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Cassava/Ecosystem Relationships and their Influence on Breeding Strategy

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Summary The influence of ecosystems on cassava (*Manihot esculenta* Crantz) cultivars and the *possible reasons* for this are discussed as well as the effect of distinct vegetative production factors edaphic and climatic constraints and disease and pest stresses on regional and introduced varieties Decentralised improvement programmes in different ecosystems based on 10 years research are suggested and selected according to socioagro-economic studies related to actual and/or potential production of cassava

Introduction

Cassava (*Manihot esculenta* Crantz) originated in America with a major centre of diversity in South America and a secondary centre in Guatemala and Mexico (Leon 1977 Lozano 1977) where it has been cultivated for more than 5000 years Some 400 years ago the crop was introduced in Africa and more recently in Asia (Jennings 1976 Leon 1977 Mauny 1953) It is composed of clones under cultivation no wild types have been found (Leon 1977)

The species has 36 chromosomes and is generally regarded as tetraploid (Toro and Garcia 1977) Clones are highly heterozygous (CIAT 1976 Kawano *et al* 1978) but not heterogeneous mainly because of vegetative propagation and inbreeding depression

In a multiclonal population cassava has a very high rate of selfing (Kawano *et al* 1978) however selfed plants are not competitive with crosses due to strong inbreeding depression (Kawano 1978 Kawano *et al* 1978) Plants grown from botanical seed do not compete well with those grown from vegetative cuttings or with weeds thus plants from true seed are not common in traditional farming systems

Cassava has been traditionally cultivated under mixed cropping systems where stem cuttings of different clones are planted on recently cleared land This system is still being used to a great extent in the Americas (J K Lynam personal communication) Monocropping has only recently been introduced but still with the traditional multiclonal cassava population

These early plantations were isolated locally by forests and regionally by mountains The American cassava growing areas are characterised by a great diversity of edaphic and climatic conditions Soils vary in pH (3 0–9 5) texture macro- and/or micronutrient deficiencies salinity or mineral toxicity e g aluminum and organic matter content Climatic conditions are often dependent on elevation except for Paraguay and south eastern Brazil and Peru temperatures can be stable or fluctuating averaging from 8 to 33 C there are equatorial to subequatorial *photoperiods* semi desert to very wet regions (500–6000 mm/year) with 1 or 2 rainy or dry periods of 1 to 8 months/year and relative humidities ranging from 15% to near saturation during a *given period* of the year All these factors combine to form a great number of different ecosystems

Due to their relative isolation farmers usually plant vegetative material obtained from a previous crop or from neighbouring farms Clone introductions have occurred only occasionally each being selected by the farmer on comparison with the performance of local clones as regards adaptation to the ecosystem yield stability and resistance to diseases and pests found in the new ecosystem

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Although research has shown that *M esculenta* has a high yield potential (Cock 1974 Kawano 1978) commercial yield/unit area is very low (FAO 1971) This has been generally attributed to inadequate agronomic practices as well as to the lack of improved high yielding cultivars resistant to diseases and attack by pests Great advances in cultural practices have been reported (CIAT 1976 1977 1978 1979 Toro and Garcia 1977) but promising selections or improved lines have given variable results when grown in regions other than those from where they were selected This suggests that regional testing of varieties and programmes for incorporating specific resistance to the different pressures or negative production factors (NPFs) in a given ecosystem are required

The relationships between the cassava plant and the NPFs existing in the different cassava growing areas are studied on the basis of experimental results obtained over the past 10 years at CIAT with emphasis on pathological problems their impact on breeding strategies is discussed

Breeding programmes impact of past strategies

Cassava breeding programmes are relatively recent one of the first was initiated 50 years ago at the Instituto Agronomico de Campinas Brazil (Normanha and Pereira 1950) Later a breeding programme in Africa began work on the development of varieties resistant to African mosaic disease (Storey and Nichols 1938) During the past decade the International Institute of Tropical Agriculture (IITA) Nigeria and the Centro Internacional de Agricultura Tropical (CIAT) as well as several national programmes initiated breeding projects (Mauny 1953 Nestel 1974)

IITA s breeding programme involves massive crossing and selection against two major diseases cassava bacterial blight (CBB) and African mosaic disease and their dissemination Improved true seed from different interpollinated superior females with sources of resistance and other agronomic traits is sent to different locations in Africa CIAT s programme has used conventional crossing of superior lines following a pedigree method selected material at one centre is vegetatively disseminated and tested in three different locations

The impact of these programmes on the species to date however has been limited Regional cultivars probably have most of the genetic traits characteristic of the first domesticated and selected clones having been selected over the centuries for ecological adaptability resistance to diseases and pests and good agronomic characteristics These clones constitute an excellent source of basic material for breeding programmes the success of which depends on their correct identification and use

Experimental results related to breeding strategies

Results of research over the past ten years have led us to believe that (a) disease and pest incidence and severity of attack are related to the ecological characteristics of a given region (b) pathogenic race specialisation among cassava diseases appears to be rare (c) stable resistance to most major NPFs exists in *M esculenta* (d) clones in existence today are regionally adapted cultivars that have persisted in a given ecosystem because of certain desirable characters and (e) clones with resistance to the main NPFs in an ecosystem can be found

Recent studies have shown that diseases and pests are often restricted to certain regions and if present become severe only during a certain season Cercospora leaf spots *Cercosporidium* (*Cercospora*) *henningsii* Allescher and *Cercospora viscosae* Muller and Chupp anthracnose *Colletotrichum* and *Gloeosporium* spp and rusts *Uromyces* spp are not found or are only mild during dry periods or in semi desert regions (CIAT 1976 Lozano 1978 Lozano and Booth 1974 Teri Thurston and Lozano 1978) whereas CBB *Xanthomonas manihotis* (Arthaud-Berthet & Bondar) Starr and superelongation *Sphaceloma manihoticola* Bitanc & Jenk are severe only during periods of prolonged rainfall (Krauz Lozano and Thurston 1978 Lozano 1975 Lozano 1978) Moreover CBB infection is moderate in areas where temperatures are stable independent of the rainy season or the amount of rainfall in a given period (CIAT 1979 Takatsu 1977) Concentric ring leaf spot *Phyllosticta* spp and white leaf spot *Phaeoramularia manihotis* = *Cercospora caribaea* Chupp and Ciferri occur in 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 (Lozano and Booth 1974) Phytophthora and Pythium root rots are most prevalent in heavy undrained soils (Booth 1978 Lozano and Booth 1974 Oliveros Lozano and Booth 1974) whereas Armillaria Rosellinia and Rigidoporus root rots cause heavy losses when cassava is planted following forest or perennial crops (Booth 1978 Lozano and Booth 1974) Stem rots are severe in areas where relative humidities are near saturation for prolonged periods Incidence of African mosaic is particularly high when there are high populations of its vector *Bemisia* spp in the rainy season (Bock and Guthrie 1977 Leuschner

1977) This is also the case in bacterial stem rot caused by *Erwinia carotovora* var *carotovora* (Jones) Bergey *et al* found in association with fruitflies (Lozano and Bellotti 1979) Populations of mites thrips and lacebugs are particularly high when there are prolonged dry periods (Bellotti and van Schoonhoven 1978) With one exception (CIAT 1978 1979 the causal agent of superelongation which possibly evolved on a different euphorbia host(s)) to date there does not appear to be any evidence of race specialisation among cassava pathogens Our research on the pathogenic variability of the causal agents of bacterial blight Cercospora leaf spots (three species) concentric ring leaf spot and anthracnose (three species of *Colletotrichum* and two of *Gloeosporium*) have shown that their variability is due to aggressiveness not to a gene for gene relationship with their host

This apparent lack of race specialisation could be due to the fact that cassava a homogeneous long season crop (8–18 months) is basically heterozygous (CIAT 1976 Kawano *et al* 1978) and that its major pests are not obligate parasites

Resistance to NPFs particularly diseases and pests appears to be stable which is to be expected in regional varieties because those with unstable resistance could not survive in a crop that has 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 resistance faster than the crop could evolve it

In the Caicedonia area in Colombia for example the variety Chiroza has given steady yields of around 26 t/ha over the last seven years (S Garcia personal communication) Llanera in the Eastern Plains region and Valluna in Santander de Quilichao have been giving consistent yields for many years supporting the statement that stable resistance does exist and has been exploited by farmers for many years

Clones grown in traditional systems are regionally adapted having been selected over time in ecosystems with distinct sets of NPFs Clones selected and developed in areas where there are few NPFs usually give steady yields at these sites but when grown in other ecosystems these same clones tend to show greater fluctuation in yield from year to year (Table 1) This is due to the fact that varieties selected in areas with few NPFs do not have resistance to all the NPFs at other sites therefore yields will vary depending on the stress exerted from one year to another

Considerable decreases in yield have been recorded when a regionally adapted variety is grown in another ecosystem with different NPFs An example is the case of lines CMC 92 and M Col 22 the former adapted to the Popayan region of Colombia and the latter adapted to CIAT conditions (Table 2) When CMC 92 was grown at CIAT its yield decreased from 20 to 8 t/ha Yields of M Col 22 fell from 40 to almost nothing (0–1 t/ha) when grown at Popayan The same has been recorded for the variety Santa Catarina in Brazil (A Takatsu personal communication) and several varieties from Kenya when planted elsewhere in Africa (E Terry personal communication)

Resistance to most NPFs existing in the different ecosystems probably exists in *M esculenta* since it has been selected under a wide range of ecosystems The highest expression of resistance is found where stress due to NPFs

TABLE 1 FLUCTUATION IN YIELDS OF MATERIALS SELECTED AT CIAT AND PLANTED AT EIGHT LOCATIONS IN COLOMBIA OVER A THREE YEAR PERIOD (1975–1977)

Site	Mean yield (t/ha)	Variation s d	Standardised variation c v
Media Luna	12 7	5 0	39 7
Carimagua	15 3	9 1	59 2
Nataima	23 3	6 0	25 8
Rio Negro	23 3	6 5	27 8
Caicedonia	31 0	10 5	34 0
Pereira	29 3	11 6	39 5
Popayan	9 0	2 7	29 4
CIAT	31 0	3 0	9 7

TABLE 2 SOME NEGATIVE PRODUCTION FACTORS (NPFs) THAT REDUCE YIELDS IN FOUR DIFFERENT ECOSYSTEMS IN COLOMBIA

NPFs	Location			
	Popayan	Darien	Carimagua	CIAT
Climatic conditions				
Mean temperature (°C)	18.0 (+)	19.5 (+)	26.1 (–)	24.0 (–)
Rainfall (mm/year)	2500 (–)	1500 (–)	2031 (–)	1000 (+)
Rainfall duration (month)	6 (2 periods) (–)	6 (2 periods) (–)	8 (1 period) (+)	5 (2 periods) (–)
Edaphic conditions				
pH	4.1 (+)	4.3 (+)	4.7 (+)	6.8 (–)
Al concentration	High (+)	High (+)	High (+)	Low (–)
Fertility	Good (–)	Medium low (+)	Low (+)	Good (–)
Texture	Clay loam (–)	Silt loam (–)	Sandy loam (–)	Clay (±)
Diseases				
Concentric ring 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

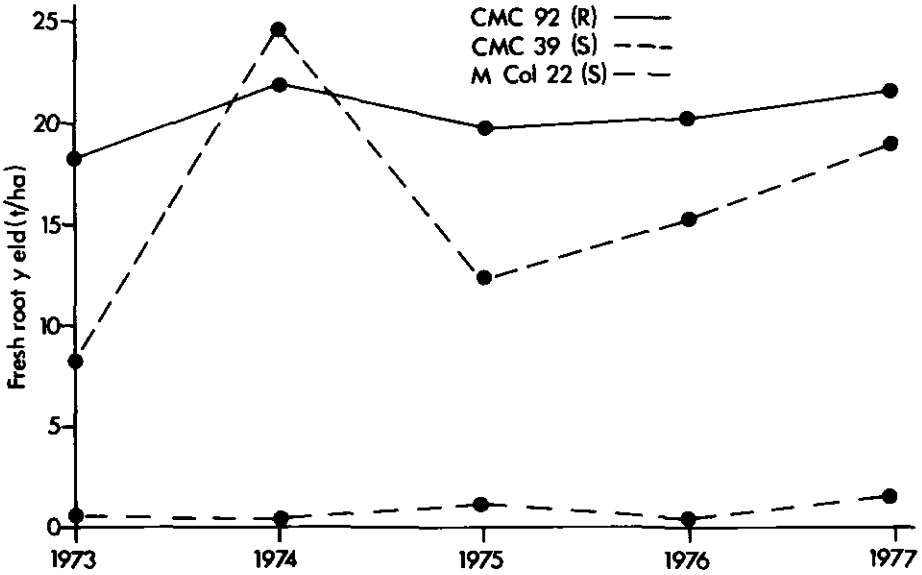
is highest Thus far clones with resistance to the following adverse factors have been reported low levels of phosphorus high levels of aluminum saline soils (Howeler 1978) stable low temperatures (Irikura Cock and Kawano 1979) *Cercospora* spp *Phoma* sp *Colletotrichum* and *Gloeosporium* spp *Sphaceloma manihoticola* (Krauz Lozano and Thurston 1978 Lozano 1978 Lozano and Booth 1974) African mosaic (Bock and Guthrie 1977 Hahn 1979) mites thrips and lacebugs (Bellotti and van Schoonhoven 1978 CIAT 1979)

Resistance to specific sets of NPFs

Although sources of resistance to all major diseases as well as to several insects and tolerance to adverse edaphic and climatic conditions have been identified combining these characters into one variety poses a serious problem for breeding programmes since it requires a large number of crosses and several generations of testing Consequently emphasis has been placed on identifying lines tolerant to many NPFs Work at CIAT has concentrated on two regions in Colombia each with different adverse factors that can greatly reduce yield (Table 1)

Popayan ecosystem

The major NPFs at this site are leaf spot diseases low temperatures and low soil pH Reactions of a resistant line CMC 92 an intermediate line CMC 39 (resistant to low temperatures and pH but not to leaf spot diseases) and a susceptible line M Col 22 were studied over a 5-year period (Fig 1)



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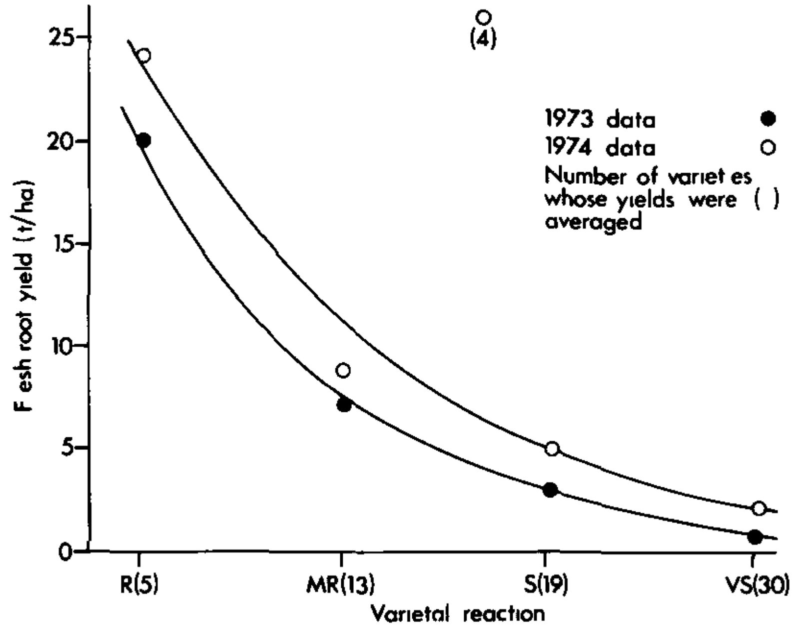

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The susceptible line consistently yielded from 0–1 t/ha whereas that of the intermediate line fluctuated between 8 and 26 t/ha depending on the intensity of disease present mainly determined by amount of rainfall (Table 3) The resistant line consistently yielded 18–22 t/ha

In a two-year screening trial it was shown that yield was related to resistance to the NPFs in this ecosystem (Fig 2) In the second year four lines that had been rated as susceptible the first year appeared to be resistant since they yielded as well as the resistant lines Further studies revealed that they were resistant to the edaphic and climatic constraints but not to the disease problems (CIAT 1979) Since the second year was abnormally dry there were few disease pressures thus these varieties yielded well

TABLE 3 FIELD EVALUATION IN THE POPAYAN ECOSYSTEM OF RESISTANCE TO NEGATIVE PRODUCTION FACTORS (NPFs) IN RELATION TO RAINFALL

Growing cycle	Reaction to NPFs†			Rainfall (mm)
	M Col 22	CMC 39	CMC 92	
Year 1	4 9‡	4 1	2 1	3119
Year 2	3 5	2 0	1 5	2475
Year 3	4 8	4 0	1 9	3103
Year 4	5 0	3 9	1 9	3319
Year 5	4 8	3 5	2 0	3365

El t 1760 m m t mp t 18 C (4 C m 20°C ma)
†A g data t ke f om 36 pl ts/ ty o e a 15-mo th p od
‡1 m l pl t g owth d se s p t tta k
2 l ss th 30% leaf f ll d t d se o pe t attack d/o l mat d ph f t s m l pla t g owth
3 p to 80% leaf fall d st m ca ke o j es d t d ease o p t tt k and/o othe cl mat edaph f t s sl ght t t g d y llow g
4 t tal d f l t tem a ke s st t g d l ght d eback d to d se p t d/o l mat daph facto s
5 ev e t t g pl t d th d to d e pe t a d/ l m t o edaph c f to

Carimagua ecosystem

Although *this area is* representative of much larger areas with a tremendous potential for increased production there are many NPFs such as bacterial blight superelongation low soil *fertility low* pH aluminium toxicity and mites (Table 2) In selection trials of 800 clones over a two year period eight were selected as resistant

Recommended breeding strategy

The foregoing considerations suggest that in order to breed for varieties with a wide type resistance that is to several NPFs the breeding programme should be decentralised Several representative ecosystems should be chosen as selection sites where parental material and progeny should be evaluated for both resistance and agronomic characters over several years Hybridisation for different ecosystems could be done on a centralised basis Large quantities of vegetative material selected at various sites can be returned to a central location for hybridisation by using the technique of Lozano and Wholey (1974) for production of CBB and other disease free planting material

The progress of these improvement programmes 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 In some areas for example the local varieties may lack resistance to one factor but other wise are well adapted with yield and quality In this case the local variety should be improved by incorporating the resistance crossing the local variety or varieties with a resistant one(s) and then selecting for resistance and the characteristics of the local variety Several cycles would be required to accomplish this An extreme case would be an area where there are no good local varieties for example Carimagua In this case a large number of possible parents would have to be evaluated before beginning a recurrent population improvement programme (random crosses between parents selection of progeny random crosses *between* selections etc)

These decentralised programmes would produce varieties with the necessary resistance for the ecosystem in question in addition to stable high yields They would then be distributed to similar ecosystems and evaluated for several years The validity of this distribution strategy is supported by the yield results of several varieties adapted to CIAT or Popayan and Darien for example and their respective yields at the other site (Table 4) With several regionally located breeding programmes the unstable yields frequently exhibited by introduced high yielding varieties bred in ecologically different areas could be avoided

TABLE 4 YIELD (T/HA) OF DIFFERENT CLONES WITH DIFFERENT REACTIONS TO NEGATIVE PRODUCTION FACTORS (NPFs) EXISTING IN POPAYAN DARIEN AND CIAT ECOSYSTEMS (SEE TABLE 2)

Clone	Popayan	Darien	CIAT
CMC 92	22 3	26 6	8 2
Morada	16 5	18 3	
M Col 80	13 7	15 3	
M Col 235	14 5	11 5	
M Col 230	11 3	10 3	
M Col 307	6 5	6 7	
CMC 39	8 6	8 8	13 0
M Col 22	0 3	0 0	39 4
M Mex 59	0 9	2 4	33 1
CMC 40	3 8	5 3	42 2
CMC 84	1 0	4 0	40 3
CMC 76	0 5	1 4	36 0
M Col 113	5 0	2 5	26 8
CMC 9	0 5	0 1	31 7
M Mex 23	1 0	1 0	34 3

Data taken during 1974–1975 by the Agronomy and Pathology sections of the Cassava Production Program at CIAT (CIAT 1976 1977)

Lastly it should be kept in mind that cassava is in equilibrium with its pests and diseases at present and great care should be taken not to upset this balance thereby encouraging the development of pathogenic specialisation

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