nearly all the harvest is processed into animal feed or starch. Second only to rice, cassava is Thailand's major export crop, making Thailand the principal cassava-exporting country in the world. In 1983 the country exported 7.9 million tons of cassava products, earning US\$731 million. About 95% of the production is exported, mostly as pellets (90%), followed by chips (6%), and flour (4%). The most important market is the European Economic Community (EEC), amounting to 4.5 million tons in 1983. Domestic use is about 5%, in the form of starch for industrial use and pellets for animal feed.

In Thailand cassava occupies the third largest area next to rice and corn (Table 1). The area under cassava increased from about 328,000 ha in 1972-1973 to over 1.3 million ha in 1982-1983 (Table 2). The minor fluctuations from year to year are mainly the result of price fluctuations which, in turn, are influenced by the foreign market.

In the past, the main cassava area was the eastern part of the central plain region. Today, this has shifted to the northeast region, which accounts for 60% of the total area, followed by the central plains (37%), and the north (3%). Total cassava production increased more than fourfold in the past 10 years, from about 4 million tons in 1973 to about 19.3 million tons in 1983 (Table 2), registering a high growth rate of 19.3% per annum. The increase took place almost entirely because of increased planted area. There was no increase in yield during this period, with national averages ranging from 12-16 t/ha.

* Field Crop Research Institute, Department of Agriculture, Thailand.

Table 1. Planted area and production of major field crops in Thailand, 1981-1982.

Crop	Planted area (ha in thousands)	Production (t in thousands)
Rice	9,590	17,774
Corn	1,570	3,448
Cassava	1,270	17,744 ^a
Mung bean	486	283
Sorghum	280	273
Scybean	127	131
Peanut	122	146

a. Fresh root.

SOURCE: Field Crop Research Institute, Thailand.

Table 2. Cassava area, production, and yield in Thailand.

Year	Area (ha in thousands)	Production (t in thousands)	Yield (t/ha)
1972-1973	328	3,974	12.1
1973-1974	432	5,668	13.1
1974-1975	473	6,240	13.2
1975-1976	593	8,100	13.6
1976-1977	679	10,138	14.5
1977-1978	960	12,372	12.9
1978-1979	1,010	15,048	14.9
1979-1980	1,041	11,136	10.7
1980-1981	1,270	17,744	14.0
1981-1982	1,236	17,788	14.4
1982-1983	1,385	19,316	13.9

SOURCE: Office of Agricultural Economics, Thailand.

Production systems and principal constraints

Edaphoclimatic conditions

In the two major cassava-growing regions (northeast and central plains) the rains begin in May (over 100 mm/month) and end in October. Both regions are predominantly dry for 6 consecutive months (November to April), receiving less than 50 mm rainfall per month.

Cassava is grown mostly on gray Podzolic soils which are highly leached with a low base saturation (35%-50%) and low amounts of nitrogen, available phosphorus, and potassium. They are light in structure and moderately to excessively drained. Available moisture storage ranges from 60-80 mm per metre of soil. The pH is 5.0-6.0 in the surface soil and decreases with depth. Subsoil pH ranges from 4.5-5.0 in the subsurface to as low as 3.8-4.0 at the lowest depth.

Cultivars

Fresh cassava roots for direct human consumption are grown on a small scale for making desserts. Only one cultivar of this type, Ha Na Tee, is known and is planted on a very small scale. Cassava for industrial use is grown on a much larger scale for pellet and chip making and for starch extraction.

The great majority of the cassava area is planted with a single genotype, Rayong 1. All evidence shows that it is a typical farmers' cultivar. Yet Rayong 1 is basically high yielding and its flexibility under suboptimal conditions is striking. It is suitable for harvest in 12 months or more, but it is not an ideal type for early harvest. Hence, it is not suitable for relay or sequence cropping systems. The selection and recommendation of Rayong 1 has been one of the most important factors of successful cassava production in Thailand.

Biological yield constraints

Cassava bacterial blight (CBB) caused by *Xanthomonas campestris* pv. *manihotis* is the only major disease of cassava that is widespread in the country. Rayong 1 is susceptible to CBB, although, it is not known how much economic damage CBB is causing. Brown leaf spot caused by *Cercosporidium henningsii* and mites (*Tetranychus truncatus*) are commonly observed, but their effects on yields are not well understood.

At present, Thai cassava faces a small number of disease and pest problems. However, this is no guarantee for the future because of the dynamic nature of biological yield constraints. With more than 1 million ha planted to a single genotype, the crop is extremely vulnerable to any change in the disease or pest pattern. Diversification of cassava genotypes is important and care should be taken to avoid accidental introduction of diseases and pests.

Varietal improvement program

A national average yield of 14 t/ha is rather low compared with experimental yields of 50 t/ha or more in Thailand and at the Centro Internacional de Agricultura Tropical (CIAT) in Colombia. There are also clones with much higher contents of root dry matter than Rayong 1. Hence, there appears to be considerable potential for yield improvement through breeding.

Germplasm introduction. Before 1960, some 20 cultivars were introduced to Thailand, probably from Malaysia, Java, and Mauritius (Table 3). From this stock, the venerable Rayong 1 emerged. More clones were introduced from Java in 1963 and from the Virgin Islands in 1965. The first introduction from CIAT took place in 1970.

Table 3. Introduction of cassava germplasm to Thailand (through the Thai Department of Agriculture).

Year	Number of genotypes introduced	Origin
Before 1960	about 20 cultivars	Malaysia, Java, Mauritius
1963	7 cultivars	Java
1965	44 clones	Virgin Islands
1970	5 cultivars	CIAT ^a Colombia
1975	900 seeds	CIAT
1977	10 clones 6170 seeds	CIAT CIAT
1978	7720 seeds	CIAT
1979	10 clones	CIAT
1980	3050 seeds	CIAT
1981	1400 seeds	CIAT
1982	7450 seeds	CIAT
1983	7900 seeds	CIAT
1984	6650 seeds	CIAT

a. CIAT = Centro Internacional de Agricultura Tropical.

SOURCE: Field Crop Research Institute, Thailand.

Introduction of CIAT germplasm through true seed was begun in 1975. Ten hybrid clones were introduced in the form of meristem culture from CIAT in 1979. Introduction of CIAT seed populations from better defined cross parents started in 1982. Many introductions are now being utilized in the breeding program.

Germplasm introduced from CIAT contributed to an important increase in genetic variation. Many crosses were made between Thai and CIAT clones each year, supplemented by some crosses between Thai clones. Many hybrid seeds from CIAT have also been directly incorporated into testing. From the CIAT hybrid seeds introduced in 1975, two cultivars were developed, Rayong 2 and Rayong 3.

Rayong 1. Cassava breeding research began with the collection of local cultivars throughout the country and their systematic evaluation in 1956 at Rayong Field Crop Research Center, Rayong Province. There were few genotypes and the leading cultivar from many locations was identified as being of the same genotype. It was called Local Rayong, to be used in comparison with introduced cultivars. It appeared that Local Rayong yielded better than the introduced cultivars, and was, therefore, renamed Rayong 1 by the Department of Agriculture in 1975.

Breeding program. A breeding program based on open-pollinated seeds from Rayong 1 and introduced cultivars was begun in 1971. Not much was gained from the selections from open-pollinated seeds. Controlled hybridization started in 1975 by utilizing limited germplasm from Java, the Virgin Islands, and CIAT. With the return of researchers trained at CIAT since 1977, the breeding program at Rayong Center formed the core of the national program.

The major objectives of the cassava breeding program are:

High yield in terms of dry matter and starch production per unit area;

Good adaptation to local production environments, including adverse soil conditions and drought tolerance;

Early maturity;

Diversification of germplasm, including resistance to diseases and pests; and

Good plant type for intercropping and ease of harvest.

Breeding for high yield is based not only on yield but also on high harvest index and high root dry matter. High-yielding cultivars will contribute to higher productivity, hence, lowering the cost of production and gaining higher competitiveness against feed grains. Higher dry matter content will lead to lower product costs through lower costs of processing.

Breeding for early maturity is done by high yield selection at early harvest. Early cultivars will increase the opportunities for better land use, cropping systems, and crop rotation to avoid soil erosion. Breeding for pest resistance emphasizes CBB and mites. Breeding for drought tolerance also aims at finding cultivars suitable for late rainy-season plantings.

Varietal testing

Hybridization. Some 12,000-20,000 seeds from 200-250 crosses are obtained every year at the Rayong Center. The majority of these come from controlled pollinations among Thai and CIAT clones. Some open-pollinated seeds are also collected. About 6000-8000 hybrid seeds introduced from CIAT are added to these every year.

Seedling trials. From 15,000-20,000 F_1 seeds are planted annually. Selection is based on plant vigor, disease and insect incidence, harvest index, and yield. About 10% of the plants are selected for single-row trials.

Single-row trials. Selected plants from the seedling trials are planted in single rows of 10 plants. Every 10 rows, Rayong 1 is planted as a check variety. About 10%-20% selection is practiced, based on designed objectives.

Preliminary yield trials. Selected clones from the single-row trials are planted in 5 x 12 m plots with two replications at the Rayong Center.

Standard yield trials. About 20 clones are evaluated in 5 x 12 m plots with four replications in two or three major cassava stations.

Regional yield trials. About 10-15 clones including local cultivars are evaluated in 5 x 12 m plots with four replications in 6 to 10 stations scattered in major cassava-growing areas.

Farmers' field trials. Promising clones from regional yield trials (usually three to five) are tested in farm trials in 5 x 12 m plots with four replications. The trials are conducted on farmers' land and with farm labor but managed by the researchers. The number of trials depends on the resources available.

Farmers' field tests. The best clones are compared with the farmers' crop in farmers' fields using farmers' techniques. Many large plots (1600 m²) are required. Extension workers of the Department of Agricultural Extension participate in the evaluation along with the farmers. When the best material is approved, it is named and released by the Department of Agriculture.

Production of planting material. Promising clones are multiplied on a small scale in research stations. Once a cultivar is named and released, limited multiplication plots are kept in the research stations. This material is turned over to the extension workers from the Department of Agricultural Extension, who in turn use it for demonstration and multiplication in selected farmers' fields.

Distribution of planting material. Distribution of a released cultivar to farmers is done mainly by extension workers. Materials are obtained from selected farmers in the previous season. Research stations also distribute materials to nearby farmers.

Achievements

Recommended cultivars

Rayong 1 is basically a farmers' cultivar. However, it was collected, selected, purified, named, and recommended by the Department of Agriculture. It is a high-yielding cultivar with a moderately high harvest index. Production of high-quality stakes and good sprouting under dry conditions make this cultivar highly versatile. Data from CIAT suggest that Rayong 1 is superior to most Latin American cultivars under conditions similar to the Thai cassava areas.

Rayong 2 was selected from hybrid seeds of the CM 305 cross, introduced from CIAT in 1975. Its fresh root yield, dry matter content, and starch content (calculated from the Reimann scale) are similar to Rayong 1 (Table 4). This cultivar is good for making fried chips and other products for table use and outyields Ha Na Tee, a traditional table-type cultivar (Table 5). Its yellow flesh is high in carotene. Some agronomic characteristics of Rayong 2, which was released in 1984, are shown in Table 6.

Rayong 3 was developed from the hybrid seed of the CM 407 cross which was introduced from CIAT in 1975. The results of experiments conducted from 1979 to 1984 showed that dry matter content and starch content of Rayong 3 were higher than Rayong 1 and root yield was similar

to Rayong 1 (Table 7). Some characteristics of Rayong 3 are compared with those of Rayong 1 in Table 8. Higher starch content brings a higher price for Rayong 3 roots. The price differs by US\$0.74 per ton for each 1% of starch. Higher dry matter content of Rayong 3 is also welcomed by the chippers because it requires a shorter time to dry.

Table 4. Yields of Rayong 1 (R1) and Rayong 2 (R2) in various trials in Thailand, 1979-1984.

Trial	No. of trials	Fresh yield (t/ha)		Dry yield (t/ha)		Dry matter (%)		Starch content (%)	
		R1	R2	R1	R2	R1	R2	R1	R2
		Preliminary	1	32.1	43.0	9.8	12.9	30.5	30.0
Standard	5	28.8	25.9	7.8	7.4	26.8	24.7	16.3	14.3
Regional	21	28.2	27.4	9.5	7.8	34.1	33.9	21.4	22.6
Onfarm	18	20.8	17.4	5.9	4.5	28.2	26.2	17.6	15.6
Average		24.3	22.5	7.3	6.7	30.3	29.2	19.6	18.5
Relative to R1 (%)		100	93	100	92	100	96	100	94

SOURCE: Field Crop Research Institute, Thailand.

Table 5. Comparison of fresh root yields between Rayong 2 and Ha Na Tee cultivars in various research stations and farmers' fields, 1984, Thailand.

Trial	Location	Fresh root yield (t/ha)	
		Rayong 2	Ha Na Tee
Regional	Khon Kaen	20.4	18.2
Regional	Ubon	22.7	19.0
Regional	Ban Mae Samrong	16.0	10.3
Farmers' fields	Patthalung	16.2	12.3
Farmers' fields	Nakhon Ratchasima	13.4	12.3
Farmers' fields	Nakhon Ratchasima	13.0	10.6
Average		17.3	13.9
Relative to Ha Na Tee (%)		124	100

SOURCE: Field Crop Research Institute, Thailand.

Table 6. Characteristics of Rayong 2 compared with Rayong 1, 1984, Thailand.

Characteristic	Rayong 2	Rayong 1
Height (cm)	285	282
Outer root skin color	Light brown	Cream
Flesh color	Light yellow	White
Root yield (t/ha)	21.5	23.5
Dry matter content (%)	29.8	30.8
Starch content (%)	19.0	20.0
HCN ^a (peeled root) (ppm)	24	43
Carotene (μ g/100 g)	502	80
Vitamin A (IU/100 g)	83	130
CBB ^b resistance	Moderately susceptible	Moderately susceptible

a. HCN = hydrogen cyanide.

b. CBB = cassava bacterial blight disease.

— SOURCE: Field Crop Research Institute, Thailand.

Table 7. Yields of Rayong 1 (R1) and Rayong 3 (R3) in various yield trials from 1979 to 1984, Thailand.

Trial	No. of trials	Fresh yield (t/ha)		Dry yield (t/ha)		Dry matter (%)		Starch content (%)	
		R1	R3	R1	R3	R1	R3	R1	R3
		Preliminary	1	32.1	40.7	9.8	15.4	30.5	37.9
Standard	5	28.8	24.8	7.8	8.1	26.8	32.2	16.3	20.8
Regional	23	27.2	22.8	9.0	8.8	33.2	38.5	22.1	26.6
Onfarm	81	20.5	28.4	6.0	6.7	29.4	36.6	18.7	24.8
Average		22.5	19.7	6.7	7.3	30.0	37.0	19.2	25.2
Relative to P.1 (%)		100	88	100	109	100	132	100	132

SOURCE: Field Crop Research Institute, Thailand.

Table 8. Characteristics of Rayong 3 compared with Rayong 1, Thailand.

Characteristic	Rayong 3	Rayong 1
Height (cm)	174	282
Fresh root yield (t/ha)	19.7	22.5
Dry matter content (%)	37.0	30.0
Dry yield (t/ha)	7.3	6.7
Starch content (%)	25.2	19.2
Starch yield (t/ha)	5.0	4.3
Harvest index	0.57	0.45
HCN ^a in roots	Medium	High
CBB ^b resistance	Moderately susceptible	Moderately susceptible

a. HCN = hydrogen cyanide.

b. CBB = cassava bacterial blight disease.

SOURCE: Field Crop Research Institute, Thailand.

Promising clones

Currently, the best selection sources are the crosses between Thai and CIAT clones. They are particularly good for early harvest. One selected hybrid clone, CMR 24-63-43, is outyielding Rayong 1 by 40% in fresh yield and 50% in dry yield when harvested at 6-7 months (Table 9). At a 12-month harvest, the clone OMR 23-29-15 is outyielding Rayong 1 by 40% in fresh yield and 54% in dry yield. Its starch content is also higher than Rayong 1 (Table 10).

New cultivars in farmers' fields

Rayong 3 was released in 1983. Planting material had been multiplied in farmers' fields simultaneously with the final evaluation. Materials harvested in 1984 were distributed to farmers to grow in about 100 ha to be harvested in 1985.

The results of 1983 and 1984 in farmers' fields showed that Rayong 3 yielded 19.2 t/ha fresh root with 36.0% dry matter content, giving 6.9 t/ha dry yield (Table 11). Starch content, dry matter content, and dry yield of Rayong 3 were higher than those of Rayong 1. Yields of Rayong 1 and Rayong 3 in farmers' fields were lower than their yields in research stations, but yields of Rayong 3 declined less than those of Rayong 1.

Table 9. Comparison between yields of a promising early clone, CMR 24-63-43 (CMR), and Rayong 1 (R1) in various trials, harvested at 6-7 months, Thailand.

Year	Trial	No. of trials	Fresh yield (t/ha)		Dry yield (t/ha)		Dry matter (%)		Starch content (%)	
			R1	CMR	R1	CMR	R1	CMR	R1	CMR
1982-1983	Prelim.	1	15.2	23.3	5.4	9.4	35.4	40.0	24.1	28.8
1983-1984	Standard	2	18.2	23.4	6.7	8.3	36.8	35.3	25.3	24.0
	Average		16.7	23.3	6.0	8.9	36.1	38.1	24.7	26.4
	Relative to R1 (%)		100	139	100	148	100	105	100	107

SOURCE: Field Crop Research Institute, Thailand.

Table 10. Comparison between yields of a promising clone, OMR 23-29-15 (OMR), and Rayong 1 (R1) in various trials, Thailand.

Year	Trial	No. of trials	Fresh yield (t/ha)		Dry yield (t/ha)		Dry matter (%)		Starch content (%)	
			R1	OMR	R1	OMR	R1	OMR	R1	OMR
1982-1983	Prelim.	1	19.9	23.5	5.3	7.4	26.9	31.6	16.4	20.7
1983-1984	Standard	2	25.2	37.4	7.2	11.5	28.5	30.7	17.9	19.9
	Average		23.5	32.8	6.6	10.2	28.0	31.1	17.4	20.2
	Relative to R1 (%)		100	140	100	154	100	111	100	114

SOURCE: Field Crop Research Institute, Thailand.

Table 11. Comparison between experiment station yields and farmers' yields for Rayong 1 (R1) and Rayong 3 (R3), Thailand.

Location	No. of trials	Fresh yield (t/ha)		Dry yield (t/ha)		Dry matter (%)		Starch content (%)	
		R1	R3	R1	R3	R1	R3	R1	R3
Exp. stations	25	27.7	23.7	8.8	8.9	31.9	37.4	21.0	25.6
Farmers	42	21.5	19.2	6.2	6.9	29.0	36.0	18.3	24.3
Relative to stations (%)		78	81	70	77	91	97	87	95

SOURCE: Field Crop Research Institute, Thailand.

Constraints and prospects

Thai farmers prefer to adopt new cultivars in the hope that higher yield and higher price can be attained without large additional costs. The major constraint in releasing a new cultivar is the low propagation rate of cassava which makes availability of large quantities of planting material difficult. There is no government or private cassava multiplication farm available. Starting with about 100 ha of Rayong 3 in 1984, and a multiplication rate of 1 to 10, it would require at least five to six years to plant this cultivar in 0.6 million ha, half of the total cassava planting area.

Rapid propagation techniques or simple two-node propagation may help hasten production of planting material and distribution of newly released cultivars, but these methods may involve high costs.

Large yield increases through new cultivars will not be realized in the near future. Rayong 3 offers higher starch content. However, it may not replace Rayong 1 on a large scale because its total dry matter yield does not much exceed that of Rayong 1. There are a number of promising hybrid clones being developed for high yield and early maturity, but it will take some time before any of these pass to production fields.

Whether we can obtain new clones whose yielding capacity is sufficiently high to significantly reduce production costs depends on future work. Higher yielding cultivars will provide the opportunity for better competition in the international market. Higher yielding cultivars also may help farmers to withdraw cassava from erosion-threatened areas. Early cultivars, on the other hand, will increase chances for better land use through better cropping systems and rotation to avoid soil erosion.

Summary

Cassava is one of the most important economic crops in Thailand. It is produced by small farmers and its products are exported mainly to the EEC. The production has steadily increased during the last two decades through expansion of planted area. The national average yield has been stagnant at about 14 t/ha, which is higher than the world average, yet low compared with the potential of the crop.

Major production problems are declining soil fertility, soil erosion, and limited genetic diversity of the crop. The research network of the Department of Agriculture has identified the high-yielding, versatile

cultivar, Rayong 1. Latin American germplasm provided by CIAT in Colombia is now well incorporated into the breeding system. High-yielding capacity and early maturity are important selection targets.

The Thai cassava breeding program includes every step of varietal improvement. Selected clones are evaluated in research stations located in the major cassava-planting areas. Extension workers and farmers are involved in testing the promising clones before the release of new cultivars.

Recently, two cultivars, Rayong 2 and Rayong 3, were released. Both were developed from CIAT hybrid seeds. Rayong 3 contains high starch and dry matter content. Rayong 2 is good for table use. These two cultivars have performed well both in research stations and farmers' fields. There are now many promising clones with high-yielding ability and earliness at various stages of evaluation.

A superior cassava cultivar will provide opportunity for reducing the costs of production, increasing farmers' income, and making the product more competitive in the international market.

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From Advanced Cassava Lines to Farmers' Fields: Nigeria

James E. Okeke and L. S. O. Ene*

Introduction

Cassava (*Manihot esculenta* Crantz) has been in cultivation in Nigeria for over 400 years (Mauny, 1953) and is one of the oldest Nigerian food crops. It provides the daily carbohydrate needs of over half the population of the country and sustains the people (estimated as being between 90 and 100 million) during adverse situations when other food crops fail. Its importance has increased with the diversification of the use of its roots in industry and in feed for poultry and livestock. Nigeria currently produces 12 million tons on 1.2 million hectares as against an estimated potential demand of 24 million tons.

Cassava is usually planted in mixtures with maize, yams, and vegetables. Most of the cassava is grown in the southern half of the country between latitudes 5° N and 10° N under humid tropical rainforest conditions. The "bitter" varieties are commonly grown in the southern belt, largely under subsistence technology with low yields of 6 t/ha and 8-10 t/ha in mixed and single cropping systems, respectively. The northern savanna and Sahel regions (above latitude 10° N with rainfall of less than 1000 mm in 3 months of the year) grow the "sweet" types which are boiled and consumed as food (*rogo*) without processing to remove the cyanogenic glucoside. Frequent droughts in these parts have, however, necessitated massive cultivation of bitter varieties alongside the sweet types for making *gari*, a fermentation product of the bitter varieties and the staple carbohydrate across the country.

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Production constraints

Only about 20% of the potential productivity of the cassava crop is realized by the great majority of Nigerian farmers who produce over 90% of the total national output from fragmented holdings of 0.2-0.5 ha. The main constraint is the low yield potential of indigenous varieties which have evolved over the centuries and adapted to specific ecosystems and cultivation practices. Because cassava planting materials are bulky, there has been limited exchange of varieties among farmers and, therefore, limited crop improvement through selection from "natural" hybrids and recombinants.

Genetic improvement

Breeding objectives at the National Root Crops Research Institute (NRCRI) are based on primary production constraints. These are mainly inherently low-yielding cassava varieties, which are also susceptible to pests and diseases. Thus, the emphasis in Nigeria has been on the development of high-yielding varieties with good quality characteristics that are resistant to pests and diseases. Early attempts (about 1940) were made at collecting and introducing promising materials (Umanah, 1977). As a result, the Gold Coast Hybrid 7 (GCH 7) was selected, having an average yield of 9 t/ha and a yield improvement of 28% over local varieties. Consistent and systematic cassava improvement started with the introduction by Beck and Chant (1958) of an interspecific hybrid, 58308, from Amani in East Africa. This hybrid clone has a high general combining ability for resistance to cassava mosaic disease (CMD) and cassava bacterial blight (CBB), and has low hydrogen cyanide content (Hahn et al., 1979). Great leaps were made in the 1970s with the release of high-yielding varieties which were also resistant to CMD and CBB (IITA, 1980). The International Institute of Tropical Agriculture (IITA), in collaboration with NRCRI, conducted systematic ecological adaptation trials and made recommendations for various zones of Nigeria.

The emergence of the cassava mealybug (CMB) (*Phenacoccus manihoti* Mat.-Ferr.) and green spider mite (CGM) (*Mononychellus tanajoa* (Bondar)) in Nigeria in 1979 (Akinlosotu and Leuschner, 1979) posed a serious breeding problem. NRCRI screened its 1002 accessions in the germplasm collection along with the improved varieties already in use by farmers. So far, no cassava variety with immunity to the pests has been identified at NRCRI. However, 82 varieties with good levels of tolerance

to the pests were selected. They constitute a promising source population which is being improved, using cyclic recombinations and selection procedures. The variety 58308 is used in both controlled and open crosses to ensure desirable parental gene contribution. Hybrid clones are subjected to various levels of selection pressure for 3 years before reaching advanced yield trials. Selection parameters include resistance/tolerance to pests and diseases, yield, tuber shape, starch content, dry matter, and yield of various derived food products. Table 1 shows currently recommended improved varieties and their performance in comparison with indigenous varieties.

Table 1. Performance of improved cassava varieties compared to local varieties, 1982-1983, Nigeria.

Variety	Fresh root yield (t/ha)	Mean increase over local variety (%)	Dry matter (%)	Gari yield (t/ha)	Foofoo yield (t/ha)	Reaction ^a to	
						Diseases ^b	Pests ^c
Improved							
U/41044	37.0	220	28.4	6.7	7.4	HT	T
U/7706	35.5	208	30.0	7.0	7.7	R	T
NR/8231 ^d	35.2	206	28.0	6.9	7.2	R	T
NR/8208 ^d	31.0	170	32.0	7.3	7.7	R	T
TMS 30555 ^e	32.5	182	26.2	4.2	5.4	R	T
TMS 30211	28.0	143	25.0	3.9	4.2	R	T
TMS 30572	23.1	100	31.3	4.2	5.6	R	T
TMS 50395	32.7	180	26.2	4.3	4.9	R	T
TMS 50207	30.0	160	25.9	4.2	4.5	R	T
TMS 30001	21.8	89	27.9	3.3	3.7	R	T
Unimproved							
Nwugo	12.2	0	35.3	2.7	3.6	P	P
53101	10.8	0	34.0	2.5	2.9	P	P

a. HT = highly tolerant; T = tolerant; R = resistant; P = poor.

b. Diseases were: cassava mosaic disease and cassava bacterial blight.

c. Pests were: cassava mealybug and cassava green spider mite.

d. Currently under multiplication for distribution.

e. The TMS series was released by International Institute of Tropical Agriculture (IITA).

SOURCE: NRCRI (National Root Crops Research Institute). 1984. Briefs on cassava.

Multiplication and distribution

A nationwide program for the production and distribution of cassava planting material was initiated in Nigeria against a background of declining supply caused by CMB and CGM and the inherently low multiplication rate of cassava relative to the grains. The national research agencies, IITA, and the National Seed Service (NSS) are improving the availability of cassava planting material through research for better multiplication methods and active distribution.

Methods of increasing stake production

Pruning and spacing. Studies were carried out at Umudike (lat. 5°29' N, long. 7°35' E, elevation 122 m) in 1979 and 1980 on the effect of pruning and spacing on the production of stakes. Results showed that the multiplication rate of 1 ha of mature cassava to 14 ha of new crop can be increased to 1:30 by pruning stems every four months over a 12-month period (Table 2). The efficiency of the practice, however, depended on the

Table 2. Mean number of 20-cm stakes produced by cassava varieties 60506 and Nwugo as affected by pruning frequency and spacing, Nigeria.

Spacing (cm)	Pruning frequency over 12 months	Stakes (thousands/ha) ^a produced by variety	
		60506	Nwugo
100 x 100	No pruning	135	140
	Every 6 months	195	175
	Every 4 months	210	213
	Every 3 months	202	198
75 x 100	No pruning	170	200
	Every 6 months	216	232
	Every 4 months	315	294
	Every 3 months	240	216
50 x 100	No pruning	225	202
	Every 6 months	220	210
	Every 4 months	284	270
	Every 3 months	238	240
25 x 100	No pruning	190	180
	Every 6 months	193	200
	Every 4 months	238	241
	Every 3 months	205	198

a. SE \pm 5.8.

SOURCE: NRCRI (National Root Crops Research Institute). Annual report, 1980. Nigeria.

variety. Closer spacing within the row on 1-metre ridges increased the number of stakes significantly. The best arrangement was planting at 0.75 x 1 m and pruning once every 4 months for 12 months.

Node number and planting position. In studies using three varieties (60506, TMS 30395, and TMS 30211), it was shown that vertical, horizontal, or angular (40° - 45°) planting position had no effect on the number of 20-cm stakes produced (Table 3). However, stake production was significantly affected by node number and variety. Ten-node stakes produced significantly higher numbers of stakes than 2- or 4-node stakes. Generally, production of planting material increased with higher number of nodes on the stake. Significant varietal differences were also observed.

Table 3. Effect of node number and planting position on production of 20-cm stakes from three cassava varieties in a rainforest zone, Umudike, Nigeria.

Variety ^a	Planting position ^b	Stakes (thousands/ha) according to no. of nodes ^c				
		2	4	6	8	10
TMS 30395	Horizontal	140	240	241	326	315
	Vertical	220	260	410	404	467
	Inclined	287	301	390	390	410
TMS 30211	Horizontal	197	212	298	229	278
	Vertical	200	273	290	315	393
	Inclined	157	229	253	327	377
60506	Horizontal	123	138	179	136	226
	Vertical	0	158	147	180	192
	Inclined	0	207	165	292	342

a. SE for variety mean: $\pm 29,000$.

b. SE for planting position: $\pm 13,000$.

c. SE for node number: $\pm 31,000$.

SOURCE: NRCRI (National Root Crops Research Institute). Annual report, 1981. Nigeria.

Rapid multiplication techniques. The rapid propagation techniques of Wholey and Cock (1977) and Cock et al. (1976) were studied and adapted for farmers' use. Ene (1978a) studied some factors affecting production of propagules and recommended the period between November and April as the best season for propagule production. A method for massive production of propagules was described in another study (Ene, 1978b). It was shown that one mature plant could, within 14 months, produce from about 30,000 to 60,000 propagules which could perform as well as normal 20-cm

stakes in terms of root yield and production of dry matter and starch. Sterile conditions and humidity chambers were maintained in these studies as they are essential for obtaining disease-free propagules. The methods of Lozano and Wholey (1974) and Porno et al. (1976) to obtain disease-free materials were also tried.

Okeke (1981) studied a rapid multiplication technique using healthy cassava cultivars in which the type of rooting medium and sterilization of media were investigated. It was found that unsterilized soil was as good as other media for rooting stakes: propagules rooted best and accumulated the greatest amount of dry matter within 47 days in unsterilized soil (Tables 4 and 5). It was concluded that for rapid multiplication of improved, disease-free materials, a farmer would require a nursery bed of

Table 4. Effect of growth media on stake sprouting and linear growth rate of propagules.

Growth medium	Mean no. propagules per stake after 34 days ^a		Mean linear growth rate (cm/day) after 47 days ^b	
	Sterilized	Unsterilized	Sterilized	Unsterilized
Soil: compost (1:1)	8.6	8.6	0.33	1.05
Soil: compost (2:1)	8.1	8.3	0.40	0.56
Soil: compost (1:2)	9.1	9.4	1.03	1.32
Soil + N-P-K-Mg	9.5	9.8	0.49	0.94
Soil	9.3	9.7	0.48	1.06

a. SE \pm 0.34.

b. SE \pm 0.06.

SOURCE: Okeke et al., 1986, p. 200.

Table 5. Effect of growth media on top growth of propagules.

Growth medium	Mean dry weight after 47 days (g/plant)
Distilled water	4.30
Sterilized soil	3.95
Unsterilized soil	5.80
Sterilized soil + N-P-K-Mg	2.59
Unsterilized soil + N-P-K-Mg	5.06
Sterilized soil: compost (1:1)	3.16
Unsterilized soil: compost (1:1)	3.72

SOURCE: Okeke et al., 1986, p. 200.

well-drained soil near a water source, shade, and polyethylene bags. This method has proved successful in the rapid multiplication of breeder's materials.

Institutional arrangement

The NSS of the Federal Department of Agriculture in Nigeria has the responsibility, country-wide, to produce foundation seed, including cassava stakes. Its sources of supply are IITA and NRCRI. The NSS supplies the various state multiplication units with certified seed for distribution to their farmers. It has three regional centers where stage II foundation seed is produced for distribution to state ministries of agriculture in the cassava belt of Nigeria. The NSS also engages contract growers to help in the multiplication of improved cassava varieties.

The federal government assists the Cassava Multiplication Programme by:

Creating a grid of multiplication plots for elite cassava varieties in locations close to states that will receive the stakes;

Assisting with a grant of US\$700/ha for up to 15 ha; and

Assisting the research centers with funds for the rapid multiplication of desirable cassava clones.

Participating states are responsible for providing trucks for transportation and monitoring the sites to ensure good husbandry, clean materials, and pure stands of the improved varieties.

Impact of improved varieties

The improved cassava varieties are first distributed to farmers registered under the National Accelerated Food Production Program (NAFPP), together with production technology packages. Results from "minikit" trials show that substantial genetic improvement has been achieved. Table 6 shows that there were differences among locations and that fertilizer input was necessary to elicit appreciable responses from most of the improved varieties. However, the farmers' preferences constitute the key to wide adoption of any improved varieties. Results of a survey of farmers' preferences made in four states in the southeastern cassava belt are presented in Table 7. The preferences were based on yield, *gari* and *fofofo* qualities, and pest and disease resistance.

Table 6. Root yields (t/ha) according to treatment and variety in minikit trials, Nigeria, 1979.

Treatment and cultivar	Location							
	Mbom	Ukwa	Umuahia	Ariam	Izombe	Ngwa	Ahiaeke	Afara
Fertilized								
TMS 30572	35.7	36.1	42.2	30.0	30.4	31.5	38.4	8.6
TMS 30568	34.0	33.6	21.9	35.5	25.0	36.6	44.2	—
TMS 30211	40.6	35.1	—	—	52.3	40.2	38.4	34.6
TMS 30555	16.1	34.3	—	41.2	19.2	45.6	29.2	8.2
Local	19.5	45.4	20.3	25.0	22.0	49.7	30.0	10.0
U/42046	—	—	5.8	—	—	—	—	—
1525	—	—	16.1	—	—	—	—	—
U/41044	—	—	—	49.2	—	—	—	23.5
Unfertilized								
TMS 30572	7.2	25.4	26.4	24.4	21.3	—	—	8.2
TMS 30568	13.4	5.1	22.3	25.6	22.2	—	—	—
TMS 30211	16.9	4.4	—	—	16.4	—	—	34.4
TMS 30555	9.1	15.1	—	18.0	10.0	—	—	4.8
Local	9.0	19.3	22.3	15.1	16.5	—	—	6.8
U/42046	—	—	24.9	—	—	—	—	—
1525	—	—	29.0	—	—	—	—	—
U/41044	—	—	—	19.8	—	—	—	11.5

SOURCE: Proc. 5th NAFPP (National Accelerated Food Production Program) Workshop, Umudike, Nigeria, 1981. p. 18.

Table 7. Cassava varieties preferred by farmers in four southeastern states of Nigeria.

Rank	State			
	Imo	Anambra	Rivers	Cross River
1	TMS 30572	TMS 30572	TMS 30211/TMS 30001	Local
2	Local	Local	TMS 30555	TMS 30211
3	30372/30395A	TMS 30211	TMS 30572	30395A
4	1525	—	TMS 30555/Local	U/41044

SOURCE: Proc. 5th NAFPP (National Accelerated Food Production Program) Workshop, Umudike, Nigeria, 1981. p. 40.

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From Advanced Cassava Lines to Farmers' Fields: Philippines

*Algerico M. Mariscal**

Background to varietal improvement

Cassava (*Manihot esculenta* Crantz) has been cultivated in the Philippines since before World War I on subsistence farms, using only the traditional varieties. During World War II cassava became a staple for the many Filipinos who sought refuge in the mountains. Several early workers attempted to investigate the crop's potential in the production of starch, flour, animal feeds, and alcohol (Roxas and Mario, 1921; Sison, 1921). Realizing the multiple uses of cassava, the Philippine Congress passed the Republic Act 657, known as the Cassava Flour Law in 1951 (Acena, 1953). This Act encouraged and promoted the production, processing, and consumption of cassava flour as a measure to conserve dollars and regulate the importation of wheat. After that, however, very little effort was expended to improve cassava production, possibly because of the lack of outstanding varieties and lack of strong support from the agencies involved.

Early work on cassava focused on production and utilization problems (Molinyawe, 1967). Breeding activities were mainly variety trials of a few local and introduced varieties. Recognizing the potential of root crops, the Philippine Council for Agriculture and Resources Research (PCARR)¹ conceived in 1973 a national program for research on root crops. An assessment of the root crop industry was made and research needs were identified, prompting the establishment of a national research center and a network of research stations. Consequently, the Visayas State College of Agriculture (ViSCA) at Baybay, Leyte, located in the top root crop

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1. In 1982 the name was changed to Philippine Council for Agriculture and Resources Research and Development (PCARRD).

production and consumption area in the country, was chosen as the site of the National Root Crop Research Center. The national root crops program was finally formulated toward the second half of 1975 and implemented in mid-1976 under the joint leadership of PCARRD and ViSCA, with major contributions from the International Development Research Centre (IDRC), Canada.

On March 21, 1977, the President of the Philippines signed the Presidential Decree No. 1107, converting the National Root Crop Research Center into the Philippine Root Crop Research and Training Center (PRCRTC) to spearhead root crop research in the country. Cassava varietal improvement became an essential component of the Center's research thrust.

On March 29, 1980, PRCRTC recommended three cassava varieties to the farmers (Table 1). These varieties are the products of multilocational testing conducted over several seasons utilizing PRCRTC's pool of cassava germplasm. The Center now maintains a germplasm collection of more than 400 accessions of local and foreign origin.

In 1973 the University of the Philippines at Los Baños (UPLB), through a National Science Development Board (now National Science and Technology Authority) grant, initiated a research project on root crops emphasizing varietal improvement (Carpena, 1982). Two years later, the Institute of Plant Breeding (IPB) was established to take charge of breeding efforts in various plants including root crops, especially cassava and sweet potato. Through the IPB, two cassava varieties were recommended and released by the Philippine Seed Board (Philippine Seed Board, 1980). These varieties are Datu I (or UPL Ca-1) and Lakan I (or UPL Ca-2).

Table 1. Characteristics of recommended cassava varieties released by PRCRTC as of March, 1980.

Variety	Months to mature	Yield (t/ha) ^a			Alcohol production (litre/ha)
		Fresh wt	Dry wt	Starch	
PR-C 13	10-12	42	14.4	4.9	7560
PR-C 24	8-10	43	16.9	8.4	7740
PR-C 62	10-12	46	15.2	7.9	8280

a. Average yield computed from the results of a series of tests from different testing locations.

SOURCE: Philippine Root Crop Research and Training Center.

Other agencies working on cassava are the Bureau of Plant Industry of the Ministry of Agriculture and Food (BPI-MAF), and some state colleges and universities of the Philippines. BPI-MAF concentrates on varietal evaluation of existing available germplasm materials. Similarly, some colleges and universities perform cassava research for student theses and other purposes without emphasizing cassava varietal improvement. The major responsibility for varietal improvement is, therefore, left to PRCRTC and UPLB.

The major disadvantage of too many agencies involved in variety development is the complexity in identifying varieties that should be recommended for national adoption. Realizing this situation, the Philippine Council for Agriculture and Resources Research and Development (PCARRD)² launched the National Root Crop Cooperative Testing Program. This program unites all agencies involved in cassava breeding into one body without jeopardizing their respective activities. With this development PRCRTC, UPLB, and BPI-MAF are given freedom to pursue their own variety development program. However, advanced lines should pass standard selection procedures in each respective agency before they are jointly evaluated in uniform trials throughout the country.

Root crop varietal improvement group

The Philippine Seed Board was organized to approve various crops for recommendation. In 1981 the board formed a separate group called the Root Crop Varietal Improvement Group, composed of members from agencies involved in developing improved high-yielding root crop varieties for the Philippines. Its present members are from PRCRTC, UPLB, BPI-MAF, and PCARRD. Membership is open to other agencies, including those from the private sector directly involved in root crops variety development. The main function of the group is to assess and supervise the testing and evaluation of root crops and to recommend to the approving committee of the Philippine Seed Board new varieties of cassava, sweet potato, and other root crops.

National root crop cooperative testing program

The Root Crop Varietal Improvement Group monitors the National Root Crop Cooperative Testing Program whose cooperating agencies are also members of the working group. This PCARRD-initiated program was designed to foster cooperation and regular communication among

2. Prior to 1982 it was known as PCARR.

agencies involved in the development of new improved root crop varieties. PRCRTC has been chosen lead agency of this program. With its PCARRD counterpart, PRCRTC provides funds to the thirteen identified cooperating stations throughout the country (Figure 1).

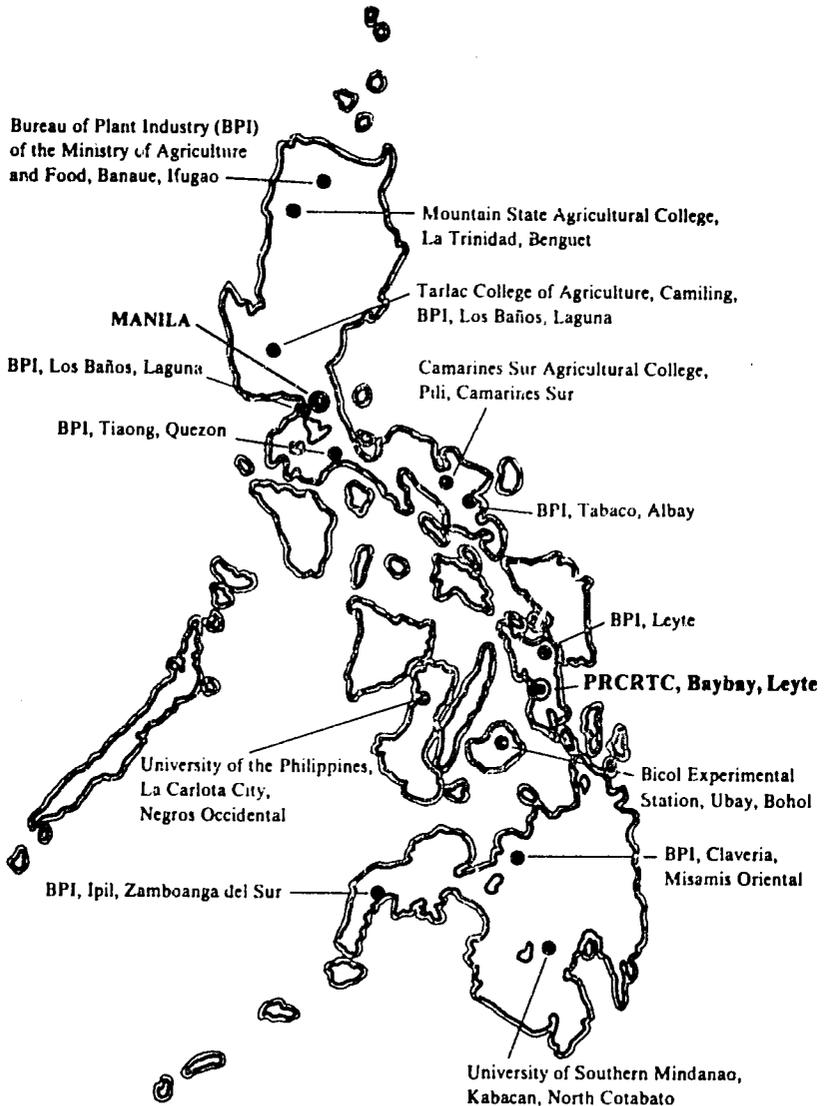


Figure 1. Location of the Philippine Root Crop Research and Training Center (PRCRTC) and cooperating stations, January 1985.

Evaluation scheme

The varietal improvement project of PRCRTC is designed to produce varieties that are best suited to farmers' resources and other conditions affecting them. Specifically, its objectives are to develop varieties that are high yielding and pest resistant, can adapt to a wide range of ecological conditions, can tolerate environmental stress, and are highly acceptable as food, feed, and industrial use. PRCRTC has adopted a scheme developed at the Centro Internacional de Agricultura Tropical (CIAT) as shown in Figure 2.

In like manner, UPLB and other agencies involved in cassava development have their own evaluation schemes. Any agency involved is required to test its entries in preliminary, general, and advanced trials before selected entries are included in the regional testing.

PRCRTC selection strategies for hybrids

F₁ field selection. Hybrids that are developed in the project, including those introduced from CIAT, are subjected to individual plant selection in the F₁ stage. Entries are planted with 2 m between rows and 1 m between hills. Harvest is at 10 months after planting and selection criteria are limited to harvest index, plant type, and general appearance of the crop.

Observational trial. Selections from F₁ field testing are entered into this stage of evaluation. Normally, five to seven stakes are prepared and planted for each selected clone in a 1 x 1 m planting pattern without replication. A check variety is planted every ten rows. Selection criteria include yield per plant, harvest index, dry matter content, and reaction to pests.

Preliminary yield trial. Entries selected from the observational trial, as well as local and exotic accessions, enter this phase of screening. Test entries are planted in four to five rows per plot without replication, following the same planting pattern as in the observational trial. Selection is based on yield per plot, dry matter, harvest index, hydrogen cyanide (HCN) content, and general appearance of the crop.

Yield trial. Selections from the preliminary yield trial are entered in this trial. Test clones are planted in four to five rows per plot, replicated two to four times. Distance of planting is 1.0 x 0.75 m. Harvesting is done 10 months after planting. Important economic characters are closely monitored at this stage and yield per hectare is computed.

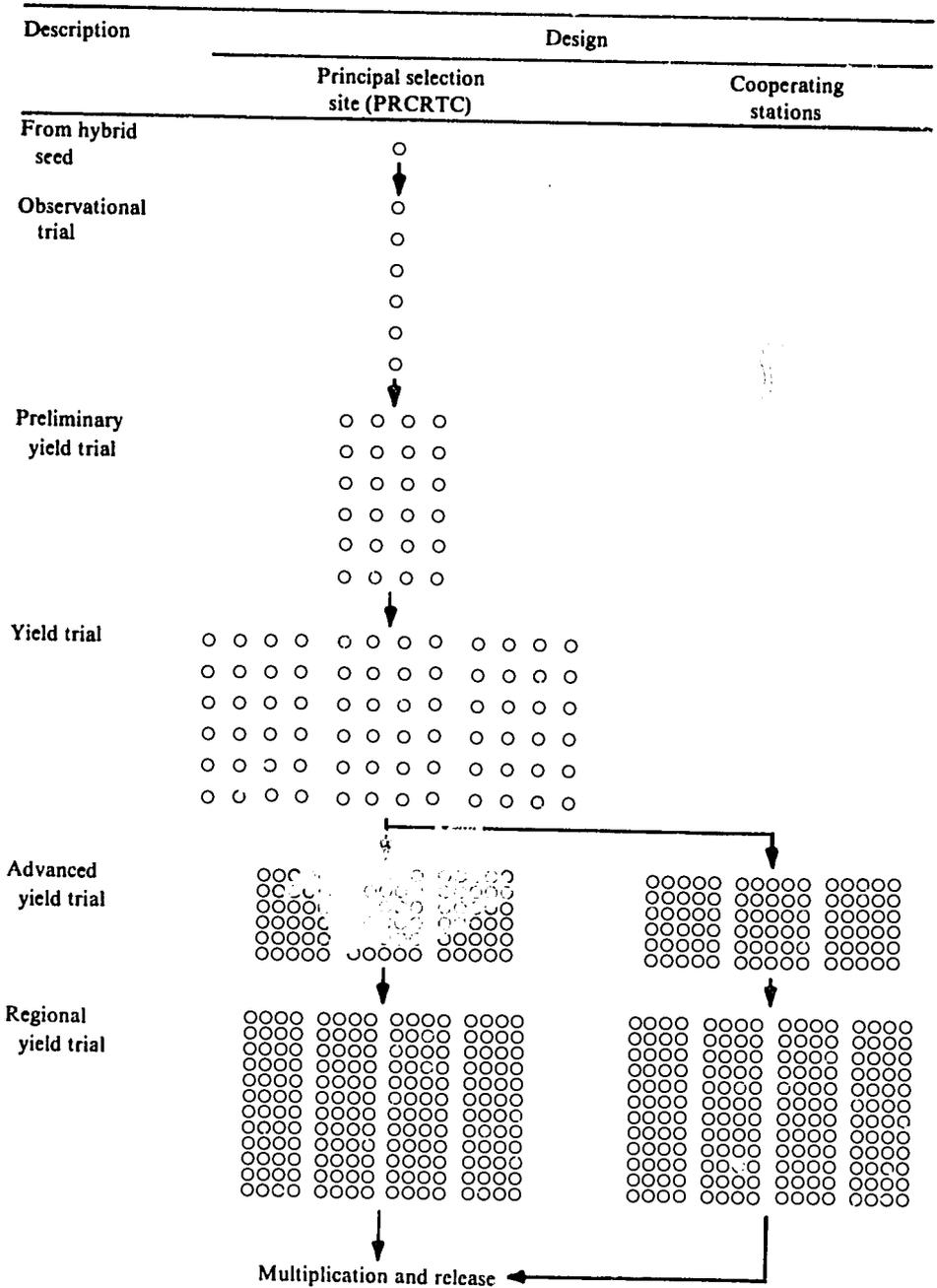


Figure 2. Stages of selection in the breeding program of the Philippine Root Crop Research and Training Center (PRCRTC). ○ = individual plant.

Advanced yield trial. This is the last stage of the agency-based selection before clones are included in the regional trials of the National Root Crop Cooperative Testing Program. A plot measuring 5 x 6 m is used for each entry and replicated three to four times. A minimum of three different testing sites is required for each selected clone before it is included in the next cycle of evaluation. Harvesting is done 10 months after planting and parameters considered are yield per hectare, dry matter content, HCN content, plant architecture, and general reaction to pests.

Philippine Seed Board regional trial. The number of entries at this stage of evaluation is determined by the Root Crop Varietal Improvement Group. Agencies involved in variety development submit lists of entries to the group for inclusion in this trial. Potential entries should have passed the advanced yield trial stage of evaluation. Under this trial, each testing site follows a uniform procedure (Appendix page 263).

Onfarm testing and varietal recommendation

Critical to success in any crop improvement program is the testing of promising cultivars in appropriate cropping systems and in farmers' fields. The present scheme adopted for varietal evaluation does not require onfarm testing prior to varietal recommendation. It is strongly suggested that such verification trials in farmers' fields be considered, inasmuch as during the series of evaluations the people involved are trained personnel, and the test sites are mostly in researcher-managed areas with relatively fertile soils, favorable rainfall, and irrigation facilities. Thus, cultivars developed with high fertilizer application and good water and weed control may be inappropriate for low-production environments characterized by low soil fertility, inadequate water and weed control, and complex disease and pest problems (Kawano and Jennings, 1980). Results obtained from field experiments vary greatly from those obtained from farmers' fields (Table 2).

At this point, one can assess the major constraints in the transfer of experimental results to farm production. It is easy to get 60 t/ha of cassava under favorable experimental field conditions, but in farmers' fields which have less productive environments, such results can hardly be attained. Onfarm testing, therefore, is very important in transferring technology from experimental sites to farmers' fields. Any validation on the farm cannot depend on a transplanting of experimental station technology which is unrealistic or unavailable to farmers (Francis, 1970). In the

Table 2. Yield of promising cassava varieties in experiment stations^a and farmers' fields, 1980-1981, Philippines.

Variety	Experiment stations (t/ha)	Farmers' fields (t/ha)
Golden Yellow	23.9	15.7
Kadabao	20.0	11.7
Hawaiian 5	35.6	19.3
Java Brown	26.7	13.3
Local check	18.4	11.0

a. Camarines Sur State Agricultural College, Bicol region, Philippines.

SOURCE: Philippines Root Crop Research and Training Center. 1981.

regard, enough replication throughout the region of application must be accomplished to assure adequate evaluation over the range of possible soil and climatic conditions that a new variety could face. This replication of testing is generally limited by a lack of resources, but ingenious schemes may be devised to maximize participation by farmers and utilization of limited inputs.

The present evaluation scheme adopted by the cassava Varietal Improvement Group requires a selection or hybrid to pass at least two normal growing-season tests over a minimum of six locations prior to recommendation to the Philippine Seed Board. Unless called upon by the Philippine Seed Board, the Varietal Improvement Group meets only in April and November. In the meetings, results of various tests are discussed. Entries to be dropped or retained, and new entries for testing are determined. During the meeting the group also selects varieties for recommendation to the Philippine Seed Board. A selection or hybrid is recommended to the Seed Board on the basis of superior yield, good agronomic and quality characteristics, and a high level of pest resistance. A selection not distinctly superior to existing varieties may also be recommended for release if it carries new genes for resistance against major diseases and pests, or if it is of different genetic background (Philippines Seed Board, 1983).

Once the variety or hybrid is ready for release to commercial growers or farmers, it is the responsibility of the agency developing it to maintain a continuous supply of planting material for distribution.

Present status of the national cooperative testing program

The National Root Crop Cooperative Testing Program was officially launched in 1983. After two years of existence the program has already recommended to the Philippine Seed Board sweet potato varieties for cultivation. At present, there is no recommendation for cassava because of the long growth cycle of this crop. To date, only the results of the first cropping in six of the eight test sites have been obtained (Table 3). Performance data of the 12 entries in the first cropping are very encouraging. The average yield is in the range of 19-50 t/ha. The first six entries are from PRCRTC (the majority of these come from CIAT), while the remaining entries are from UPLB. The second cropping is expected to be finished by the first half of 1985. Overall results will then be evaluated for possible recommendation to the Seed Board.

PRCRTC, as well as UPLB, continuously evaluates improved populations for possible inclusion in regional trials. CIAT germplasm is intensively screened at PRCRTC at different stages of evaluation. Hybridization work using promising CIAT and local materials has been done and a series of initial evaluations is still in progress. CIAT materials previously introduced to PRCRTC have a very bright prospect for varietal release. Table 4 shows that the yields of promising clones are almost twice as high as the yields of local varieties at the zero fertilizer level. Those clones which have very high harvest indexes and root dry matter contents are planted in advanced trials for possible inclusion in the regional testing.

Table 3. Yield (t/ha)^a data from cassava regional trials of the Philippine Seed Board, 1983-1984 planting season.

Entry	Region ^b						Average
	PRCRTC Leyte	BPI-MAF Zamboanga del Sur	UPLB Laguna	USM North Cotabato	BPI-MAF Bohol	UP Negros Occidental	
Golden Yellow	13.6	25.6	20.0	32.9	20.8	40.5	25.5
CM 323-52	26.2	36.4	59.2	45.1	30.0	38.3	39.2
CMC 40	—	24.8	42.4	42.0	28.0	38.3	35.1
CM 308-197	20.3	16.4	63.2	42.5	39.9	46.2	38.1
M Col 1684	31.3	42.8	—	48.1	44.0	56.4	44.5
M PTR 26	19.0	32.8	—	22.9	15.0	44.1	26.8
Bogor 397	43.6	31.4	36.7	43.5	32.9	—	37.6
G 50-3	49.2	31.3	—	80.2	41.0	—	50.4
Datu I (check)	41.2	50.7	64.3	41.2	—	54.2	50.3
Vassourinha	29.8	38.8	—	34.0	14.5	46.3	32.7
M Mex 59	23.2	40.2	—	—	15.5	45.1	31.0
M Ven 218	22.8	36.1	—	41.1	12.4	40.0	30.5
CV (%)	19.2	30.0	17.0	26.5	24.6	18.2	

a. Average of four replications per location harvested at 10 months. Entries without yield data are due to more than 30% of hills missing and therefore not included for computation.

b. BPI-MAF = Bureau of Plant Industry of the Ministry of Agriculture and Food

PRCRTC = Philippine Root Crop Research and Training Center

UP = University of the Philippines (at)

UPLB = University of the Philippines at Los Baños

USM = University of Southern Mindanao.

SOURCE: Data bank of the Root Crop Varietal Improvement Group, Philippine Seed Board.

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Table 4. Characteristics of selected clones from preliminary yield trial, Philippine Root Crop Research and Training Center, 1984-1985.

Clone	Parents	Dry root yield (t/ha)	Fresh root yield (t/ha)	Root dry matter content (%)	Harvest index
CM 3422-7	CM 630-122 x CM 728-2	19.8	61.7	31.7	.74
CM 3320-11	M Bra 12 x CM 523-7	19.4	56.7	34.3	.58
CM 3318-3	M Bra 12 x CM 342-170	18.8	59.4	31.6	.64
CM 3318-11	M Bra 12 x CM 342-170	18.4	60.0	30.6	.72
CM 3318-9	M Bra 12 x CM 342-170	18.2	58.9	30.9	.78
CM 3422-3	CM 630-122 x CM 728-2	17.7	52.8	33.6	.66
CM 323-52	M Col 22 x M Mex 59	17.7	56.1	31.6	.72
CM 3320-5	M Bra 12 x CM 523-7	16.6	46.7	35.5	.62
CM 3318-12	M Bra 12 x CM 342-170	16.5	51.7	31.7	.58
CM 3306-5	M Col 22 x CM 523-7	15.9	45.0	35.9	.65
CM 3380-11	CM 586-1 x CM 523-7	15.9	47.2	33.6	.66
CM 3318-10	M Bra 12 x CM 342-170	15.7	45.0	34.9	.67
CM 3341-4	CM 342-170 x CM 523-7	15.6	47.8	32.7	.76
CM 3341-2	CM 342-170 x CM 523-7	14.9	46.7	32.0	.74
CMC 40		14.4	47.8	30.7	.57
M Col 1684		14.3	44.4	32.3	.68
CM 3340	CM 342-170 x CM 586-1	13.9	45.6	30.5	.67
CM 3380-30	CM 586-1 x CM 523-7	13.1	42.8	30.7	.71
Kadabao (local)		11.6	35.7	31.6	.59
Golden Yellow (local)		8.5	27.3	30.2	.46

SOURCE: Philippine Root Crop Research and Training Center.

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Appendix

Procedures for conducting cassava regional trials: cultural practices

Land preparation. The area is plowed twice when a buffalo-drawn plow is used. Two harrowings at 1-week intervals are done thereafter. When a tractor-drawn plow and harrow are available, one plowing and one harrowing may be sufficient. Ridgesspaced at 1 m are constructed after the last harrowing.

Stake selection and preparation. Stakes are taken from at least 7-month-old cassava plants which are free of insect pests and diseases. The mature portion of the stem is cut into stakes 25 cm long unless the variety has long internodes, in which case each stake would have at least three nodes.

Planting time. This will be specified by the Working Group. Replanting is done not later than 2 weeks after planting. Replanted hills are not harvested, however, and should therefore be tagged.

Planting method and spacing. Stakes are planted vertically at the crest of ridges with two-thirds of the length buried in the ground. Spacing between hills is 75 cm.

Fertilization. The rate is 60-60-60/ha applied basally on a per-row, per-plot basis, 10 cm from the base of the plant toward the side of the ridge. Application is at planting time or not later than 2 weeks after planting.

Insect control. Any available recommended insecticide is used to control mite infestation.

Weeding. This is done according to the traditional practice in the area. As a rule, weeding should be done as often as is necessary until the canopies completely cover the area between rows.

Irrigation. Where irrigation water is available, the crop is irrigated during the long dry spells, especially during the first 3 months of the growing season.

Harvesting. This is done 8-10 months after planting. The two middle rows, except the end hills and replanted hills, are harvested in each plot. The number of hills harvested per plot is recorded. Plots with more than 30% of missing hills are not included. The yield is calculated, using only completely bordered plants. Plots with less than 10 such hills are discarded. Results from an entry with more than one missing plot (replication) are not included for that season. The yield is calculated by lifting and separating the roots from the stems, removing the adhering soil. The roots are sorted into marketable roots (those at least 3 cm in diameter) and nonmarketable ones and weighed.

Procedures for conducting cassava regional trials: plot size, experimental design, and field layout

Plot size including guard rows. The plots consist of four rows, 1 m apart, and 12 hills long (8.25 m from one end hill to another). Hills are spaced at 75 cm. Only the completely bordered hills in the two middle rows are harvested for yield estimates.

Experimental design. A randomized complete block design with four replications is used.

Field layout. Since in most cases the uniformity of the area cannot be assumed and the direction of the gradient is not known, plots must be laid out in such a way that the shape of a replication is as square as possible. Thus, a replication consists of two or more sub-blocks. For example, for a 12-entry trial each replication consists of two sub-blocks. Sub-blocks are 0.75 m apart (that is, if there are no furrows).

Border rows. At least three rows on each side and at least seven hills (4.5 m row) on each end of the area are planted. There will be no border rows or vacant spaces between replications except for the required row and sub-block spacings.

Data collection. The data collected are:

Total marketable yield based on root size;

Dry matter or starch content (for selected stations only);

Resistance to lodging (optional or to be considered as an additional desirable character);

Resistant to pests and diseases (optional or to be considered as an additional desirable character);

Shelf life under ambient conditions;

Eating quality and acceptability (for table varieties); and

Hydrogen cyanide (HCN) content (for selected stations).

From Advanced Cassava Lines to Farmers' Fields: Sierra Leone

Mohamed T. Dahniya*

Introduction

Cassava (*Manihot esculenta* Crantz) is the second most important food crop after rice in Sierra Leone, where both the roots and leaves are consumed by the people. In 1970-1971 it was estimated that the mean root yield of cassava in Sierra Leone was 2.2 t/ha (Central Statistics Office, 1972). It was as a result of this very low yield that cassava improvement work was initiated in the country less than 10 years ago with the active support of the International Institute of Tropical Agriculture (IITA) in Ibadan, Nigeria.

Production problems

The major production problems of cassava in Sierra Leone include diseases, pests, weed infestation, and poor cultural practices (Dahniya, 1981).

Cassava mosaic disease (CMD) and cassava bacterial blight (CBB) are the most widespread economic diseases in Sierra Leone but accurate estimates of crop loss are unavailable. Cultivars with a high degree of resistance to these diseases are now available.

Severe cases of cassava brown leaf spot (*Cercospora henningsii*) and cassava anthracnose (*Colletotrichum* spp.) have been observed. White thread fungus, caused by *Fomes lignosus*, is also a serious root disease that is widespread in the country.

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Termites may eat up newly planted stakes, especially if there is a dry period after planting. During the severe dry season, grasshoppers (*Zonocerus variegatus*) do considerable damage as a result of their feeding activities.

The cassava green spider mite (*Mononychellus tanajoa*) was first observed in the country in 1983. An outbreak of the cassava mealybug (*Phenacoccus manihoti*) was reported in February 1985. These pests can do considerable damage to cassava, especially in the northern part of the country where the crop is planted towards the end of the rainy season after the rice harvest.

Weeds are one of the most important constraints to cassava production in Sierra Leone. Observations at Njala revealed that because of the high rainfall, cassava needs at least three properly timed weeding before harvest.

Mammals, particularly monkeys, grasscutters, and squirrels, feed on the roots of the plants and this leads not only to yield reduction but also assists in the spread of various root rots.

Some of the cultural factors limiting cassava production in Sierra Leone include the predominant use of low-yielding varieties, poor land preparation, late planting, and lack of fertilization.

Varietal improvement

Against the background of the above problems, cassava improvement work was initiated in Sierra Leone less than 10 years ago in a cooperative venture between IITA in Nigeria, the Rice Research Station in Rokupr, and later Njala University College of the University of Sierra Leone. The main objective of the program is to develop cultivars which are high yielding, resistant to the major diseases and insect pests, adapted to a wide range of environments in the country, and possessing good consumer acceptability.

The improvement procedure involves raising thousands of seedlings derived from open-pollinated seeds obtained both locally and from IITA. These go from the seedling nursery through the preliminary, intermediate, advanced, and uniform yield trials to farm-level testing and farmer evaluation.

As a result of the improvement program, the Rice Research Station released three varieties in 1978 called Rocass 1, 2, and 3 while Njala University College has released another three between 1980 and 1983, named Nucass 1, 2, and 3.

Onfarm trials and demonstrations

Cassava trials and demonstrations have been conducted in cooperation with the Adaptive Crop Research and Extension (ACRE) Project which has its headquarters at Njala.

The project was established in 1980 with the support of the United States Agency for International Development (USAID) and the Sierra Leone Ministry of Agriculture and Natural Resources. The main objective of the project is to increase the agricultural productivity of small farmers through adaptive crop research, crop demonstrations, and an effective extension service. Its main areas of activities are within a radius of 25 miles of Njala in the south, Kenema in the east, Rokupr in the northwest, Makeni in the north, and Kabala in the far north (Figure 1).

In addition, the Project's improved cassava varieties are evaluated by extension officers of the Ministry of Agriculture and Natural Resources various integrated agricultural development projects, and voluntary agencies involved in agricultural extension programs.

Table 1 lists the number of cassava research trials and demonstrations conducted during the 1981-1982 and 1982-1983 planting seasons by the ACRE Project. Under the system of shifting cultivation that is predominant in the country, rice is the main crop. Because cassava is a crop of relatively long duration, it has to remain in the field for several months after the rice has been harvested. As a result, some of the participating farmers do not take as much care of the crop as is necessary. There have been incidences of rodent damage and unauthorized harvesting of the trials and demonstrations. Nevertheless, results from the trials and demonstrations have shown clearly that the new cultivars are superior to the local varieties in terms of root yields.

Table 2 shows the results of a demonstration in farmers' fields in three zones during 1982-1983. In this demonstration, an attempt was made to compare an improved variety (Rocass 1) under intermediate management with a local variety under local management. Under intermediate management, the plants are set 1 m apart on 1-metre ridges and given timely

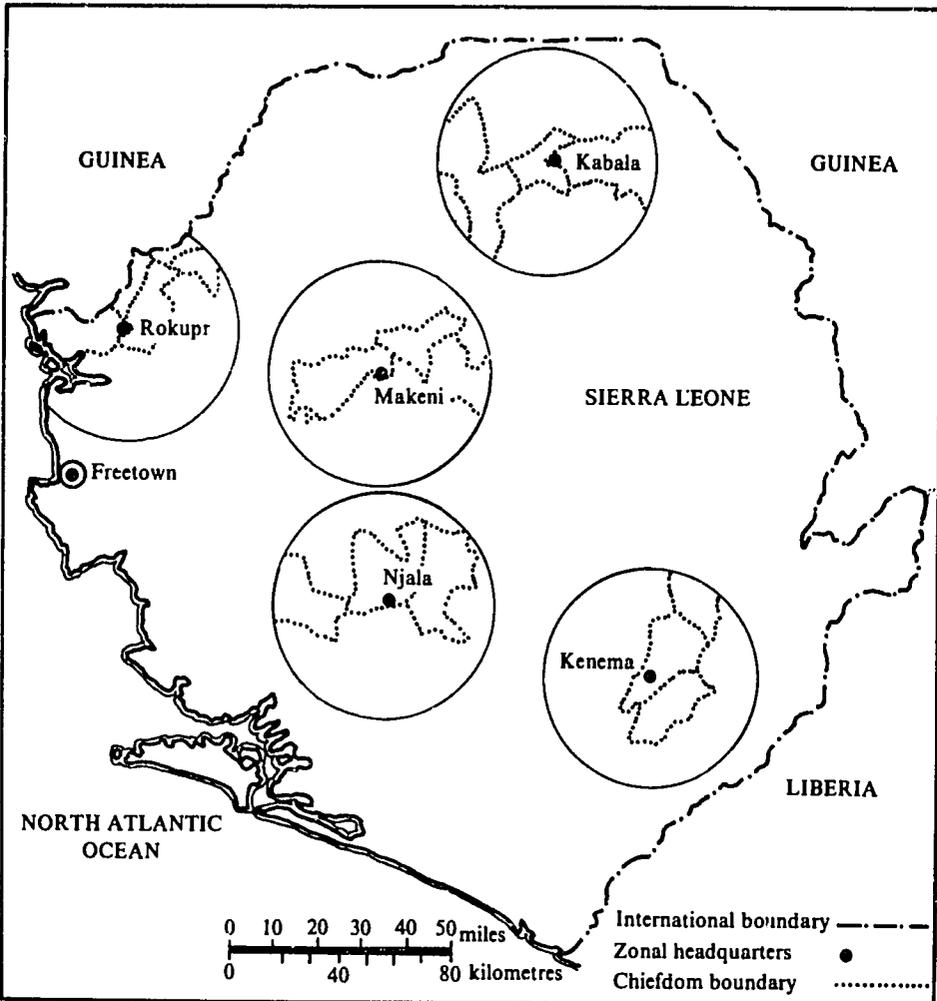


Figure 1. Operational zones of the ACRE (Adaptive Crop Research and Extension) Project, Sierra Leone.

weeding, but no fertilization. Local management refers to growing the crop as the farmer would, on hills or raised beds without uniform spacing or fertilization, and weeding as convenient. The results show that in all three zones, the root yields obtained with the improved variety under intermediate management were superior to those of the local variety under local management.

Table 1. Cassava trials and demonstrations conducted by ACRE Project between 1981 and 1983, Sierra Leone.

Zone	Trials		Demonstrations	
	1981-1982	1982-1983	1981-1982	1982-1983
Kenema	8	12	13	7
Njala	8	12	11	6
Rokupr	8	12	10	6
Kabala	12	12	8	6
Makeni	4	12	10	6
Total	40	60	52	31

Table 2. Comparison of local and improved cassava varieties under local and intermediate management, Sierra Leone, 1983.

Variety	Management level	Fresh root yield (t/ha)		
		Njala	Kenema	Rokupr
Improved (Rocass 1)	Intermediate	12.5	12.7	14.2
Local	Local	5.4	6.5	6.1

Table 3 presents the results of one of the cassava uniform yield trials during 1982-1983 at Warima in the Northern Province under the auspices of the Magbosi Integrated Agricultural Development Project. Warima is an important cassava-growing village and this trial attracted many cassava growers in the area. The crop was planted on upland gravelly soil without fertilization. The results show clearly that the improved local and prereleased varieties outyielded the two local varieties.

Distribution of planting materials

Besides the usual onfarm trials and demonstrations, minikits (small packages of improved cassava planting materials) are supplied. Minikit distribution is so organized as to bring together a large number of farmers for the purpose of training and to encourage them to obtain improved planting materials for use on their own farms. In 1983 a total of 152,696 cassava stakes were distributed to farmers as minikits in the five ACRE Project operational zones.

Table 3. Performance of cassava clones in the 1982-1983 uniform yield trial at Warima, Sierra Leone.

Clone	No. of marketable roots/plant	No. of roots/plant	Marketable fresh root yield (t/ha)	Total fresh root yield (t/ha)
80/11	2.3	5.2	7.7	11.4
80/14	2.4	6.3	8.0	12.9
80/22	2.1	6.9	6.5	12.6
80/27	2.0	4.7	7.8	11.0
80/29	3.7	5.9	16.2	19.2
80/32	3.0	5.6	12.0	14.3
80/36	2.0	5.4	5.9	9.4
80/37	1.7	5.8	4.3	9.3
80/40	2.8	4.6	10.9	13.5
80/48	1.0	3.4	3.7	6.2
80/49	2.8	4.7	9.3	11.4
80/52	2.3	5.3	5.9	10.1
80/54	3.0	7.5	12.1	16.2
Nucass 1 ^a	3.2	7.4	10.7	15.6
Nucass 2 ^a	2.0	4.4	7.3	10.5
Rocass 1 ^a	2.8	5.7	9.5	12.9
Cocoa (local)	0.9	1.8	3.1	4.6
Yakanu (local)	1.3	2.7	5.2	6.9
LSD (5%)	0.7	1.4	3.3	3.2

a. Improved local clone.

Cassava planting materials are also given out to various institutions. In 1983, for example, 78,755 stakes were supplied to secondary schools, the Ministry of Agriculture and Natural Resources, integrated agricultural development projects, Peace Corps, Christian Extension Services, Meals for Millions, Seed Multiplication Project, prisons, Primary Health Care Programme, and the Masanga Leprosy Rehabilitation Centre.

In each of the five ACRE Project zones, there is a 4-ha crop multiplication site which is used almost exclusively for cassava multiplication.

Acceptability of improved varieties

During the initial stages of the crop improvement program, not much attention was paid to the acceptability of new varieties. It was only after the first varieties were released that it was realized that Sierra Leoneans have a preference for cassava plants with red petioles and pink root skin. Unfortunately, all the released varieties had white root skin and only one had red petioles. These preferences may be related to the fact that most of the sweet cassava varieties in the country have pink root skins and red petioles while the bitter types usually have white skins. Selection of clones with pink skins and red petioles is now being emphasized along with other desirable agronomic characteristics. Several promising clones have been identified.

Sierra Leoneans enjoy boiled cassava root in addition to other food forms of cassava such as *gari* and *foofoo*. The new varieties had not been evaluated for their suitability for the production of these local dishes before their release to farmers, and it was only until later it was found that Nucass 3 was unsuitable. Its multiplication and distribution have since been discontinued. Sierra Leoneans also like their boiled cassava to be soft. Unfortunately, only one of the released varieties boils to a soft texture, although the other varieties can be used in making *foofoo* or *gari*. As a result, all clones in the various trials are now routinely evaluated for their cooking characteristics.

The new cassava clones have very dense canopies. This has limited their adoption because traditionally farmers intercrop their rice with cassava and other crops. The shading effect of the new cassava clones has had an adverse effect on the productivity of the other crops. Less profuse branching behavior in clones has, therefore, become a selection criterion.

During the dry season, local farmers plant their cassava crop on raised beds in hydromorphic soils mainly for leaf production, although the roots are later harvested. Under such conditions, the roots of the new varieties may rot, unlike some of the local varieties. Attention is therefore being placed on the selection of cultivars which can tolerate damp conditions.

Of all the improved varieties, Rocass 1 is the most popular among the farmers because it has red petioles and its root cooking quality is similar to that of the local varieties. In areas where *foofoo* and *gari* production are widespread, other new clones have been particularly popular because they produce good-quality *foofoo* and *gari*.

Conclusions

Within the past few years, much progress has been made in cassava improvement in Sierra Leone. High-yielding varieties have been released and although there have been some problems with acceptability, the new varieties are slowly gaining ground, especially in areas producing *fofofo* and *gari*.

At the present time, there is a severe scarcity of foreign exchange and the country has to import large quantities of rice, the staple food crop. Cassava could therefore serve as a good supplement.

The future of cassava in Sierra Leone appears very bright because of its ease of cultivation, high root yields, good production under adverse environmental conditions, and versatility of use for human consumption and animal feed (which is increasingly important as the price of maize—the traditional animal feed—escalates). Cassava improvement work will, therefore, play an increasingly significant role in Sierra Leone's agricultural production.

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Nontraditional Techniques for Genetic Improvement of Cassava

*W. M. Roca, L. Szabados, J. Narvaez, and J. Jaynes**

Introduction

Extensive evaluation of cassava landraces at the Centro Internacional de Agricultura Tropical (CIAT) has shown that few existing varieties meet the combined requirements for adaptation, resistance, plant type, yield potential, and root quality under intensified production systems. Thus, current breeding relies on sexual hybridization to create genetic variability and selection of the desired plants (CIAT, 1985). There is still much to be done to exploit the large variability present in the various cassava collections of the world, using traditional methodologies. In spite of this, some tissue culture methods are already making an impact on cassava improvement.

Modern research operates in such areas as the production or modification of phenotypic expression and genotypic constitution, using cell culture cloning and molecular (recombinant DNA and gene transfer) approaches. Results suggest that the efficiency of traditional cassava breeding methods can be significantly increased or that certain otherwise intractable problems can be resolved.

The new genetic manipulation technologies, which fall under the term biotechnology, could aid traditional cassava breeding by allowing more rapid recovery of sexual recombinants and by exploiting or creating further genetic variability.

This paper reviews the present status of selected biotechnologies and examines their possible uses, potentials, and limitations in the genetic improvement of cassava.

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In vitro clonal propagation

In vitro techniques have been developed for the conservation and international exchange of germplasm (Roca et al., 1982) and to recover yield and vigor in traditional cultivars (Roca, 1985). Over 1500 cassava varieties have been transferred in vitro to CIAT from the major centers of genetic diversity, and nearly 70% of the 3800 clones composing the CIAT collection have been incorporated into an in vitro gene bank.

Biochemical research to characterize cassava clones by isozyme gel electrophoresis has been developed (Hussain et al., 1986). Full implementation of this technique should be useful to "fingerprint" germplasm accessions, eliminate duplicates from the collection, and eventually develop genetic markers.

Tissue culture regeneration

Vegetative propagation of cassava provides a tremendous advantage to in vitro cell and molecular manipulation. Once valuable variability has been selected, its genotype can be maintained by means of vegetative multiplication. Even epigenetic variability, common in tissue culture manipulation and stable through mitosis, can be maintained vegetatively in cassava.

Tissue culture is the route by which various forms of genetic manipulation should pass in transition from the laboratory to the field. Therefore, the ability to regenerate cassava plants by means of cell and tissue culture is a necessary step for the utilization of most biotechnologies.

In spite of the difficulties reported in regenerating plants from various cell culture systems in cassava, recent results of research in this area at CIAT are encouraging. Based on earlier work by Stamp and Henshaw (1982), plants have been regenerated through somatic cell embryogenesis using young foliar segments as initial explants. Out of 21 varieties tested: highest embryonic potential (more than 60%) was observed in 10 varieties; moderate capacity (30%-50%) for embryogenesis occurred in 7 varieties; and 4 varieties showed very low (less than 20%) somatic embryo formation (CIAT, 1985). Regenerated plants have been transplanted to the field:

Leaf mesophyll protoplasts have been isolated and cultured from 11 cassava varieties. Protoplasts regenerated cell walls and divided to form cell colonies at 50%-60% frequency. Cassava protoplast isolation and culture is now routine (CIAT, 1985). Work is underway to regenerate

plants from protoplast-derived colonies by means of somatic embryogenesis and/or organogenesis.

There are no reports on the recovery of plants from the culture of immature embryos of cassava as a means of facilitating wide crossing. Past experience in some interspecific hybridization of *Manihot* (Nassar, 1980) shows that there is apparent general crossability. However, crosses of cassava with arboreal *Manihot* species failed (for example, *M. brachyandra*, *M. leptophylla*, *M. glaziovii*, *M. pseudoglaziovii*); fruit drop was 100% three weeks after pollination (N. Nassar, personal communication). Embryo rescue and culture before fruit dropping could help to recover hybrid plants.

On the other hand, the culture of embryos from mature seed has been used to recover plants from otherwise difficult-to-regenerate seed of several wild *Manihot* species (CIAT, 1985).

If triploidy ($3x = 54$) in cassava is associated with augmented vigor and productivity (Byrne et al., 1984), the recovery of triploids from crosses at the tetraploid level could be increased through embryo rescue techniques.

Anther culture for haploid production

Haploids or dihaploids could be useful to cassava breeding in various ways. Because cassava is an allotetraploid, breeding for characters controlled by recessive genes is difficult and even more so if the character is tetrasomically inherited (Bellotti and Kawano, 1980). For example, no forms devoid of cyanogenic glycosides have been found in cassava or wild *Manihot* species (Jennings, 1976) and the incapability of producing the glycoside is reportedly due to recessive genes (Hahn et al., 1977). If this is true, then homozygosity would be needed to express acyanogenesis, which would be difficult to achieve by conventional breeding methods. Homozygous lines could be produced quickly through anther culture and chromosome doubling. Tetrasomic inheritance would be avoided in the doubled haploids, which could be used for genetic and physiological studies. The acyanogenic character would be maintained by hybridization with other lines derived from anther culture.

Hybrid seed may offer an alternative to growing cassava in the future—major problems encountered in vegetative propagation would therefore be minimized or eliminated. Because of severe inbreeding depression it is difficult to produce pure lines for use in hybrid seed production through

successive inbreeding. Homozygous lines could be quickly produced from selected parents, selected for vigor and other traits, and used for crossing, thereby facilitating the maximization of heterosis in cassava, as well as the production of uniform hybrids for commercial production.

Finally, haploids could help in the determination of genetic ratios and gene action. Since dominance effects are absent in doubled haploids (all genes are expressed), the method could also serve to detect lethal genes which may have accumulated in heterozygous clones.

The most common method to produce haploids is the culture of immature pollen (microspores) within or outside the anther. Plant regeneration depends on genotype, developmental stage of the microspore, culture medium, and anther or bud pretreatments. In an early work with cassava, floral buds of 1.2-2.5 mm, corresponding to late tetrad through late uninucleate microspore, were utilized. Chromosome counts indicated haploidy in some regenerated root tips. In some varieties nearly 100% of the anthers formed calluses, while in others callus formation was variable both between plants and even within anthers of the same plant (CIAT, 1982). To date, however, no plants have been regenerated from anther culture in cassava.

Production and modification of variability

Emerging cellular and molecular techniques provide an opportunity to genetically modify plants for development of new breeding lines, or to improve single traits of existing varieties. Somaclonal variation and protoplast fusion are the two principal topics in this category.

Somaclonal variation

Somaclonal variation is the generation of genetic variability in plants regenerated by tissue culture, without any sexual recombination phase. Variation of qualitative and quantitative characters has been observed in the regenerated plants of several crop species. The phenotypic variation of somaclones can result from epigenetic or genetic changes. Epigenetic variation is not sexually transmitted, but can be maintained vegetatively (Scowcroft and Larkin, 1982). Genotype, culture medium composition, and duration of the unorganized (callus) phase of the culture cycle seem to influence somaclonal variation.

Whether or not somaclonal variation occurs in cassava needs to be evaluated. To this end, it will be necessary to regenerate large numbers of plants from unorganized cultures for evaluation and selection in the field. Work is underway at CIAT to evaluate the phenotypic stability of cassava plants regenerated by somatic cell embryogenesis. Occurrence of somaclonal variation could be exploited to restore one or two deficiencies in otherwise good cultivars. On the other hand, a genetically *stable* regeneration system is a prerequisite for the production of "artificial seeds" using encapsulation techniques with somatic embryos.

Protoplast fusion

The fusion of protoplasts can permit the development of a hybrid having the nuclear and cytoplasmic genomes of both parents with doubled ploidy level. This technique may be useful for the transfer of cytoplasmically inherited traits and for overcoming sexual incompatibilities. Production of very large numbers of recombinants *in vitro*, followed by *in vitro* screening techniques would greatly increase the probability of identifying desired genotypes.

It has been suggested that protoplast fusion can be used to produce more heterozygous cassava tetraploids, as compared to colchicine induction, for the extraction of superior triploids (Byrne et al., 1984). In order to realize these possibilities, plant regeneration from fusion products must be accomplished.

In vitro selection

Tissue culture techniques can permit the selection of somaclones or fused protoplasts with useful agricultural characters. Compared to conventional selection, *in vitro* techniques enable the application of very high selection intensities, with or without mutagenic treatment, to a very large number of individuals: for example, one flask with 100 ml of culture medium can contain 5×10^4 callus-forming cells or 5×10^6 cells in suspension, and one gram of leaf tissue can produce $2-4 \times 10^6$ protoplasts.

In vitro selection may be limited to cases where the resistance results from properties of the cells (for example, tolerance to heavy metal, or pathotoxins) and where there is correlation between behavior of plants and cell cultures.

One possibility may be the detection of acyanogenic cassava plants. Any recessive mutant gene which confers an incapacity for producing glycosides would have little chance of becoming homozygous in an allotetraploid like cassava (Nayar, 1975). If haploids were used, the recessive mutants would appear immediately and could be stabilized by means of chromosome doubling.

Another possibility could be screening for tolerance to soil toxicity conditions. Although cassava is tolerant to acid soils, it is rather sensitive to high pH and the associated problems of salinity, alkalinity, poor drainage, and micronutrient deficiencies (Lozano et al., 1981). Through tissue culture techniques, salt-tolerant cell lines could be selected.

Recombinant DNA and gene transfer technology

The discovery of restriction endonucleases and plasmids has made it possible to cut out genes of choice from DNA isolated from any organism and to insert these genes into plasmid vectors. These plasmids are placed in a bacterium host and maintained essentially forever. The genes stored in this fashion can be retrieved for analysis and characterization.

Since purified DNA can be degraded by cell enzymes, it is necessary to use a vector system to accomplish uptake, stabilization, and replication of foreign DNA in the plant cell. While several vectors for plant transformation have been proposed, the use of Ti and Ri plasmids of *Agrobacterium* has been preferred. Following infection of a plant with *Agrobacterium*, a discrete portion of the plasmid DNA (T-DNA) covalently joins with the plant's genome (Depicker et al., 1982).

Insertion of modified T-DNA into the plant genome can be accomplished through infection of plant cells with the bacteria. Plant regeneration from transformed cell is of crucial importance for the practical utilization of genetic engineering. It seems that when the Ri plasmid of *A. rhizogenes* is used, instead of the Ti plasmid of *A. tumefaciens*, the regeneration of healthy plant is not an important constraint (Tepfer, 1984).

The transfer trait must be expressed in the mature plant and its sexual progeny, and gene expression must occur in the appropriate plant tissue or organ at the correct developmental period.

Some ways in which it may be possible to utilize recombinant DNA and gene transfer technology for the improvement of cassava are described below.

Increasing levels of total essential amino acids

The value of cassava relies on its being one of the cheapest energy sources compared to many alternative foods. Cassava roots have 30%-40% dry matter composed mainly of starch and sugar. The crude protein of cassava roots is low (about 3% on a dry matter basis), but the true protein is even lower because about half of the nitrogen in the root is nonprotein nitrogen. Cassava leaves, which are eaten in Africa and Asia, contain about 7% protein on a fresh weight basis. The quality of root protein is poor with respect to essential amino acids, especially cysteine, methionine, and tryptophan, ranging from 0.035-0.040 g per 100 g of dry weight. Leaf protein is of better quality, but deficient in methionine and tryptophan (Cock, 1985). Therefore, if it were possible to increase the levels of essential amino acids of cassava roots and leaves through genetic engineering techniques, the scope of cassava as a food would radically change. In addition to offering a more balanced food, it would result in a reduction of endemic diseases caused by cyanide toxicity in those areas where cassava intake is high and consumption of sulfo-amino acids is low.

Synthetic DNA fragments that code for polypeptides with elevated levels of essential amino acids have been constructed. This DNA has been introduced into *Agrobacterium* strains using recombinant DNA technology and its expression has been achieved (Jaynes et al., 1985). The synthetic genes code for polypeptides containing 23% lysine, 12% tryptophan, 12% methionine, 6% threonine, and 6% isoleucine. Thus, these amino acids constitute 59% of the total proteins compared to 25% of milk protein and 6% of zein.

These genes have been spliced into the T-DNA plasmid of *A. rhizogenes* under the control of a plant gene promoter and are now available for insertion into the plant genome. This would be accomplished by infecting cassava shoots in vitro. *Agrobacterium rhizogenes*-mediated plant transformation is characterized by the induction of hairy roots on the infected tissue (Tepfer, 1984). Pieces of the hairy roots can be excised from the cassava stems and cultured to form a callus. At this stage RNA and DNA extraction can be carried out for detection of foreign genes using molecular probes. Tissue culture technology will be used to regenerate plants from the transformed callus cells.

Conferring resistance to viruses by molecular interference

Replication of many plant viruses is mediated through normal translation of the viral RNA, which functions as messenger RNA ("positive

sense" single-stranded RNA), for the synthesis of viral protein at the cell's ribosomes. This finally leads to the death of the infected cell and spread of the disease.

The synthesis of DNA which codes for the RNA complementary to several plant RNA viruses has been achieved. Inactivation of a positive sense single-stranded RNA virus occurred *in vitro* after the "antisense" DNA annealed to the full length viral RNA.

Several antisense DNAs have been incorporated into *A. rhizogenes* vectors which allow the integration and expression into the genome of the plant. A cultivar whose genome carries the antisense DNA would protect itself from the incoming positive strand virus by disrupting the normal routes of virus translation.

In order to construct the antisense DNA it is necessary to elucidate the nucleotide sequence of the viral RNA using purified viral samples. Since most of the cassava viruses have single-stranded RNAs, it may even be possible to confer multiple virus resistance through these technologies.

Eliminating root cyanide

An important problem in cassava is cyanide toxicity. Besides large quantities of carbohydrates, the cassava storage roots contain varying concentrations of cyanogenic glycoside which, upon autolysis, releases hydrogen cyanide. Cyanide toxicity related to cassava consumption should be considered in improvement programs. However, no acyanogenic lines have been found in screening either cassava or wild *Manihot* germplasm (Jennings, 1976) and, as stated earlier, the lack of glycoside seems to be under the control of recessive genes. It should be possible to locate the genes responsible in the plant for the production of the cyanogenic glycosides. Then, by utilizing the aforementioned antisense concept, their genes can be repressed.

Reducing postharvest physiological deterioration

Finally, research aimed at delaying or preventing postharvest physiological deterioration of cassava roots is worth considering. The location of genes encoding key enzymes for the production of the phenolic compounds that accumulate at the onset of deterioration, after harvest (Wheatley, 1982), could pave the way for the application of a biotechnological approach to inhibit the expression of such genes; perhaps through an antisense RNA mechanism similar to the one referred to above. However,

before biotechnology can be applied, basic biochemical research on the deterioration process is necessary.

Recombinant DNA and gene transfer technology offer great potential for introducing desirable traits into cassava when associated with tissue culture techniques. However, these technologies should be regarded as additional tools which, when allied with traditional techniques, can enlarge the scope of breeding and increase the possibility of crop improvement.

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Workshop Conclusions and Recommendations

*Clair H. Hershey and Kazuo Kawano**

Cassava has a relatively short history of the application of modern breeding techniques and the dissemination of new information is often inadequate. The present workshop, the first ever of its type in cassava, was valuable as a means of updating cassava breeders from around the world on the work in progress in other countries and as a format for exchanging ideas on future directions. Conclusions and recommendations of the workshop were summarized in the final session, chaired by Dr. S. K. Hahn. Also included here are short summaries of the roundtable discussion on *National Programs and International Centers and Data Management and Information Exchange*.

Germplasm

Only a few institutions are at present in a position to provide adequate long-term maintenance of major international cassava collections. The International Agricultural Research Centers (IARCs) have taken on special responsibility in this area, particularly the Centro Internacional de Agricultura Tropical (CIAT) which is located near the centers of diversity of the genus *Manihot*. National programs have generally been concerned with collecting and maintaining national germplasm resources. In vitro methods are being used at some of the major gene banks as a means of achieving higher maintenance security, lower long-term maintenance costs, and ease of exchange.

Most of the germplasm at the Centers has been evaluated and described for important agronomic traits—which information is available upon request. The IARCs have a major responsibility in providing germplasm with specific traits for given programs. There is a need for more germplasm

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collection and the International Board for Plant Genetic Resources (IBPGR) has given high priority to funding such collections.

Germplasm may be distributed internationally in the form of stakes, in vitro cultures, or as true seed. International exchange of stakes is generally not recommended, since there is higher risk of transporting pests and pathogens as compared to in vitro methods. True seed cannot duplicate parental genotypes, but constitute an effective means of distributing a gene pool. Considerable work still needs to be done on virus-indexing methods to provide for secure exchange of virus-free germplasm.

Few germplasm accessions meet the total needs of modern cassava cultivation systems and genetic improvement is basic to bringing about transformation of varieties for higher productivity.

Genetics and cytogenetics

In spite of its importance as a major food crop, relatively little is known about cassava genetics and cytogenetics. The Central Tuber Crops Research Institute (CTCRI) in India has played a major role in elucidating what is known about cassava cytogenetics. All the *Manihot* species so far studied have 36 chromosomes and cassava has been described as a segmental allotetraploid. Since normal bivalent pairing occurs for most clones, it may be expected that many traits are inherited in normal diploid fashion and the complications of breeding with tetrasomic inheritance may not occur to any significant extent. The cytogenetics of interspecific crosses has barely been explored and such research must accompany any attempts to utilize genes from wild species in breeding programs.

Hybridization and breeding methodologies

Vegetatively propagated crops are possibly the least complicated of any group of species for developing a breeding strategy. Any genotype, once created, can be indefinitely maintained and reproduced through vegetative propagation. The production of variability through hybridization is relatively easy in cassava and either hand pollination or "controlled" open pollination systems can be effectively used. Open pollination systems are increasingly being used as an alternative, especially in programs where labor is unavailable for controlled pollination. Studies need to be done on the best ways to accomplish near-random mating in open-pollination systems.

Breeding methodologies applicable to cassava are similar to those of other outcrossing species and simplified by vegetative propagation. Population improvement methods, though not well-developed for cassava, should be the most effective means of improving multiple traits, each controlled by several to many genes. The IARCs should concentrate on developing broad-based populations improved for the more universally required traits, while national programs select for local adaptation, agronomic practices, and utilization. The IARCs, as germplasm centers, should be able to provide, upon request, sources for high expression of all the important traits.

Breeding for specific objectives

Most cassava breeding programs find it necessary to work simultaneously toward several objectives. Nevertheless, it is essential to analyze and develop a strategy for each individual objective. In the workshop, some of the most common areas of breeding objectives were discussed: yield potential, yield stability, pest and disease resistance, and root quality.

Cassava is now relatively well understood from the point of view of physiological traits related to yield, although the application of physiological principles to yield selection is not widespread. Selection for yields potential needs to be placed in the perspective of the types of environment in which the crop is grown. There was a broad consensus among participants that cassava's competitive advantage compared to many other crops is its ability to yield reasonably well under suboptimal conditions of water availability and/or soil fertility. Therefore, yield selection should be done under conditions similar to the conditions of soil and climate in the target production area rather than aiming for maximum yield under optimal conditions, except in those few cases where they are characteristic of the target production area.

Since cassava is a long-season crop, the repeated applications of fungicides or insecticides necessary to control pests and diseases are often uneconomical. Furthermore, such applications can often lead to an imbalance in pest-predator populations which ultimately results in even higher pest levels. Host-plant resistance should be one of the main components of a pest and disease management strategy. Resistance has been found to all the key pests and diseases. For most, adequate resistance has been found in *M. esculenta*, though resistance to cassava mosaic disease was transferred from *M. glaziovii*. Resistance sources have been

identified for many pests and diseases, but in only a few cases have these sources been systematically used in breeding improved varieties.

Although on a worldwide basis there are a large number of pests and diseases affecting cassava, in a given region those of economic importance are generally limited. Soil, climate, and cropping system determine which pests and diseases are potentially important and the breeder generally can limit resistance breeding work to only a few key pests or diseases.

Because cassava enters such a wide range of markets requirements for root quality also vary accordingly. There is still a poor understanding of many of the factors influencing quality, particularly for the fresh market which has the most stringent quality requirements. For industrial purposes, starch content is often the most critical quality component, but root size, ease of peeling, and hydrogen cyanide (HCN) content may also be important. Because cassava is generally grown under rainfed, unfertilized conditions, root quality may be subject to wide variation resulting from influences of the environment. Breeding for stability of expression of quality traits across environmental variations should be an important objective.

Selection methodology

It was generally accepted that one of the major means of improving yield in cassava was through improving dry matter distribution within the plant, that is, harvest index. Harvest index may be especially important as a selection criterion in early selection stages under conditions of intergenotypic competition. It appears, at least under more favorable conditions, that harvest index in mixture is more closely correlated with yield in monoculture than is yield itself. Nevertheless, there appears to be enough variability for this phenomenon across environments that each breeding program should confirm the validity of different selection criteria based on local results.

Most breeding programs wish to improve upon local cultivars. In some cases, however, introduction of new varieties for the sole purpose of increasing genetic diversity of the crop may be justified. Thailand is one example where nearly the entire cassava area is planted to a single variety, Rayong 1. New varieties, even if they merely equal Rayong 1 in yield performance, could reduce the genetic vulnerability to a newly introduced pest or disease, or to an outbreak of an already present one because of changes in cultural patterns.

There was a general feeling of the need for more standardization of evaluation criteria used by different cassava breeders, so that information obtained in one program is understood in others.

Yield stability

Cassava, as a rainfed crop often grown under multiple environmental stress conditions, is subject to greater yield instability than high input crops where environmental variability is controlled. On the other hand, the physiological nature of cassava (for example, no critical stage of yield formation) allows the crop to produce under conditions where many other crops would fail completely. One of the objectives of many breeding programs is to limit the degree of instability through varietal adaptation. Lack of stability can be caused by any one of a range of environmental factors, including temperature, photoperiod, cropping system, soil conditions, and pests and diseases. In order to make progress in breeding for improved stability, the components causing instability in the target region must first be identified. It appears to be impractical to breed for very wide adaptability in cassava, and distinct agroecological zones often need to be defined within which stability can be sought.

Nontraditional breeding techniques

The biotechnology era is bound to affect, to a greater or lesser degree, the breeding of virtually all crops, and cassava will be no exception. At this early stage it is not possible to predict specific impact, but general areas of application can be postulated. Indeed, the workshop participants felt strongly that the new biotechnology should be viewed as another set of tools with which to further progress in cassava breeding; that these tools will not replace, but rather will complement more traditional techniques. The continued concentration on traditional techniques may be especially critical in a crop like cassava which often requires simultaneous manipulation of several gene complexes to achieve breeding goals.

Advanced lines to farmers' fields

Most national programs have some system for testing, multiplying, releasing, and extending new cassava varieties to farmers' fields. As with any other activity, this is done by various means and with varying degrees of effectiveness in different countries. There is no commercial seed

industry in cassava anywhere in the world. As a result, these activities are always the function of the state. But most programs find themselves in a highly experimental, relatively undeveloped area: that of extending new varieties of a vegetatively propagated crop to small, low-resource farmers.

Questions still remain about the appropriate number of testing sites and for how many years, before the release of a variety. Cassava yields generally demonstrate quite high coefficients of variation, perhaps because of a combination of the types of environment (variable) in which it is grown and because of the nature of the crop itself. The low multiplication rate of cassava is an inhibition to rapid dissemination of new varieties. Various rapid multiplication methods have been described. However, these all involve considerable effort and expense and can only be applied when a high level of confidence in the performance of a variety justifies their use. These limitations suggest that varietal release strategies should not necessarily be modeled after those used for seed-propagated crops. The relatively slow dissemination of new varieties (resulting from a low multiplication rate) has the advantage that most deficiencies can be detected before a large area is planted to a new variety.

Complementary roles of national programs and international centers

The most important steps to be taken by a national program are to collect, characterize, evaluate, and select local germplasm. This is especially so in such a germplasm-rich country as Brazil. National programs are encouraged to introduce appropriate germplasm provided by IARCs. At the same time they are encouraged to contribute their own germplasm to the IARCs for maintenance of duplicates, general evaluation, redistribution to national programs, and incorporation into gene pools developed by IARCs.

In countries where local germplasm is not particularly rich, maintaining a small working germplasm collection is recommended. Maintaining a vast number of introduced germplasm entries by a national program is discouraged. It has often been the experience that local traditional cultivars are excellent sources of genes for local adaptation.

IARCs are expected to maintain a comprehensive germplasm collection, develop improved gene pools adjusted to the needs of national programs, and distribute the materials through safe and efficient means to the national programs.

IARCs must recognize the sovereignty of national programs in releasing new varieties. Any variety releases must be done by or through national programs. The more the national programs take responsibility for germplasm introduction, evaluation and release, the more healthy will be the relationship between the IARCs and the national programs.

Seeds are unanimously welcomed as the major means of germplasm transfer from IARCs to national programs. Meristem-cultured clones are used for introducing specific characters for hybridization schemes or for possible varietal selection in the areas where growing conditions are similar to that of selection sites of the IARCs. There is general reluctance toward exchange of stem cuttings. Evaluation of local germplasm and careful description of breeding objectives should precede the introduction of exotic germplasm. Introduced germplasm should usually be tailored to compensate for specific deficiencies in local germplasm.

IARCs are also expected to take an active role in providing relevant information for national programs to better focus and strengthen their breeding activities. Information services and training offered by the IARCs actually inspired the formation of cassava research programs in many countries in the past. Feedback information from national programs to IARCs is also much needed. Thus, germplasm and training and information services remain the major function of the IARCs.

Data management and information exchanges

Although the principal product of a breeder's work is usually a set of plant genotypes, the accompanying information is an essential part of the package. Data management practices and information exchange among cassava breeders should be improved. There is a need for some degree of standardization to maximize "exchangeability" of information. Too often, the only data provided in summary reports are fresh root yields. This in itself is virtually meaningless to anyone seeking information on the potential usefulness of a clone for given conditions. At the minimum, basic information on climate, soils, fertilization, and other cultural practices should be included in reports. Since fresh root yield is rarely the only criterion of importance to farmers, other key information should be included, especially root dry matter content (or starch), an indication of plant form (height, branching habit), and reaction to pests and diseases. Within a country, and sometimes across countries, it should be possible to include common reference or check varieties so that the data would have more relative meaning.

Cassava breeders tend to publish little and this needs to be improved because the technical bulletins of institutions (where data are likely to be found) are generally not widely available. Periodic workshops such as the present one should be encouraged—they are invaluable for information exchange.

List of Acronyms and Abbreviations Used in the Proceedings of the Workshop on Cassava Breeding

Acronym	Institution	Country
ACRE	Adaptive Crop Research and Extension Project	Sierra Leone
BES	Bicol Experimental Station	Philippines
BNB	Banco de Nordeste do Brasil	Brazil
BPI-MAF	Bureau of Plant Industry of the Ministry of Agriculture and Food	Philippines
CATIE	Centro Agronómico Tropical de Investigación y Enseñanza	Costa Rica
CENARGEN	Centro Nacional de Recursos Genéticos	Brazil
CIAT	Centro Internacional de Agricultura Tropical	Colombia
CIP	Centro Internacional de la Papa	Peru
CNPMF	Centro Nacional de Pesquisa de Mandioca e Fruticultura	Brazil
CNRCIP	Cameroon National Root Crop Improvement Program	Cameroon
CPAC	Centro de Pesquisa Agropecuária dos Cerrados	Brazil
CPATU	Centro de Pesquisa Agropecuária do Trópico Umido	Brazil
CRIFC	Central Research Institute for Food Crops	Indonesia
CSAC	Camarines Sur Agricultural College	Philippines
CTCRI	Central Tuber Crops Research Institute	India
EEC	European Economic Community	Belgium

Acronym	Institution	Country
EMBRAPA	Empresa Brasileira de Pesquisa Agropecuária	Brazil
EMCAPA	Empresa Capichaba de Pesquisa Agropecuária	Brazil
EMPASC	Empresa de Pesquisa Agropecuária de Santa Catarina	Brazil
EPACE	Empresa de Pesquisa Agropecuária do Ceará	Brazil
ESALQ	Escola Superior de Agricultura Luiz de Queiroz	Brazil
IAC	Instituto Agrônômico de Campinas	Brazil
IADS	International Agricultural Development Service	USA
IARC	International Agricultural Research Center	Various
IBPGR	International Board for Plant Genetic Resources	Italy
IDRC	International Development Research Centre	Canada
IFARD	International Federation of Agricultural Research Systems for Development	Italy
IFS	International Foundation of Science	Sweden
IITA	International Institute of Tropical Agriculture	Nigeria
INERA	Institut National pour l'Etude et la Recherche Agronomique	Zaire
INIA	Instituto Nacional de Investigaciones Agrícolas	Mexico
IPA	Instituto Pernambucano de Pesquisa Agropecuária	Brazil
IPB	Institute of Plant Breeding	Philippines

Acronym	Institution	Country
IPEAL	Instituto de Pesquisas e Experimentação Agropecuárias do Leste (now CNPMF)	Brazil
IRRI	International Rice Research Institute	Philippines
ISAR	Institut des Sciences Agronomiques du Rwanda	Zaire
MARDI	Malaysian Agricultural Research and Development Institute	Malaysia
MSAC	Mountain State Agricultural College	Philippines
NAFPP	National Accelerated Food Production Program	Nigeria
NRCRI	National Root Crop Research Institute	Nigeria
NSS	National Seed Service	Nigeria
PCARR	Philippine Council for Agriculture and Resources Research (now PCARRD)	Philippines
PCARRD	Philippine Council for Agriculture and Resources Research and Development	Philippines
PRCRTC	Philippine Root Crop Research and Training Center	Philippines
PRONAM	Programme National Manioc	Zaire
TCA	Tarlac College of Agriculture	Philippines
UEPA.Ec	Unidades de Execução de Pesquisa de Ambito Estadual e Territorial	Brazil
UFBA	Universidade Federal da Bahia	Brazil
UNDP	United Nations Development Programme	USA
UP	University of the Philippines (interchangeable with UPLB)	Philippines
UPLB	University of the Philippines at Los Baños (interchangeable with UP)	Philippines

Acronym	Institution	Country
USAID	United States Agency for International Development	USA
USM	University of Southern Mindanao	Philippines
ViSCA	Visayas State College of Agriculture	Philippines

Abbreviation Description

CAD	Cassava anthracnose disease
CBB	Cassava bacterial blight
CEC	Cation-exchange capacity
CGM	Cassava green spider mite
CGR	Crop growth rate
CMB	Cassava mealybug
CMD	Cassava mosaic disease (also known as African mosaic disease)
CV	Coefficient of variation (statistical)
DM	Dry matter
DNA	Deoxyribonucleic acid
ECZ	Edaphoclimatic zone
ESRP	Efficiency of storage root production
HCN	Hydrogen cyanide (also known as prussic acid)
HFGS	High fructose-glucose syrups
ISS	Initial plant weight at which storage root production starts
LAI	Leaf area index
LSD	Least significant difference (statistical)
MM	<i>Mononychellus</i> mite
PBA	<i>Plant Breeding Abstracts</i>

Abbreviation Description

PMC	Pollen mother cells
RNA	Ribonucleic acid
SD	Standard deviation of sample (statistical)
SE	Standard error of mean (statistical)
SE	Superelongation disease
vpm	vppm = Volumetric parts per million

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