The Relationships Between Cassava (Manihot esculenta Crantz), Ecosystems, Diseases and Pests and Their Influence on Breeding Strategy

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During this decade a great deal of effort has been devoted to cassava research by two international institutes (the Centro Internacional de Agricultura Tropical, CIAT, and the International Institute of Tropical Agriculture, IITA) and several national institutions and programs (25). This is due to the importance of cassava in the tropics not only as a staple for humans and a potential feedstuff for animal diets but also for industrial uses (29).

Even though cassava has a high yield potential (8, 14), commercial yield/unit area is relatively low (9). This has been attributed to the limited use of adequate cultural practices and to the lack of improved high-yielding cultivars resistant to the attack of diseases and pests (8). Great advances in cultural practices have been reported (4, 5, 6, 7, 33), but selected or improved lines have not behaved as expected when planted in regions different from those where they were selected or developed. This suggests that cassava clones have been selected for regional conditions that vary with respect to disease and pest pressures as well as climatic and edaphic factors. These four groups constitute negative production factors (NPFs = factors that can decrease the yield of a crop).

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The production of improved lines that are adapted to various similar ecosystems requires the identification and use of clones resistant and/or tolerant to the largest number of NPFs within each ecosystem. Our investigations on cassava during the last ten years have led us to believe that (a) the severity of cassava diseases and pests in a given region is related to the ecological characteristics of the region; (b) pathogenic race specialization among the diseases and pests of cassava appears to be rare; (c) there is stable resistance to most major NPFs in M. esculenta; (d) existing clones are regionally adapted varieties; and (e) in M. esculenta there are clones that have resistance to all the NPFs in any given ecosystem.

The species

M. esculenta, which originated in America with a major center of diversity in South America and a secondary center in Guatemala and Mexico (17, 20), is composed of clones under cultivation. No wild clones or ancestors have been found (17).

The species has 36 chromosomes and is generally regarded as tetraploid (34). Clones are highly heterozygous (4, 15) but not heterogeneous, primarily because of vegetative propagation and inbreeding depression.

Cassava has a very high rate of selfing in a multiclonal population (15), but exhibits strong inbreeding depression (14, 15) so that selfed plants are not competitive with crosses. Cassava plants grown from seed have a poor competitive ability in comparison to those grown from vegetative cuttings and to weeds;thus plants from true seed are not common in traditional farming systems.

Domestication of the species

The time and place of domestication of cassava are not known. Archeological evidence shows that cassava has been cultivated for more than 5000 years in the extensive geographical area from southern Brazil and Peru to Mexico. Fossilized leaves and roots more than 4300 years old have been found in Mexico and Peru. Carved stones and bones found in Venezuelan and Colombian tombs were probably used to grind the roots. Cassava flour was commonly traded in 2500 B.C. (13, 17). Archeological evidence (ceramics) and historical information indicate that cassava was used more frequently for human consumption in South America than in Central America (13). This suggests that in the centers of origin, cassava has been cultivated over a wide geographical area for several thousand years. Cassava was introduced into Africa from the Americas (approximately 400 years ago) and more recently into Asia from the Americas and Africa (17, 24).

American cassava-growing areas

The American cassava-growing areas, where cassava has been cultivated for centuries, are characterized by a great diversity of edaphic and climatic conditions. The soil varies in pH (3.0-9.5), in texture, in nutritional deficiencies of macro- and/or micronutrients, in salt or mineral toxicity (e.g., Al) and in organic matter content. The climate, which is characterized by extreme differences in temperature as well as intensity and duration of rainfall, is related to elevation (except for Paraguay and south-eastern temperate Brazil and Peru). Due to the mountainous geography and large expanse of the cassava belt, a great variety of climatic conditions are found. These vary between stable or fluctuating temperatures, ranging from 8 to 33°C (average); equatorial to subequatorial photoperiods; semidesert (500 mm/year) to very wet (6000 mm/yr) regions with 1 or 2 definite or indefinite rainy or dry periods of 1 to 8 months/yr; and relative humidities that range from 15% to near saturation during a given period of the year. All these edaphic and climatic factors combine to form a great number of ecosystems with different ecological characteristics. In many instances, because of mountain delimitations, adjacent areas have notably different environments.

Traditional practices

Cassava is traditionally cultivated under a mixed cropping system by planting stem cuttings of different clones in small holes made after clearing the forest. This system is still being used in a considerable percentage of the cassava-growing areas in the Americas (J.K. Lynam, CIAT's cassava economist; personal communication). Only recently has the monocropping system, with better soil preparation and weed control, been introduced. This is now being intensively expanded, but with the traditional multiclonal cassava population.

Early cassava plantations were isolated locally by forests and regionally by mountains. Each of these regions, generally ecologically different, were scattered along the cassava-growing area from southern Brazil and Peru to Mexico. Trade between these regions was probably limited to the more valuable commercial products; and therefore cassava, being a bulky product of little value, was probably seldom traded among regions. Cassava growers usually plant vegetative material obtained from a previous crop, or from neighboring farms.

Introductions have occurred only occasionally. Each introduction was selected by growers in relation to its adaptation to the ecosystem, yield stability and, intrinsically, resistance to diseases and pests present in the new ecosystem by comparing its performance with that of the existing local clones. Consequently, the clones in existence today are regionally adapted cultivars that have persisted vegetatively in each ecosystem because of desirable characters. Resistance to the NPFs existing in the ecosystems has contributed to the survival and stable productivity of the clones.

Impact of breeding programs

Cassava breeding programs are relatively recent. Fifty years ago one of the first cassava breeding programs was initiated at the Instituto Agronômico de Campinas, Brazil (27). Later, in Africa, a breeding program was initiated to produce varieties resistant to African mosaic (30). During this decade IITA, CIAT and several national progr[illegible] initiated breeding projects in several tropical countries (25, 26). The impact of breeding programs on the species to date is still very limited. Regional cultivars probably have most of the genetic traits characteristic of the first domesticated and selected clones. Those varieties that have been developed in the distinct areas have been selected by farmers over the centuries for ecological adaptability, resistance to diseases and pests as well as for good agronomic characteristics.

The more popular clones in each ecosystem may contain wider resistance to NPFs peculiar to the ecosystem where they are grown. These clones are preferred by traditional growers in each ecosystem constitute the best basic material for breeding programs. The success of such programs depends on the correct identification, the appropiate use and improvement of these clones for specific NPFs that arise in each region. This requires regional testing of varieties and programs for incorporating specific resistances according to where they will be used.

General discussion and conclusions

Based on the above considerations related to the characteristics of the crop, centers of origin, and the traditional system of cultivation, the following conclusions were made:

1. The existence and/or severity of diseases and pests of cassava are related to the characteristics of the ecosystem. Recent studies of some cassava diseases and pests have shown that they are restricted to certain regions, and if present, are severe only during a certain season (wet or dry). For example: (a) Cercospora leaf spot [Cercosporidium (Cercospora) henningsii and Cercospora vicosae], anthracnose (Colletotrichum and Gloeosporium spp.) and rusts (Uromyces spp.) are not found or are only mild

during dry periods or in semidesert-cassava-growing regions (4, 21, 23, 32). (b) Cassava bacterial blight and superelongation are severe only during periods of prolonged rainfall (16, 19, 21). (c) Cassava bacterial blight infection is moderate in areas where temperatures are stable, independent of the rainy season and of the amount of rainfall in a given period (7, 31). (d) Phoma (Phyllosticta) spp. and white leaf spots (Phaeoramularia manihotis = Cercospora caribaea) are present only in those regions where temperatures fall below 18°C during the rainy season and during the winter in the subtropical zones of southern Brazil and Peru, northern Argentina, Uruguay and Paraguay (23). (e) Phytophthora and Pythium root rots are most prevalent in heavy undrained soils (3, 23, 28), whereas Armillariella, Rosellinia and Rigidoporus root rots cause heavy losses when cassava is planted following forest or perennial crops (3, 23). (f) Stem rots are severe in areas where relative humidities are near saturation for prolonged periods. (h) The incidence of African mosaic is particularly high when there are high populations of its vector, Bemisia spp., in the rainy season (2, 18). This is also the case of bacterial stem rot, (caused by Erwinia carotovora p.v. carotovora) (23). (i) Mite, thrip and lacebug populations are particularly high and their attack very severe when there are prolonged dry periods (1). This indicates that in many instances the climatic and edaphic characteristics of a region can determine, both qualitatively and quantitatively, the pathological and entomological flora and fauna.

2. Among the pathogens and pests of cassava there does not appear to be any evidence of race specialization to date. Our investigations on pathogenic variability of the causal agents of cassava bacterial blight, Cercospora leaf spots (three species), Phoma leaf spot and anthracnose (three Colletotrichum and two Gloeosporium spp.) have shown that their variability is due to aggressiveness and not to a gene-for-gene relationship with their host. An exception appears to be the causal agent of superelongation, which possibly evolved on a different euphorbia host(s)(6, 7). This lack of pathogenic race specialization could be due to the fact that cassava, a homogeneous and long-season crop (8-18 months) is basically heterozygous and that its major pests are not obligate parasites (some minor pests such as rust and powdery mildew are). Moreover, the geographical and ecological barriers have prevented wide dispersion and/or introduction of pests.

3. Resistance to NPFs, particularly diseases and pests, appears to be stable. This is to be expected in regional varieties because unstable resistance could not last in a crop that has a relatively static genetic composition and in which susceptible material is always present. Assuming that pathogens and pests have a greater capacity for genetic change than this vegetatively propagated crop, they would overcome the resistance faster than the crop could evolve it.

In Popayán, where the major negative production factors are leaf spot diseases, low temperature and low soil pH, a resistant variety (CMC 92), an intermediate-resistant variety (CMC 39)(resistant to low temperatures and pH, but not to the leaf spot diseases), and a susceptible variety (M Col 22) were grown for five years (Fig. 1, Table 1).

The susceptible variety consistently yielded between 0 and 1 t/ha. Yield of the variety that lacked good resistance to leaf spot diseases fluctuated between 8 and 26 t/ha, depending on the intensity of disease present, which is mainly determined by the amount of rainfall (Table 2). The resistant variety consistently yielded 18-22 tons over all five years. In the Caicedonia area, the variety Chiroza has been grown for the last seven years and has steadily given yields around 27 t/ha (Samuel Garcia, Coffee Federation, personal communication). Other local varieties in other areas such as Llanera in the Llanos and Valluna in Santander de Quilichao have been giving consistent yields for many years. This supports the statement that stable resistance does exist and has been exploited in the cultivation of the crop for many years.

4. Cassava clones are regionally adapted varieties; they have been selected over time in regions with distinct sets of NPFs. Clones selected and developed where there are few NPFs usually give steady yields in these sites, but when grown in other ecologically different sites that have different sets of NPFs, these clones tend to show greater fluctuation in yield from year to year (Fig. 2). Yield variation at the other sites is due to the fact that varieties selected in areas with few NPFs do not have resistance

to all the NPFs that exist at the other sites; therefore, yields will fluctuate, depending on the stress exerted from one year to another. Stress is affected by factors such as rainfall and temperature. Dramatic decreases in yield have been recorded when a variety that is regionally adapted is grown in another region that has a dramatically different set of NPFs. An example of this is the case of CMC 92 and M Col 22. CMC 92 is adapted to the Popayán region; and when grown at CIAT, its yield decreases from 20 to 8 t/ha. On the other hand, M Col 22 is a variety adapted to CIAT conditions; and when grown in Popayán, its yield falls from 40 to 0-1 t/ha (Fig. 3). This has also been recorded with the variety Santa Catarina in Brazil (Takatsu, personal communication) and several varieties from Nairobi, Kenya, when planted in other regions of Africa (Terry, personal communication).

5. M. esculenta probably has resistance to most NPFs existing in the different ecosystems since it has been selected under a wide range of ecosystems that contain most of the possible NPFs. The highest expression of resistance is found where stress due to NPFs is highest. Thus far, resistant clones have been reported to the following adverse factors: low levels of P, high levels of Al, saline soils (11), stable, low temperatures (12), Cercospora spp., Phoma sp., Colletotrichum and Gloeosporium spp., S. manihoticola (16, 21, 23), African mosaic (2, 10), mites, thrips and lacebugs (1, 7). Resistance to other NPFs that have not been studied as of yet probably exists.

6. In M. esculenta it is possible to find clones with resistance

to all the NPFs in a given ecosystem. Screening in two extreme cassava-growing regions supports this statement. In Popayán (several leaf disease pressures, low temperatures, low soil pH) several clones were selected in a two-year trial (Table 1). In this trial yield was related to varietal resistance to the NPFs in the area (Fig. 4). In the second year four varieties that had been rated as susceptible the first year appeared to be resistant since they yielded as much as the resistant varieties. Further studies revealed that they were resistant to the edaphic and temperature constraints of the region but not to the disease problems (7). The second year was abnormally dry and therefore there were few disease pressures; without these pressures, these varieties yielded well. In selection trials of 800 clones at Carimagua (Table 1) over two years, eight clones were selected as resistant to the NPFs in this area (bacterial blight, super-elongation, low soil fertility, low pH, Al toxicity, mites). The existence of regional varieties that have given consistent yield over many years in extreme ecosystems confirms that there are varieties that have the necessary resistance to the NPFs that exist in any given region.

7. The above considerations suggest that in order to breed for varieties that have a wide-type resistance (i.e., to several NPFs), the breeding program should be decentralized. Several representative ecosystems should be chosen as selection sites. At each site parental material and progeny should be evaluated over several years for both resistance and agronomic characte-

ristics. The progress of these varietial improvement programs would depend greatly on the genetics of the desired traits, the number of traits that have to be incorporated, the effectiveness of the evaluation techniques and the number of progeny evaluated yearly. For example, in some areas the local varieties lack resistance to one factor but are otherwise varieties with good, stable yields. In this case, one would try to improve the local variety by incorporating the resistance by crossing the local variety with a resistant one and then selecting for resistance and the characteristics of local-type variety; several cycles may be necessary to obtain this. The other extreme would be an area such as Carimagua in the Llanos Orientales of Colombia, where there are no good local varieties. In this case one would have to evaluate a large number of possible parents and then use the selected material as parents to begin a recurrent population improvement program (random crosses between parents, selection of progeny, random crosses between selections, etc.).

These programs would produce varieties that have the necessary resistance for the ecosystem in question and give a stable, high yield. These varieties would then be distributed to similar ecosystems and evaluated for several years. The validity of the distribution strategy is supported by the yield results of several varieties that are adapted to CIAT or Popayán and their respective yields at CIAT, Popayán and Darién. CIAT-adapted varieties do not yield well at Popayán or Darién, both which are very different from CIAT. Popayán-adapted varieties do not yield well at CIAT but do well in Darién, which has a similar ecosystem (Tables 1 and 3). With several regionally located breeding programs, the unstable yields frequently exhibited by high-yielding introduced varieties bred in ecologically different areas could be avoided. Lastly, we have to keep in mind that cassava is still in equilibrium with its pests and diseases and that uncontrolled breeding programs may encourage the development of pathogenic specialization. Therefore, we must proceed carefully in order to maintain the diversity that exists.

Table 1. Some climatic and edaphic factors, diseases and pests that induce yield reduction (negative production factors, NPFs) at Popayán, Darién, Carimagua and CIAT.

NPFs	Location			
	Popayán	Darién	Carimagua	CIAT
Climatic				
Mean temperature (°C)	18.0(+)*	19.5(+)	26.1(-)	24.0(-)
Rainfall (mm/year)	2500(-)	1500(-)	2031(-)	1000(+)
Rainfall duration (months)	6(2 periods)(-)	6(2 periods)(-)	8(1 period)(+)	5(2 periods)(-)
Edaphic				
pH	4.1(+)	4.3(+)	4.7(+)	6.8(-)
Al concentration	High(+)	High(+)	High(+)	Low(-)
Soil fertility	Good(-)	Medium-low(+)	Low(+)	Good(-)
Soil texture	Clay loam(-)	Silt loam(-)	Sandy loam(-)	Clay(±)
Diseases				
Phoma leaf spot	+	+	-	-
Anthracnose	+	+	+	-
White leaf spot	+	+	-	-
Bacterial blight	-	-	+	-
Superelongation	-	-	+	-
Brown leaf spot	-	-	+	±
Cercospora leaf blight	-	-	+	+
Pests				
Mites: *Oligonychus* sp.	±	±	±	±
Mononychellus sp.	-	-	+	+
Thrips	+	+	+	+
Scale insects	-	-	+	-
Stemborers	-	-	+	+
Lacebugs	-	-	-	+

* + = severe damage; ± = moderate damage; - = no damage

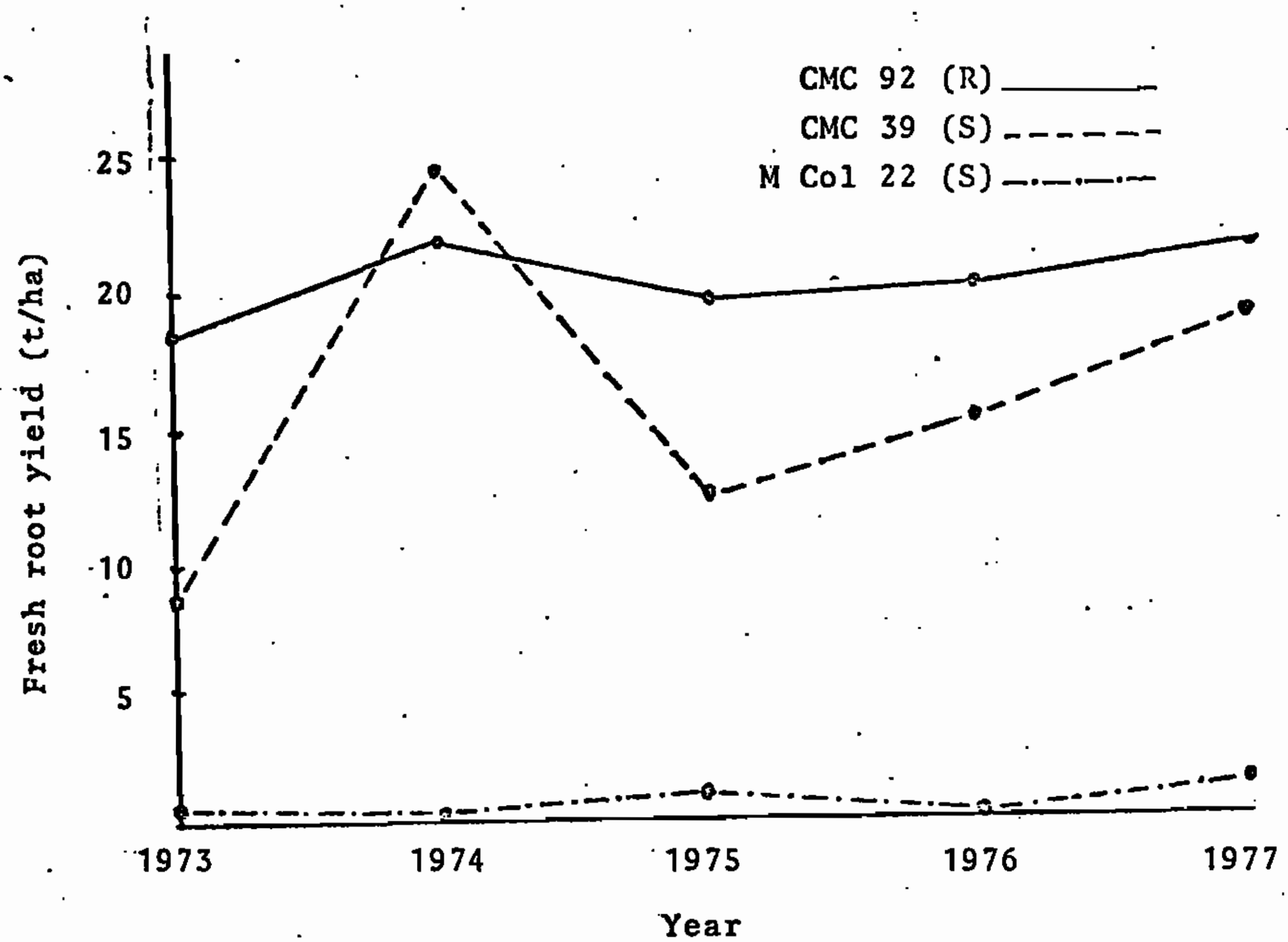

Figure 1. Yields of three varieties in Popayán over five years.

Table 2. Field evaluation of resistance to negative production factors (NPFs) in the Popayán ecosystem in relation to rainfall*.

Growing cycle (15 months)	Reaction to the Popayán NPFs/variety** M Col 22	CMC 39	CMC 92	Rainfall during 15-month cycle (mm)
1972-73	4.9***	4.1	2.1	3119
1973-74	3.5	2.0	1.5	2475
1974-75	4.8	4.0	1.9	3103
1975-76	5.0	3.9	1.9	3319
1976-77	4.8	3.5	2.0	3365

* Elevation 1760 m, mean temperature 18°C (4°C min, 20°C max).

** Average data taken from 36 plants/variety over a 15-month period.

***Reaction to NPFs: 1 = normal plant growth, no disease or pest attack; 2 = less than 30% leaf fall due to disease or pest attack and/or environmental or edaphic factors, normal plant growth; 3 = up to 80% leaf fall and stem cankers or injuries due to disease or pest attack and/or other environmental or edaphic factors, slight stunting and yellowing; 4 = total defoliation, stem cankers, stunting and slight dieback due to disease, pest and/or edaphic or environmental factors; 5 = severe stunting or plant death due to disease, pest and/or edaphic or environmental factors.

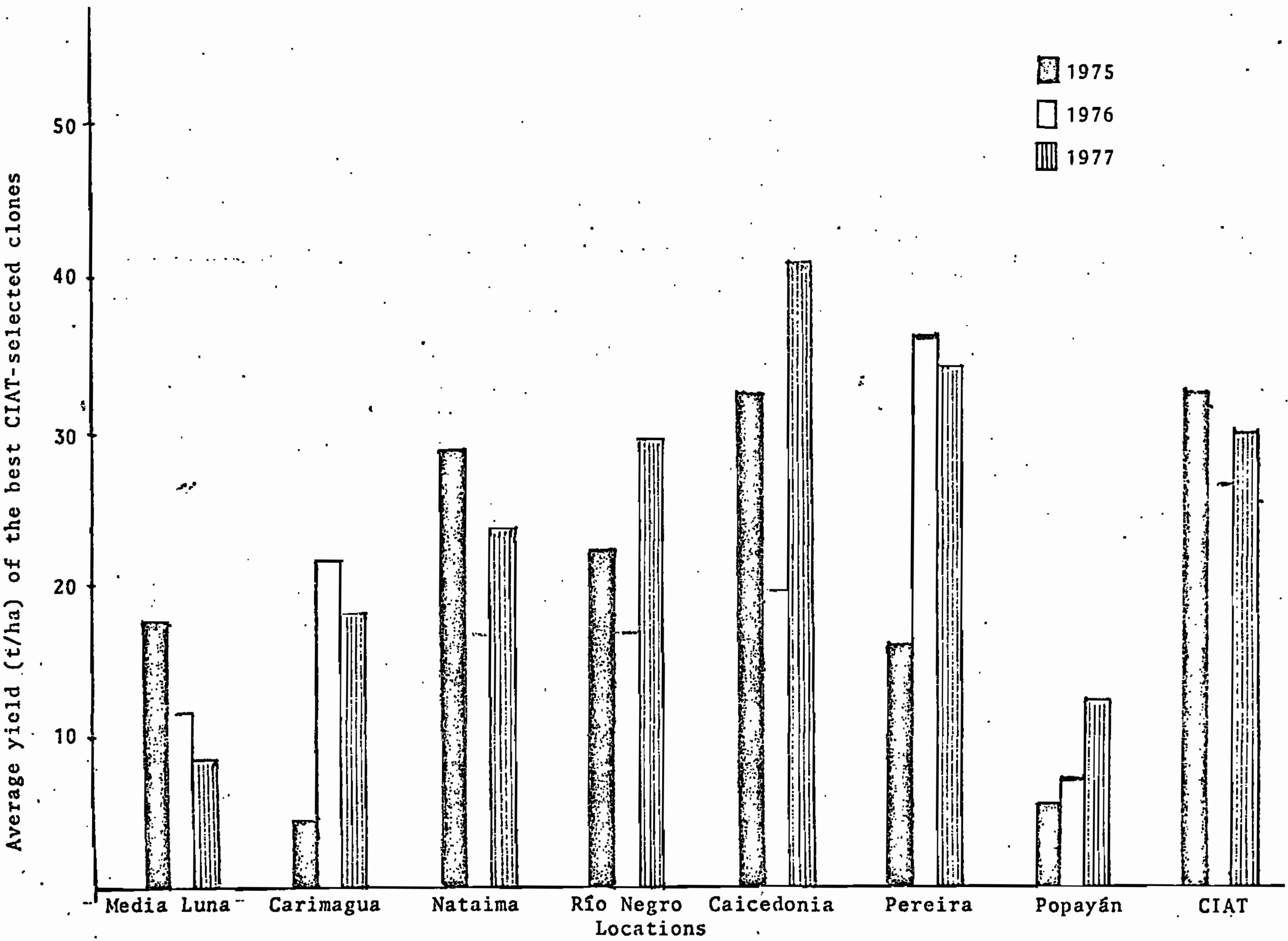

Figure 2. Fluctuation in yields of CIAT-selected materials at eight locations over a three-year period.

Table 3. Yield of different clones with different reactions to negative production factors (NPFs) existing in Popayán (rainfall 1760 mm, mean temperature 18°C, altitude 1760 m), Darién (rainfall 1500 mm, mean temperature 19.5°C, altitude 1450 m) and CIAT (rainfall 901 mm, mean temperature 23.5°C, altitude 1000 m).

Clone	Yield (t/ha)* and reaction to NPF					
	Popayán		Darién		CIAT	
	Yield	Reaction	Yield	Reaction	Yield	Reaction
CMC 92	22.3	R**	26.6	R	8.2	R
Morada	16.5	R	18.3	R		-
M Col 80	13.7	R	15.3	R		R
M Col 235	14.5	R	11.5	R		R
M Col 230	11.3	R	10.3	R		R
M Col 307	6.5	T	6.7	T		R
CMC 39	8.6	T	8.8	T	13.0	R
M Col 22	0.3	S	0.0	S	39.4	R
M Mex 59	0.9	S	2.4	S	33.1	R
CMC 40	3.8	S	5.3	S	42.2	R
CMC 84	1.0	S	4.0	S	40.3	R
CMC 76	0.5	S	1.4	S	36.0	R
M Col 113	5.0	S	2.5	S	26.8	R
CMC 9	0.5	S	0.1	S	31.7	R
M Mex 23	1.0	S	1.0	S	34.3	R

*Data taken during 1974-75 by the Agronomy and Pathology sections of the Cassava Production Program at CIAT (4,5).

**R = plants with less than 50% defoliation and normal growth; T = plants show slight stunting and/or total defoliation but recover during dry periods; S = severe stunting, dieback and/or death. Partial or no recovery during dry periods.

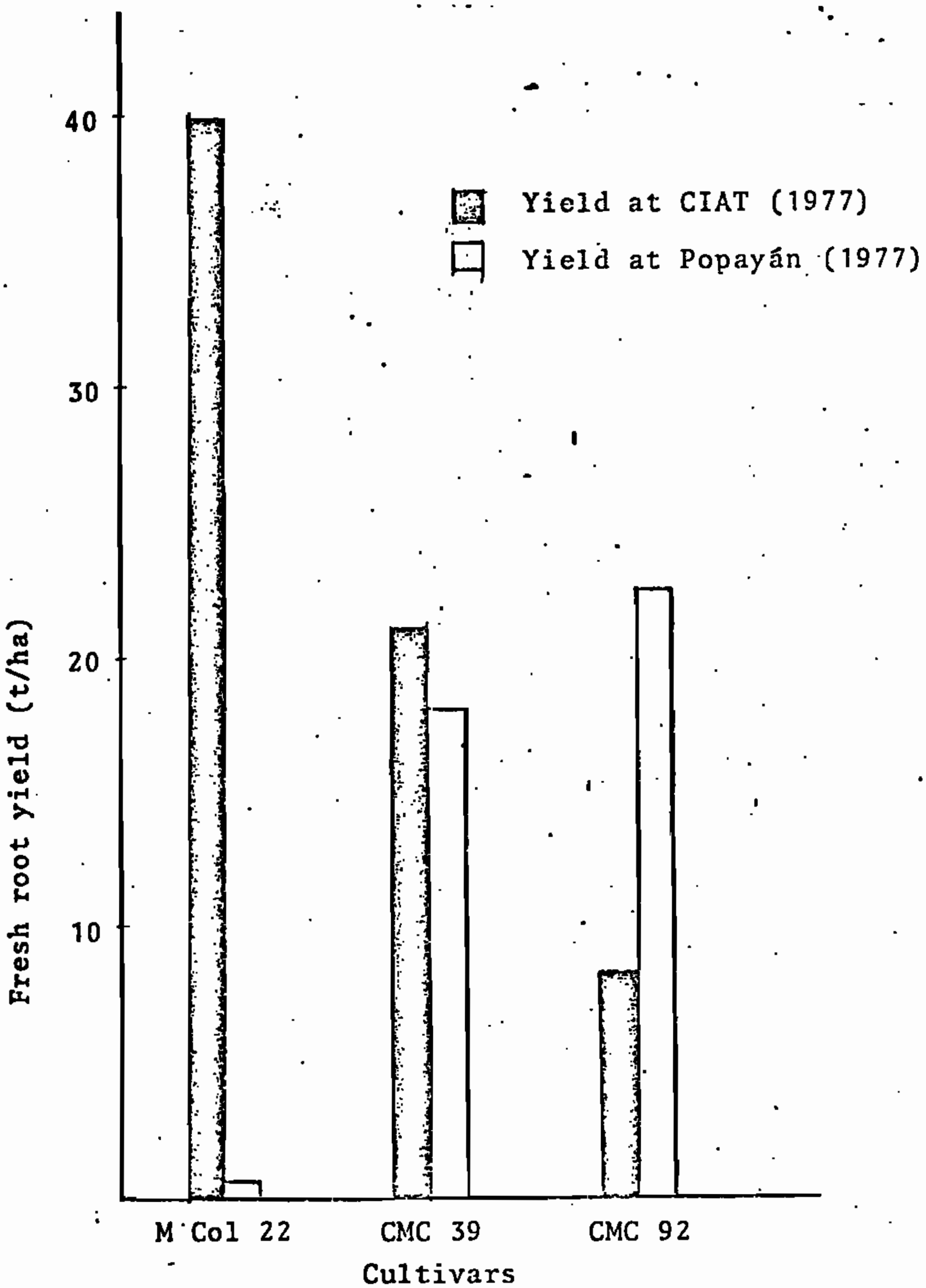

Figure 3. Yield of three varieties in CIAT and Popayán ecosystems.

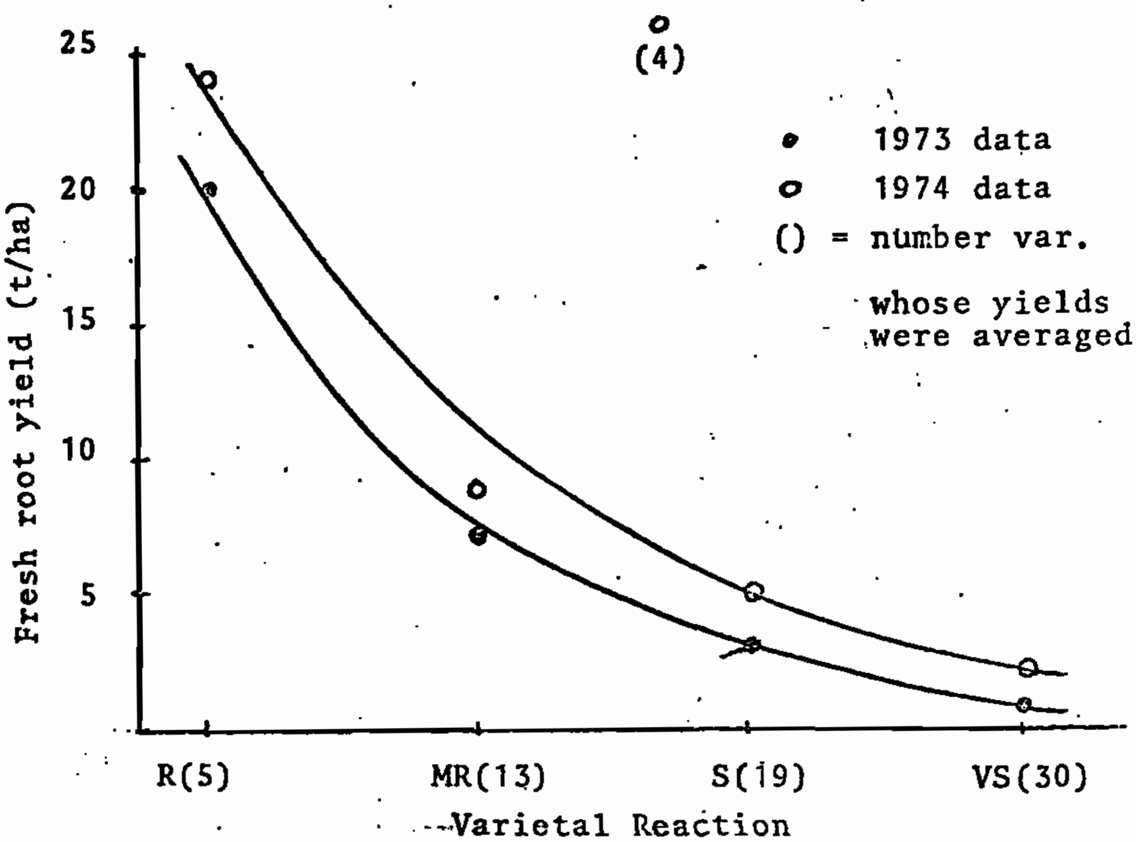

Figure. 4 Yield of 67 varieties at Popayán in relation to the negative production factors of this ecosystem.

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