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BREEDING CASSAVA FOR ADAPTATION TO A NEW ECOSYSTEM: A CASE STUDY FROM THE COLOMBIAN LIANOS

Sélection du manioc pour son Adaptation à un nouvel Ecosystème: Une Etude de Cas dans les Plaines Colombiennes

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SUMMARY

Cassava (*Manihot esculenta Crantz*) has often been described as a rustic crop which suffers little damage from pests and diseases. More recent evidence has shown that taking cassava clones from their native habitat, or submitting them to intensified cultural practices, can result in high and unstable pest and pathogen populations. A case study is presented for a breeding program carried out over a ten-year period at the Carimagua experiment station in the middle of the Colombian llanos. Breeding methodology is described and the dynamics of pest and pathogen fluctuations are traced. Significant genetic advance over selection cycles is observed through comparison with standard checks. General principles are suggested for breeding cassava for new ecosystems created by introduction of the crop to new areas, through changes in cultural practices, or by introduction of new pests or diseases into an area.

RESUME

Le manioc (Manihot esculenta Crantz) *a souvent été décrit comme une culture rustique peu affectée par maladies et parasites. Des évidences plus récentes ont montré que le transfert de clones hors de leur habitat d'origine ou leur utilisation en culture intensive pouvait conduire à des niveaux variables et élevés de populations parasitaires. Une étude de cas est présentée à partir d'une sélection conduite sur une dizaine d'années à Carimagua au milieu des plaines colombiennes. La méthode de sélection est décrite de même que les dynamiques des fluctuations parasitaires. Un progrès génétique significatif est observé au cours des cycles de sélection par rapport aux témoins classiques. Des principes généraux sont suggérés pour la sélection du manioc en vue de nouveaux écosystèmes découlant de passage dans de nouvelles aires ou de modifications culturales.*

INTRODUCTION

Cassava's ability to produce high root yields in drough-prone areas and on soils of low fertility status, with minimal inputs of fertilizers or pesticides, makes it a crop ideally suited to many small farms in the tropics. Cassava has historically been considered a rustic crop with few serious pest[1] problems (Purseglove, 1968). Evidence accumalated over the past several years, however, his shown that this belief is based primarily on observations of regionally evolved and selected varieties grown under traditonal cultural practicies (LOZANO _et al_., 1980). Within these systems, the pest populations are often in balance with their natural enemies and the host plant, and are thus maintained at low levels.

Although it is still widely grown as a small-farmer crop in traditional agricultural systems, new varieties and new production technology are increasingly being adopted by farmers. In additions, the crop is expanding into new areas as population pressures move agriculture into more marginal lands. Such changes, either in cultural practices or in variety, can result in an imbalance in the established equilibrium, with a subsequent pest outbreak. As cassava is a long-season crop, insecticides or fungicides would have to be applied over a long period to provide satisfactory protection. Its low value however, generally makes this uneconomical. For many pest problems the best control strategy is through host plant resistance.

This paper describes an example from the Colombian llanos where heavy pest outbreaks occured following the introduction of susceptible varieties and intensive cultivation practices into a region where previously there were only scattered plantings of cassava. Through a concerted interdisciplinary genetic improvement program over a ten-year period, a high level of resistance to the major disease problems, combined with improved yield potential, has been achieved. Insect and mite resistance is recently receiving more attention. From this experience a generalized strategy may be suggested for optimizing the possibility of developing high and stable resistance, especially for potentially destabilizing situations created by changes of variety or cultural practices, or introduction of new pests.

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[1] The term "pest" will be used throughout the paper to refer to pathogens, mites, and/or insects.

MATERIAL AND METHODS

The Centro Internacional de Agricultura Tropical (CIAT) concentrates its cassava breeding efforts on the development of germplasm tolerant to the prevalent stresses of major present and potential cassava-growing areas, and on selection for high and stable yields under low agronomic inputs. For purposes of its breeding strategy CIAT has divided cassava-growing regions into six basic classifications (edapho-climatic zones), defined primarily in terms of climatic and soil variables, and secondarily by pest and disease problems (HERSHEY, 1984). Within this classification, Edaphoclimatic Zone 2 (ECZ 2) is described as the moderate to high rainfall lowland tropics, with an extended dry season and acid, infertile soils. The savannas of southern Mexico, the llanos of Colombia and Venezuela, and parts of the Campo Cerrado of Brazil are considered to be regions within ECZ 2. As the primary evaluation and selection site for this broadly defined zone, CIAT collaborates with the Instituto Colombiano Agropecuario (ICA) on the ICA station of Carimagua in the middle of the Colombian llanos (Table 1).

Cassava is traditionally grown throughout the inhabited areas of the Colombian llanos, both by indigenous peoples and more recently by colonists. However, as human population density is very low, plantings are widely scattered. The crop is generally planted as a backyard crop for home consumption. Commercialization is minimal due to lack of accessible markets. The diversity of native cassava germplasm in the region is attested to by CIAT's collection of over 100 local varieties from the Department of Meta alone, which encompasses only a small proportion of the total llanos. As a whole, the varieties from this region have moderate resistance to Cassava Bacterial Blight (CBB, caused by *Xanthososoma campestris pv. manihotis)*, and Superelongation Disease (SED, caused by *Elsinoe brasiliensis*, and are susceptible to mites and thrips (HERSHEY, In press).

The results presented in this paper are from an ongoing breeding program initiated at Carimagua in 1974. CIAT Annual Reports describe in detail the goals, methodology and results of this program. Selection over the years has been applied to a wide range of traits, including germination ability, early vigor, plant architecture, pest resistance (principally CBB and SED, but also lacebug *(Vatiga spp.)* and mites *Mononychellus spp.)*, root yield, root HCN and root dry matter content. Nevertheless, the highest selection intensity has been applied to root yield and root dry matter content, on the assumption that final root yield is the best integrator of a wide range of adaptation, resistance and productivity factors.

The breeding methodology has changed somewhat over the years, but the consistently involved some form of recurrent selection, with parental selection based on phenotype and progeny performance, followed by recombination, and progeny selection through a number of cycles of vegetative propagation.

Table 1. Edaphoclimatic description of Carimagua experiment station.

Location	Climate	Soils
Longitude : 4.5°N	T_{max} (daily mean; °C): 30.8	Classification: oxisol (Typic Haplustax)
Latitude: 71.3° W	T_{min} (daily mean; °C): 22.0	Structure: Clayey, Kaolinitic
Altitude: 150 masl	Annual precip. (mm): 2100	PH: 4.7
	Months 100 mm rainfall: 4	Organic matter (%): 3.2
	Rainy season: April to November	P (Bray II ppm): 1.9
		K (meq/100 g): 0.14
		Al (% saturation): 80-90

Results are presented here only for advanced yield trials. These consisted of plots of 25 plants with 2-3 replications. At harvest, the central 9 plants were harvested, leaving a surrounding border row to minimize intergenotypic competition effects. Yield trials have included varying numbers of genotypes, with a mean of about 75 per season. Each trial contained several standard checks, including local varieties and promising selections. As some of the checks have changed over time, results of only two checks which were included in all trials over the period are included here. these were M Col 1438 (Llanera), a local variety from the llanos, and M Col 1684, a germplasm accession with high yield potential from the Colombian Amazon region.

Yield trials were planted in two different periods of each year. "A season" trials were planted near the beginning of the rainy season, usually in April or May, and "B season" trials were planted near the end of the rainy season, usually in September or October. Experimental plots were prepared with ridges and trials were planted at a population of 12,500 plants/ha. Dolomitic lime was incorporated at the rate of 0.5 t/ha at the time of land preparation. Soon after planting, fertilizer was applied by banding at the base of the plants, at a rate of 50 to 75 kg/ha N, 100 to 150 kg/ha each of P_2O_5 and K_2O, and 10 kg/ha of Zn. Good weed control was maintained by a combination of herbicide and hand weeding. No insecticide, fungicide or irrigation was applied to any trial. During the growing cycle, data were taken on various delopmental parameters, and pest damage levels. At harvest, yield, root dry matter and root HCN levels were calculated. Selected clones from each yield trial were repeated the following cycle, and new genotypes were advanced from the preliminary yield trials at Carimagua.

Breeding trials were begun in the A season of 1974 (1974A) with a single row planting of 300 germplasm bank accessions selected previously in the CIAT headquarters station at Palmira (CIAT-Palmira), which is kept free of CBB and SED. Subsequent trials consisted mostly of hybrid clones, but also included some selected germplasm accessions. During the 1975B and 1976B plantings, CBB infections were kept at a minimum by using CBB-free planting material from CIAT-Palmir, and planting in isolated sites within the Carimagua station. Even with these precautions, disease incidence increased rapidly because of foci of infections at neighboring farms. Beginning in 1977A the decision was made to allow disease epidemics to take their natural course, and concentrate instead on selecting resistant clones. Thus, concerted disease resistance breeding began with the 1977A planting. In 1977 and 1978 an extensive germplasm screening was carried out to identify new sources of resistance and adaptation. Selected accessions entered yield trials and hybridization blocks in subsequent years.

The selection program in Carimagua is a continuing, long-term project, with gradual improvement expected in a multitude of agronomic traits.

RESULTS AND DISCUSSION

YIELD TRENDS

The mean fresh root yields of the Carimagua advanced yield trials from 1975B to 1984A are shown in Figure 1. Trial mean yields, mean yields of the two check varieties (M Col 1684 and Llanera), and mean yield of the five highest yielding clones are presented. In the first years of the yield trial (1975 and 1976 plantings), root yields of over 25 t/ha were achieved by the highest yielding clones, and the checks averaged almost 30 t/ha. From 1976B to 1977A yields dropped rapidly to below 10 t/ha, as CBB and SED reached epidemic levels. In subsequent years, yields have fluctuated at levels always below the maxima achieved for the respective categories during the period when CBB was artificially avoided. Nevertheless, an overall tendency for increasing yields over time of the experimental materials (excluding checks) can be observed.

Previous studies (CIAT, 1985) have suggested that the yield constraints affecting cassava at the Carimagua station may be quite distinct depending upon the planting season. In the A season plantings, CBB and SED are devastating on susceptible clones, while in second semester plantings, the crop can achieve good growth and yield formation before the heavy rains of April and May favor disease epidemics. Based on this information, yield trends for A and B season results were analyzed separately.

A series of regression equations were calculated for yield data, where year and season of planting were taken as the independent variable and yield as the dependent variable (Figure 2). Yields prior to 1977A were not considered in these analyses, as they represented artificial conditions of crop management.

Yields of the top five clones and the trial mean yields showed similar trends, with the main difference being a yield advantage ranging from 6 to 13 t/ha for the top five clones. While yields of the experimental clones from the B season remained virtually stable throughout the period, A season yields increased at a rate of about two t/ha/year.

During the same period the checks from the A and B seasons showed very different trends. For the A season planting, check yields increased slightly at an average rate of 0.48 t/ha/year, indicating that production conditions improved slightly over time. However, yields of the B season checks declined sharply at the rate of almost two t/ha/year

Figure 1. Cassava yield trends in advanced yield trials in Carimagua.

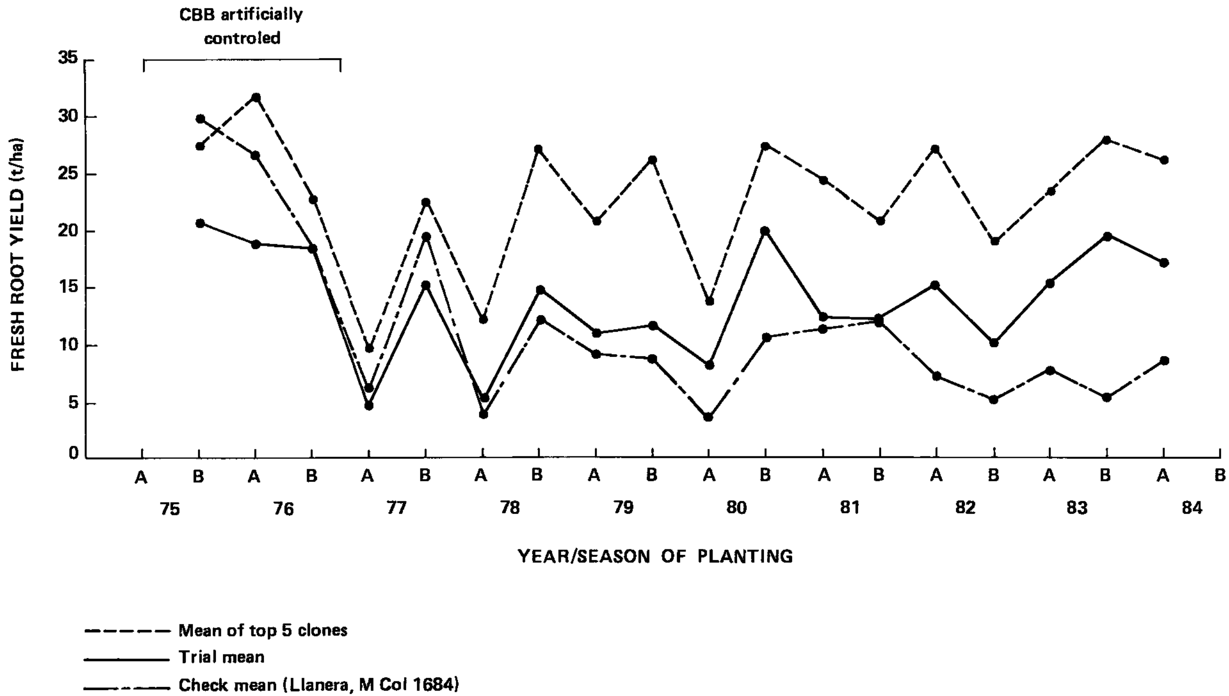
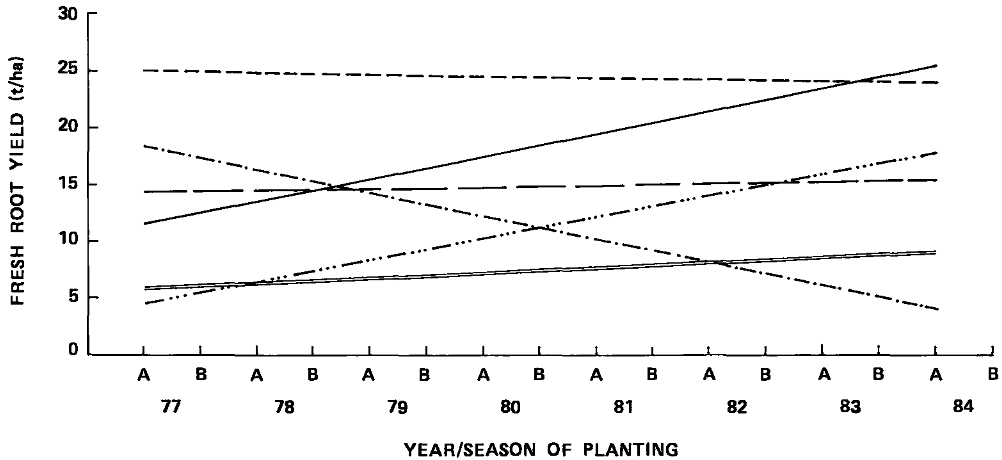


Figure 2. Regressions of yield on year/season of planting in advanced yield trials in Carimagua.



[a] x defined by 77A = 1,84A = 15

————	Top 5 clones – A season	(y = 0.97x + 10.9[a])
— — — —	Top 5 clones – B season	(y = -0.09x + 25.3)
—··· —	Trial mean – A season	(y = 0.94x + 3.7)
—— ——	Trial mean – B season	(y = 0.07x + 14.3)
════	Checks – A season (M Col 1684, Llanera)	(y = 0.24x + 5.6)
—·—·—	Checks – B season	(y = -0.95x + 18.4)

from 1977 to 1984. Thus an increase in some stress factor(s) during the B season occurred over the period.

The genetic gains due to selection can be determined by comparison of the experimental population with the constant checks. Thus, the regression line for the A season yields clearly represents true genetic progress. On the other hand, the nearly constant B season yields probably represent an equivalent rate of genetic progress when compared to the declining yields of the checks.

It is difficult to separate gains in yield potential versus gains in resistance in the Carimagua cassava populations. Since resistance ratings are subjective, tracing evaluations over years is not necessarily a precise or valid comparison. Nor is it possible to simultaneously compare different generations of selected clones, as each year the nonselected clones are discarded.

IDENTIFICATION OF YIELD CONSTRAINTS

Declining cassava yields over time can often be attributed to declining soil fertility, to build-up of pests, or to a combination of both. In Carimagua a decline in soil fertility can be discarded as a significant factor. First, soil analyses over years showed no significant change in the major nutrients. Secondly, the stability of yields of the checks in the A season plantings shows a significant decline in soil fertility to be unlikely.

Stability of yields of the checks in the A season would seem to indicate a relative stability of pest pressures since 1977. Thus disease pressure probably reached a near maximum in 1977A, soon after isolation as a means to control CBB was discontinued. Figure 3 traces CBB and SED evaluations at peak damage levels (near end of rainy season) during the growth cycle, for the check varieties from 1977B through 1984A. Although there are some year to year variations, no obvious upward or downward trend is evident, except for a rapid increase in SED incidence in 1977. It should, however, be remenbered that, as these evaluations are subjective, year to year comparisons may not strictly valid. There were strong correlations of CBB and SED damage levels with yield in all but one season (Table 2), further illustrating the high influence of disease incidence on yield.

If we discard declining soil fertility or increasing disease inoculum as potential contributors to yield decline of the checks in B season after 1977, the most plausible explanation is the increasing mite and insect populations. Up to 1980, no mite or insect damage evaluations were made in the breeding trials, as their incidence was considered to be too low and sporadic to be of major importance. From 1980 onward, increasing mite and insect populations were noted. However, the relationship of damage ratings with yield is less clear than it is with CBB or SED (Table 2). For

Figure 3. Disease damage trends across years in check varieties (Llanera, M Col 1684) in advanced yield trials in Carimagua.

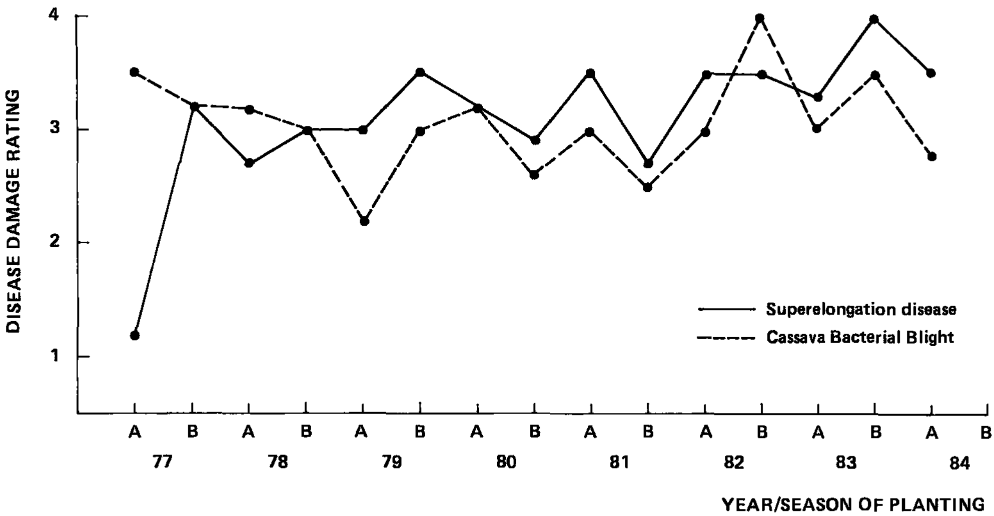


Table 2. Correlations between root yield and damage level from pest attacks Carimagua 1980-1984.

	Bacterial Blight	Superelongation Disease	Thrips	Laceburg	Mealybug	Green Cassava Mite
1980 A	--[a]	--				
B	NS	--				--
1981 A	--	--				
B	--	--				
1982 A	--	--			++	
B	--	--				NS
1983 A	--	--		NS		
B	--	--	--	--	--	NS
1984 A	--	--	NS	NS	NS	NS

a -- and ++ = highly significant (P< 0.01) negative or positive correlation respectively.

thrips, lacebug, mealybug and green cassava mite, there is at least one season when higher damage levels are significantly correlated with lower yields, but for other seasons they are not. Also, the presence and severity of the individual species of mites and insects varies widely from one season to another. The overall tendency however is clear: there is increasing insect and mite pressure in Carimagua, and these infestations appear to be most damaging to yield in B season plantings.

During the early yield trials (1975 to 1979), when most clones were susceptible to CBB and SED, A season plants were generally defoliated due to diseases by the end of the rainy season. As disease resistance levels were increased, clones planted at the begining of the rainy season entered the dry season with good foliage retention, thus creating a favorable host environment through the period when weather conditions are also favorable for mite and insect build-up.

EVOLUTION OF A BREEDING STRATEGY

The Carimagua experience in cassava breeding can be summarized in the following terms. Intensive cassava cultivation was introduced into a region where only scattered, small-scale plantations previously existed. Most of the clones initially introduced were susceptible to CBB or SED. For a few seasons, disease was partially avoided by planting clean stem pieces and locating trials in fields isolated from foci of infection. The inoculum potential however, built up by the end of each growing season, requiring continuous changes of plot location to avoid the diseases. When planting in the same plot was continuous, SED and CBB thereafter persisted in epidemic proportions. However, through recombination and selection, both disease resistance and yield potential were increased over time in the advanced selections planted in the A season.

Fungal and bacterial infections have been continously high over the years, since weather conditions during the rainy season are always favorable to their establishment, inoculum potential is high, and dispersal by wind, rain and birds creates a relatively uniform epidemic within selection plots. Under these conditions, field selection has been highly effective, without any need for greenhouse screening, artificial inoculations, or other enhancement methods.

Mite and insect populations have been much more variable over years than have the pathogens. This is probably an inherent characteristic of insect and mite populations, and can be expected to continue to be more variable from year to year as compared to foliar pathogens. Unlike the diseases, reliable insect and mite evaluations may require special manipulation of populations. These are presently being investigated for the Carimagua station.

Initially, recommendations were made to plant late in the rainy season to avoid highest disease pressure, in CBB-endemic areas. But over the long term, that strategy was not successful in Carimagua; it was, however, a useful interim strategy until mite and insect pressures began to cause serious losses in B season plantings. Yields of the A season plantings began to surpass those of the B season in 1982, and this trend appears likely to continue.

The pest pressures and climatic conditions for the two planting seasons are now so distinct that the most effective strategy seems to be to create two separate breeding populations. For the A season, high CBB and SED resistance will continue to take high priority. For the B season population, intermediate disease resistance should be combined with mite and insect resistance, and probably with drought tolerance during the early root bulking growth phase. There will continue, however, to be expensive genetic interchange between the populations, especially for characterics required in both, such as acid soil tolerance and yield and quality factors.

CONCLUSIONS

The Carimagua experience in cassava breeding is proposed as a model for extrapolation of some basic principles of resistance and yield breeding to other situations where a new ecosystem is created by change of cultural practices, change of cassava varieties, or introduction of a new pest. One of the key objectives for such situations is to develop long-term yield stability, which will depend to a large degree on maintenance of soil fertility, and on adequate resistance to potential pest problems. Only the latter aspect will be discussed here.

DEFINITION OF POTENTIAL PEST PROBLEMS

Over the past several years data on pest distribution and severity in cassava have been accumulated and analyzed to permit a reasonable prediction of the potential severity of a given pest in a given region. Although this has not yet been compiled and published in a unified form, it is possible for cassava breeders to define key pests for which to seek resistance for their target areas (BELLOTI, et al., (In press); HERSHEY, 1984; LOZANO, et al., 1984; TERRY, 1981). A detailed analysis of this, however, is beyond the scope of this paper.

Introduction of previously unreported pests into a region is wellknown for cassava, as well as many other crops. Two of the most devastating examples are the green cassava mite and the cassava mealybug in Africa (HAHN, 1984). Although introduction _per se_ is often impossible to predict, the potential threat after introduction is partially predictable. For example, SED could be devastating if introduced into the humid tropics of Africa or Asia. The mealybug would have high destructive potential if introduced to many regions with a long dry season. For all potentially important pests, a contingency plan should be developed in the case of introduction. This could include introduction and evaluation of known resistant clones or populations for adaptation, yield, and other locally important traits.

CHOICE OF A SELECTION SITE

The main selection site for a region should be representative of the region in terms of climate, general soil characteristics, and epidemic incidence of pest problems (BUDDENHAGEN, 1983; HAHN, et al., 1982; HERSHEY, 1984). Often, experiment station sites are selected to represent the most favorable conditions of a region, and thus are inappropriate for selection of cassava, since cassava for commercial production is usually relegated to the poorer soils. No attempt should be made to find selection sites isolated from the problems commonly afecting cassava in the region, either edaphoclimatic or biological.

ASSEMBLING AN APPROPRIATE GERMPLASM BASE

The base population for breeding should consist of clones with genes for all the desired traits, at moderate to high levels of expression if possible. Often local landrace varieties will have some level of resistance to existing stresses, either biological or physical. They are, however, less likely to have resistance to recently introduced or potential problems. In such cases, introduction of germplasm with known resistance will be necessary, even though local selection for further improving resistance will usually not be possible. A germplasm base for breeding should be seen as contributing balanced ecosystem adaptation - that is, a wide range of traits required for varietal acceptability in a region (BUDDENHAGEN, 1983).

Efficiency in breeding is gained by definition of long-term objectives as early as possible, including the prediction of pest problems and resistance levels required for long-term stability.

PEST POPULATION MANAGEMENT TECHNIQUES

A breeder selecting for resistance often has several options, including artificial infestation or inoculation under greenhouse, screenhouse, or field conditions; manipulation of natural populations, in the field, or use of natural populations without any manipulation. A main concern should be to achieve good uniformity of the selection environment, and reduce the error between selection environment and farmers'fields (BUDDENHAGEN, 1983; HAHN et al., 1982). The strategy to be used depends on: 1) the existence or nonexistence of a target pest problem in the selection site, 2) the levels of severity and uniformity of these pests within the selection site, and 3) the ability to discriminate among various pest problems during evaluations.

Sequential screening of different problems in cassava is often possible due to cassava's long growth cycle; during the course of the growth cycle a wide range of pests and pathogens may be present. Before considering to manipulation of populations through time of planting or other cultural practices, one should carefully study whether these practices may modify the plant's behaviour in ways that confound the breeder's ability to select appropriate genotypes. As an example, a late rainy season planting may affect overall plant adaptation to drought stress. Unless the recommandation can be made to farmers to make a similar change, this is probably not a valid selection methodology.

There is some possibility that as general resistance levels continue to rise, the inoculum potential will decrease to the level where natural, unenhanced infections/infestations will be too low or too variable to distinguish moderate susceptibility. Through continued monitoring of moderately susceptible check varieties it should be possible to determine if this point is reached.

The "safe" approach to resistance breeding is to select under higher pest pressure than would be expected under commercial conditions. This assures that resistance levels will be adequately high (not, however, that pathogen evolution will not overcome resistance) for commercial conditions. On the other hand, if pest pressure is excessively high, valuable genetic diversity may be unnecessarily discarded, thus sacrificing potential advances in breeding for other traits.

Pest control need not, of course, involve only resistance breeding. However, in a long season, low value crop like cassava, controls requiring costly inputs are not an economically viable option. Most of the key diseases and many of the insects and mites can best be controlled through host plant resistance. Biological control, and manipulation of cultural practices should be combined with resistance in an integrated management system.

LONG TERM STABILITY OF YIELD

Stability of resistance is one of the most complex problems in the field of resistance breeding. Three aspects will be briefly mentioned here. First, the possibility of pest or pathogen evolution to overcome the host resistance reaction is well-known. Evidence obtained to date for several of the major cassava pests indicates that resistance is generally of a polygenic, additive nature, and that this resistance is likely to be durable (HAHN, 1978; HAHN, et al., 1982; KAWANO, et al., 1983; ROBINSON, 1979; UMEMURA, et al., 1983). Secondly, there are continual changes in pest and pathogen populations, especially when new cultural practices are introduced, or changes in other environmental conditions occur. Thus, apart from any "breaking down" of resistance, population fluctuations can result in outbreaks. Thirdly, new pests may be introduced into a region with devastating effects.

As cassava cultivation is intensified and moves into new areas, the balance of pest problems affecting the crop will probably be of more significance to the breeder than the durability of resistance to a given pest. As yet, there are no adequate models for predicting behaviour of pest populations in cassava, even in relatively stable production systems; much less in changing systems.

Our experience in Carimagua illustrates the complexity of the problem, especially for mites and insects. The accumulation of data from similar experiences should eventually aid in defining all target pests for resistance breeding in a region of given edaphoclimatic characteristics.

Agro-ecosystems are naturally less stable than evolutionarily old natural ecosystems, but in cassava, the levels of resistance to a wide range of pest problems give rise to the hope that long-term yield stability can be achieved while simultaneously introducing improved agronomy to raise yield potential.

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