Breeding Cassava for Adaptation to Stress Conditions: Development of a Methodology

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ABSTRACT

Cassava (*Manihot esculenta* Crantz) appears to have an advantage over many tropical crops in its adaptation to marginal agricultural areas, especially in terms of drought tolerance, tolerance to high soil acidity, and ability to produce reasonably well on soils of low fertility. Wide genetic variability also exists for resistance to most disease and pest problems affecting cassava. CIAT's cassava breeding program is designed to exploit the adaptation of cassava to various physical and biological stress factors by selection over a range of moderate to high stress environments. The selection environments are described and a decentralize breeding methodology outlined.

Introduction

Empirical evidence gained over many years of cultivation as well as recent studies suggest that cassava (*Manihot esculenta* Crantz) has a comparative advantage over many crops in its adaptation to important low productivity and even marginal agricultural areas. Cassava has long been known for its ability to survive and produce reasonably in water stress situations, on soils of low fertility, on soils of high aluminum saturation and low pH, in diverse climatic conditions, and with low inputs for disease and insect control.

In a world where food production increase will rely on bringing marginal lands into production, cassava can play an important role as an efficient calorie producer especially in less resource-rich countries where the level of inputs required for more demanding crops is often economically prohibitive.

At the Centro Internacional de Agricultura Tropical (CIAT) in Cali, Colombia, the genetic improvement of cassava is being directed principally toward maximizing productivity under low input conditions. Adaptation to many biological and physical environmental stresses is being sought through breeding rather than through purchased inputs. Nevertheless, simple and inexpensive cultural practices also form an important part of the technological package.

This paper describes common stresses which limit productivity of cassava, the definition of discrete edapho-climatic zones for cassava production, the presently available germplasm base for cassava improvement, and the methodology which has been developed at CIAT for breeding for improved productivity under stress conditions.

Common Stresses in Cassava Production

In most regions, cassava is grown with zero or low fertilizer application, without irrigation, without chemical control of diseases and pests, and in generally low productivity environments. Throughout its long growing cycle, cassava commonly is exposed to a wide range of physical and biological environmental stresses.

Temperature and photoperiod

Cassava is principally grown in the lowland tropics, but extends into the northern and southern subtropics and into the highland tropics up to 2,200 m a.s.l. In the subtropics, low winter temperatures and long summer days may cause high stress for unadapted clones. CIAT studies (CIAT, 1981) suggest that long days can drastically reduce yields but that varietal differences in photoperiod sensitivity apparently exist. Likewise, Irikura et al (1979) have clearly shown that distinct genotypes are required for high altitude (mean temperature less than 22°C) compared to the lowland tropics.

Soil water availability

In many regions cassava must tolerate extended dry periods without supplemental water supply. Dry periods of 3 to 5 months or even longer are common. In addition, shorter dry periods during the rainy season are normal in low rainfall regions. Cassava is able to utilize water extremely efficiently by rapidly reducing leaf area under stress (Conner et al, 1981). Under drought stress, top growth is reduced proportionally more than root yield, often resulting in minimal reductions in root yield (Conner et al, 1981).

Ambient relative humidity

Recent physiological studies have shown cassava to be very sensitive to low relative humidity of the atmosphere. Rapid stomatal closure and highly reduced photosynthetic rates accompany stress caused by low relative humidity (CIAT, 1981).

Soil characteristics

Though soil fertility and pH status can be readily modified by addition of fertilizers and lime, this option if often not practiced by small farmers with limited economic resources. Much cassava production is on soils of low nutrient status, high aluminum saturation levels and/or low water-holding capacity.

Pests and diseases

The long growing cycle of cassava makes it a potential host over a range of environmental conditions even within the same region. Build-up of different pest and disease complexes may be favored at various periods during the growth cycle. Under traditional growing systems pests and diseases are normally not major yield constraints, the modernized cultural practices, including monocropping, higher density planting, and continuous cassava cultivation, have generally contributed to worsening pest and disease problems (Lozano et al, 1983).

Edapho-Climatic Zones for Cassava Production

The existence of such a wide range of environmental conditions for which cassava improvement must be directed, along with yield and quality considerations, makes breeding for wide adaptability across all components of environmental variability a practical impossibility. CIAT has delineated six combinations of edapho-climatic characteristics which appear to constitute a necessity for basically different genotypes (Table 1). Edapho-climatic zones (ECZ's) are defined first on the basis of temperature: lowland tropics (ECZ 1, 2, 3); middle altitude tropics (ECZ 4); highland tropics (ECZ 5) and subtropics (ECZ 6). Further division within the lowland tropics is based on rainfall distribution and soil characteristics: low to moderate rainfall with long dry season (ECZ 1); moderate to high rainfall with acid savanna soils (ECZ 2); high rainfall well distributed throughout the year (ECZ 3).

Table 1. Cassava edapho-climatic zones and their principal characteristics.

Edapho-climatic zone	General description	Representative areas
1	Lowland tropics with long dry season, low to moderate annual rainfall; high year-round temperature.	North-eastern Brazil; north coast of Colombia; northern Venezuela; Thailand, southern India; sub-Sabelian Africa.
2	Acid soil savannas; moderate to to long dry season; low relative humidity during dry season.	Llanos of Colombia and Venezuela; Cerrado of Brazil; savanna of Southern Mexico.
3	Lowland tropics with no pronounced dry season; high rainfall; constant high relative humidity.	Amazons basin region of Brazil, Colombia, Ecuador, and Peru; rainforests of Africa and Asia.
4	Medium altitude tropics; moderate dry season and temperature.	Andean zone; Costa Rica; Bolivia; Brazil; Africa; the Philippines.
5	Cool, tropical highland areas, with mean temperatures of approximate 17-20°C.	Andean zone; highlands of tropical Africa.
6	Subtropical areas, with cool winters and fluctuating daylengths.	Southern Brazil; Paraguay, northern Argentina; Cuba; Northern Mexico; southern China; Taiwan.

Potential importance of pests and diseases in cassava is largely dependent upon climatic and soil conditions of a region, along with presence of a susceptible host and cultural practices. Thus, each ECZ can be identified with a unique combination of disease and insect pest problems (Table 2). For example, bacterial blight requires minimum critical day-night temperature fluctuations to become epidemic; superelongation disease requires extended rainy periods, phoma leaf spot requires constant low temperatures, and mites and thrips are most serious during extended dry periods (Lozano et al, 1981).

Obviously, it is unlikely that any given region will have all the pests and diseases defined as potential problems for that edapho-climatic zone. Micro-environmental variations, differences in cultural practices, differences in varietal susceptibility, and whether or not the pest or pathogen has been introduced, will all affect the balance of biological problems in a given cassava plantation.

Colombia, where CIAT is headquartered, contains a wide range of climatic and soil conditions as well as most of the pest and disease problems which affect cassava. Areas representative of five of the six ECZ's have been identified in Colombia, excepting only a subtropical region with cool winters and fluctuating photoperiods. CIAT has developed intensive selection programs for ECZ's 1, 2, 4 and 5, in Colombia, and collaborates with national research programs for selection in all zones.

The Available Germplasm Base for Cassava Improvement

Cassava completed the major part of its evolution in Latin America, up to the time of the arrival of Europeans in the Americas when it was carried to Africa and Asia. Thus the present gene pool of cassava can basically be considered to have developed under the selection pressures imposed by tropical American conditions. Cassava growing areas of the Americas encompass a high diversity of climatic and soil conditions, and consequently genetic adaptation to a high diversity of conditions has evolved.

The evolution of cassava has been largely directed by conditions existing in traditional agricultural systems, including intercropping, varietal mixtures, spatial separation of cultivated areas, and fertility management by rotation and fallowing. These management conditions probably contributed to moderation of disease and insect pressures, and thus the level of genetic resistance required to maintain populations at subeconomic levels was not high. Nevertheless, the resistance which did evolve was in many cases due to multiple mechanisms, each under multigenic control. This type of resistance can be expected to be stable and durable.

Because agriculture was extensive rather than intensive, competitiveness with associated crops and root quality were more important in cassava than productivity per unit area (Kawano and Jennings, 1981). Traditional varieties often evolved with low harvest index, i.e., a large proportion of top growth compared to roots.

Many majors crops have undergone a long history of genetic modification by plant breeders, often under conditions of good land preparation, high soil fertility, irrigation and artificial disease and insect control. Under these controlled and uniform conditions of selection, inherent tolerance to environmental stresses is unnecessary. Consequently, resistance genes were lost from breeding populations, or reduced to low frequencies. If at some later time, selection for resistance was initiated, resistance had to be built upon a narrow genetic base and often resulted in single--mechanism resistance under mono--or oligogenic control.

Table 2. Importance of various physical and biological environmental factors in different edapho-climatic zones for cassava production.

Environmental factor	Controlability other than by genotype[1]	Potential for adaptation through breeding[2]	Probability of stress effects in each edapho-climatic zone[3]					
			I	II	III	IV	V	VI
Physical Environment								
Temperature	0[4]	++	0	0	0	+	+++	+++
Ambient Rel. Humidity	0	++	+++	+++	+	++	+	+
Photoperiod	0	++	+	+	+	+	+	+++
Soil water	+	++	+++	+++	+	+	+	+
Soil acidity	++	++	+	+++	++	+	++	++
Soil phosphorus	++	++	++	+++	++	++	++	++
Biological Environment								
Bacterial blight	+	+++	++	+++	+	++	+	+++
Cercospora leaf spots	+	+++	++	++	++	++	+	++
Phoma leaf spot	+	+++	0	0	0	+	+++	++
Superelongation	+	+++	++	+++	++	++	+	+++
Anthracnose	+	++	+++	+++	++	++	++	+++
Root rots	++	+	+	+	++	+++	++	+++
Green cassava mite	++	+++	+++	+++	+	++	+	+
Red spider mite	++	++	+++	++	+	++	+	+
Thrips	+	+++	+++	+++	+	+++	+	+
White fly	++	++	++	++	++	++	+	+
Hornworm	+++	+	++	++	++	++	+	++
Shoot fly	++	+	++	+	++	++	+	++
Lace bug	+	++	++	+++	+	++	+	+
Mealy bug	++	++	+++	+++	++	++	+	+
Scale insects	+++	+	++	++	++	++	++	++
Weeds	+++	+	+++	+++	+++	+++	+++	+++

[1]The degree to which a given factor can be modified in its effect on the plant, other than modification genetically of the plant.

[2]The estimated potential for changing genotype to adapt to different states of each factor, based on known genetic variability, type of gene control and heritability.

[3]Stress effects for physical factors defined as resulting from low temperature, low relative humidity, long photoperiod, low soil water availability, high soil acidity and low soil phosphorus.

[4]Subjective evaluation, where: 0 = zero or near zero, + = low, ++ = moderate, +++ = high.

In cassava, modern breeding practices have only recently been applied and the genetic base remains in a nearly untouched condition. Breeding populations include wide genetic diversity and gene frequencies for many traits have not yet been changed dramatically. This situation provides a unique opportunity in a major crop to build upon diverse sources of low and moderate resistance to environmental stress.

CIAT maintains a germplasm collection of more than 3,000 clones from most cassava-growing regions of Latin America (Table 3). This native diversity serves as the germplasm base for genetic improvement efforts.

Table 3. Origin of cassava accessions maintained at CIAT.

Country of Origin		Numbers of Accessions
Colombia		1,759
Venezuela		253
Brazil		535
Peru		150
Ecuador		125
Cuba		73
Mexico		65
Panama		21
Puerto Rico		16
Costa Rica		16
Dominican Republic		5
Paraguay		3
Bolivia		3
Malaysia		3
Thailand		1
	Total	3,028

A Breeding Strategy

The overall cassava breeding strategy at CIAT consists of: (1) germplasm accession evaluation in diverse ECZ's in Colombia; (2) parental selection and formation of gene pools for each ECZ based on performance of germplasm accessions; (3) hybrid evaluation and selection primarily within but also across ECZ's; and (4) recommendation to national programs for testing of selected clones and/or progeny of specific crosses.

The breeding scheme is basically one of simple recurrent selection, where selected hybrids are further utilized as parents to continually improve the base populations. In the present discussion, emphasis is given to breeding for stress adaptation although a wide range of other traits are also considered in the breeding program.

Evaluation sites

Evaluation for stress tolerance has historically followed one of two distinct approaches: evaluation under highly controlled conditions where only a single stress factor in permitted to be manifested, or evaluation under field conditions where environmental variability may be high and various stress factors interacting. After the accumulation of considerable experience in both approaches, CIAT now gives priority to evaluation under field conditions for most characteristics. Selection of appropriate evaluation sites thus becomes one of the most crucial aspects of a breeding program.

CIAT, as an international organization, has responsibility for development of improved cassava germplasm to meet the needs of all cassava growing countries, and not only Colombia where it is located. This obviously implies that some level of wide adaptation will be essential for the new varieties. However, we have seen that the combination of resistances/tolerances to all the potential yield-limiting stresses of cassava is a virtual impossibility. Furthermore, it is now evident that common combinations of stress exist, and that these form logical subdivisions of breeding objectives.

The principal evaluation and selection sites should then combine as many of the potential stress factors as possible for the particular edapho-climatic zone to make the final selected products as broadly relevant as possible within similar regions. Moderate and high stress situations assure that selected clones will have adequate resistance or tolerance over a wide range of conditions, including regions where particular stresses may not exist, or exist in low levels. On the other hand, selection under non-stress situations would result in clones with insufficient resistance under stress. Characteristics of principal evaluation sites are given in Table 4.

Germplasm evaluation

Most CIAT germplasm collection has been evaluated in the north coast region (ECZ 1), the eastern plains (Llanos Orientales) (ECZ 2) and at CIAT-Palmira headquarters (ECZ 4). To a smaller degree evaluations have been done in Popayán, an Andean highland site (ECZ 5). All evaluations are carried out without disease or pest control, without irrigation, and with low levels of fertilizer applications only in the lowest fertility sites. Emphasis in evaluation is for overall performance and integrated resistance to stresses as demonstrated by root yield and quality at the end of the growing season.

Colombian North Coast (ECZ 1). Under the high temperature, long dry season conditions of the north coast region of Colombia, principal stresses are from low soil fertility, a long dry season (4-5 months) and mite attack during the dry season. Bacteriosis, superelongation and root rots are problems in some years when rainfall is above normal. Low yield and low dry matter characterisize most germplasm accessions when evaluated in this region. General average yield of the germplasm evaluations in single-row trials was 1.8 kg/plant. Average dry matter content was 28.3%.

Carimagua (ECZ 2). Principal yield constrains in Carimagua in the Llanos Orientales are low native soil fertility, high aluminum saturation and low pH, bacterial blight, anthracnose, superelongation disease, mites thrips, and mealybugs. Disease problems have received the most emphasis in germplasm evaluations, as their severity precludes any reasonable yields in the absence of moderate to high resistance levels. Only about 1% to 2% of the germplasm accessions show reasonable combined resistance to the stresses in Carimagua (Table 5).

Table 4. Principal climatological and edaphic characteristics of sites for cassava germplasm evaluation in Colombia.

	Edapho - climatic zone	Altitude (masl)	Mean temperature	Annual rainfall (mm)	Soil texture	Soil pH	Organic matter (%)	P Bray II (ppm)	K (meg/100g)
Media Luna	I	10	27.2	800-1,200	Sandy loam	6.6	0.7	7.2	0.08
Valledupar	I	120	28.0	700-1,100	Sandy loam	6.9	1.1	25.0	0.22
Carimagua	II	200	26.2	1,800-2,600	Silty clay	4.7	3.2	1.9	0.14
CIAT-Palmira	IV	1,000	23.8	600-1,500	Clay	7.4	4.1	81.5	0.69
Popayan	V	1,760	18.0	1,800-2,500	Clay loam	5.5	7.4	2.0	0.04

Table 5. Combination of characters required for cassava germplasm by edapho-climatic zone in Colombia.

Target area	Principal breeding objectives for each area[1]	Level of expression	Accessions (No.)
North coast	Root yield (kg/plant)	$\geq$ 3.5	1 007
(ECZ 1)	+ Harvest index	$\geq$ 0.5	432
	+ Root dry matter (%)	$\geq$ 35	313
	+ *Mononychellus* mite damage[2]	$\leq$ 2	57
	+ Thrips damage[2]	$\leq$ 2	42
Carimagua	Bacterioris damage[2]	$\leq$ 3	55
(ECZ 2)	+ Superelongation damage[2]	$\leq$ 3	21
	+ Mononychellus mite damage[2]	$\leq$ 3	6
	+ Vatiga damage[2]	$\leq$ 3	4
Popayan	Phoma damage[2]	$\leq$ 2	17
(ECZ 5)	+ *Oligonychus* mite damage[2]	$\leq$ 2	10

[1]Data from CIAT-Palmira: root yield from single row trial, harvest index, root dry matter, mite and insect ratings. Data from Carimagua: bacteriosis and superelongation ratings. Data from Popayán: Phoma ratings.

[2]Disease, mite, and insect ratings on a 1 to 5 scale, where 1 = very low damage; 5 = very high damage.

CIAT-Palmira (ECZ 4). CIAT-Palmira headquarters are in a fertile, middle altitude inter-Andean valley, where rainfall is low but normally well distributed throughout the year. Except for root rots, disease are generally at low levels. Thrips mites and mealy bug populations can be high, especially during extended dry periods. Most cassava germplasm accessions are adapted to CIAT conditions to the extent that they can continually be maintained and multiplied. Average yield and root dry matter content of germplasm bank accessions evaluated at CIAT were 3.9 kg/plant and 35.1%, respectively.

Popayan (ECZ 5). Low ambient temperature, phoma leaf spot and anthracnose are the principal factors limiting adaptation of cassava in Popayan. Because low temperature tolerance per se is difficult to evaluate, most emphasis in preliminary evaluation of the germplasm bank is on plant vigor and disease resistance. The number of accessions with good adaptation to these stress conditions is very limited; the small number which are adapted have nearly all been collected from similar highland regions.

In summary, many germplasm accessions (which have been or still are nearly all cultivated varieties) seem to be well adapted to traditional cultural practices in areas where they evolved, in the sense that they can produce low but stable yields (Lozano et al, 1983). However, most do not seem to be able to fully exploit improved cultural practices. Yield potential, disease and insect resistance, and root quality all need to be improved. Thus the cassava program's emphasis is on creating new improved genotypes through hybridization and selection.

Parental selection and hybridization

In each zone, best-performing accessions are evaluated through several cycles. Those which give stable performance in terms of integrating edapho-climatic adaptation, resistance, yield and quality, are selected as parents and enter hybridization blocks. Single trait selection is largely avoided, as an inefficient methodology for achieving overall acceptability of hybrids. Some level of broad adaptability across zones is an additional advantage for potential parents, to avoid selection for high site-specificity for the Colombian selection sites.

Crossing blocks are separated for the low to medium altitude tropics, the highland tropics and the subtropics. For zones within the low to medium altitude tropics, crosses are directed primarily among clones adapted to the same zone, but also crosses between materials for different zones are made to transfer and recombine specific characteristics.

Hybrid selection

Ideally, selection would be in as many sites as possible, to identify the best genotypes for every different environment. On the other hand, for logistic and administrative reasons, number of sites must be limited. Studies at CIAT have developed a methodology for logical balance to breeding for wide adaptability compared to specific adaptability in the given ECZ's.

Planting of F_1's directly in principal selection sites. The maximum adaptability to a given ECZ should be achievable by initiating selection directly from the F_1 stage within the representative region. To achieve this theoretical optimum F_1 seeds have been planted directly in the fields at Carimagua, Media Luna and Popayan (Table 6). In summary, two principal problems were observed with selection beginning with the F_1 in moderate and high stress selection sites: (1) seed germination was variable and generally well below what is expected under favorable conditions; (2) plant development is generally slower for seed-derived plants, and yield formation seems to be particularly delayed.

These data suggest that selection of F_1's in diverse stress conditions may not only be difficult logistically, but also difficult for agronomic reasons.

Preliminary selection in CIAT-Palmira. Different production constraints in Carimagua (low soil fertility, CBB, superelongation) and Popayán (low temperature, phoma leaf spot), compared to CIAT-Palmira. Effectiveness of selection in CIAT conditions must be limited for eventual adaptation in these zones. One interesting case is for selection for ECZ 1 (Media Luna in CIAT program) and ECZ 4 (CIAT-Palmira) where some of the major yield constraints seem to be common.

Studies assessed the possibility of preliminary selection at CIAT-Palmira for adaptation in ECZ 1. F_1 seeds were planted directly in the field at Media Luna, and seedlings transplanted in CIAT-Palmira. At harvest, five stakes from each plant in both CIAT and Media Luna were planted in a single row trial in Media Luna. The lack of a correlation for either yield per plant or harvest index in CIAT with yield in Media Luna indicates that selection in CIAT for this zone may not be effective. A highly significant correlation was observed between root yield in the F_1 generation and root yield in the single row trial, with F_1 plants harvested in Media Luna. These data illustrate that for Media Luna conditions, selection for yield in CIAT-Palmira is much less effective than *in situ* selection at Media Luna.

Current selection scheme at CIAT. As a result of previously described studies, the current selection scheme has been developed which involves: (1) planting all F_1 progeny at CIAT headquarters where adequate care can be given to young seedlings, and where they develop normally; (2) harvest at 6 months; (3) mild selection to eliminate inferior genotypes; (4) cutting two stakes per plant, one remains in CIAT, the other sent to the principal selection site of the ECZ for which the cross was made. This intermediate selection stage following the F_1 is denoted as "F_1C_1" (first clonal generation of the F_1) to signify evaluation and selection procedures similar to that of an F_1 from true seed. Selection continues within each ECZ, and simultaneously the selected clones are maintained, evaluated and multiplied in CIAT-Palmira. At the intermediate selection stages, clones are tested across ECZ's to evaluate for reaction to a broad range of physical and biological environmental factors, and for general broad adaptation.

Throughout all stages of evaluation emphasis is given to selection for combined tolerance/resistance to the yield-limiting factors within each ECZ, as well as high yield potential and good root quality. The end result is clones having broad adaptability within each ECZ, but not necessarily across widely different zones. This strategy allows rapid progress by limiting the number of characters which must be combined for any given clone, while at the same time developing genotypes for the entire range of target area conditions. Germplasm can then be moved internationally to areas with similar edapho-climatic and pest conditions, with high probability of successful adaptation.

Table 6. Summary of results of hybrid cassava seeds direct-planted in moderate and high stress sites in Colombia.

Site	Year	Number of seeds planted	Germination (%)
Media Luna	1980	3,961	28.3
	1981	3,570	53.6
Valledupar	1981	1,935	40.9
Carimagua	1978	21,610	38.5
	1979	36,404	26.5
	1980	13,086	44.2
	1981	9,834	29.9
Popayán	1980	171	26.0

Table 7. Average yield data of promising cassava germplasm accessions and hybrid lines. Summary of seven years of trials by CIAT regional trial and varietal improvement sections at 12 Colombian locations.

Genotype		Fresh root yield (t/ha/yr)	Root dry matter Content (%)	Dry root yield (t/ha/yr)
Germplasm Accession				
M Col 22	(47)[1]	22	34	7.4
M Col 1468 or CMC 40	(55)	28	30	8.4
M Col 1684	(55)	30	31	9.3
M Ven 218	(28)	25	33	8.2
Hybrid Line				
CM 91-3	(25)	29	34	9.8
CM 321-188	(24)	33	35	11.4
CM 342-55	(22)	32	29	9.2
CM 342-170	(21)	29	33	9.4
CM 489-1	(23)	35	29	10.3
CM 507-37	(20)	28	31	8.8
CM 523-7	(20)	23	37	8.4
Local Control	(79)	17	33	5.7

[1]Figures in parenthesis indicate number of trials in which each genotype has been tested.

Source: CIAT. 1981. Cassava Program 1981 Annual Report. Cali, Colombia.

Advances in Selection

The breeding strategy has resulted from a careful evolution of experience in cassava research at CIAT and other institutes. CIAT has been selecting cassava in a range of low, moderate, and high stress environments since the earliest years of the cassava program. Regional trials data over 7 years illustrate the high potential for increasing cassava productivity with simple technology (good land preparation, stake selection and treatment, adequate planting density, and timely weed control) combined with new varieties (Table 7). In all low to medium altitude sites (selection for high altitudes is recent), selected clones have outyielded local varieties. Similar results have been observed in international trials (CIAT, 1980). In addition to many clones having high tolerance to stresses in individual ECZ's, others have been identified with broad resistance across several distinct zones. These data provide solid evidence for the potential of increasing the productivity of cassava in stressful environments by breeding combined with simple cultural practices. At the same time, these stress-tolerant clones can respond to higher productivity environments.

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