Discussion Paper

Strategies for Genetic Improvement of the CIAT Commodities

Seeking a Balance Between Broad Adaptability and Site Specificity

CIAT
Centro Internacional
de Agricultura Tropical

DISCUSSION PAPER

STRATEGIES FOR GENETIC IMPROVEMENT OF THE CIAT COMMODITIES

SEEKING A BALANCE BETWEEN BROAD ADAPTABILITY AND SITE SPECIFICITY[1]

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[1] Prepared for discussion at CIAT Annual Review, December 1982

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FOREWORD

A basic understanding of the implications of genotype by environment interactions is at the core of understanding the potential and the limitations for an International Center to develop appropriate germplasm across the target production areas We hope the present document offers some clarifications and useful suggestions related to CIAT's mandate for crop improvement, especially under rainfed conditions

The variable quality of available data, and the limited quantity of data from specifically designed trials, make drawing any solid conclusions difficult On the other hand, the amount of information from which one can draw inferences and make guesses is immense It is possible to find data to support nearly any position regarding how broadly or how specifically adapted new germplasm must or should be We have attempted to lay aside any preconceived personal or institutional biases in looking at the available information

The authors acknowledge the helpful suggestions given by the following CIAT staff in reviewing a draft version of this document James Cock, Peter Jennings, Peter Jones, Kazuo Kawano, John Lynam, Cesar Martínez, Aart van Schoonhoven, Shree Singh and Jose Toledo It has not been possible to incorporate all suggestions, however, due to time constraints The document represents the opinions of the authors and is not a statement of any individual program policy nor of center policy It is intended primarily to foment open discussion on the directions of present and future breeding activities in CIAT's crop commodities, i e , tropical pastures, beans, cassava and upland rice

INTRODUCTION

A major part of the research activities of the International Agricultural Research Centers (IARC's) is crop genetic improvement Indeed the public image of the IARC's is based largely on the yield increases realized in developing countries in the tropics through wide adoption of the products of the rice (IRRI and CIAT) and wheat (CIMMYT) breeding programs

The IARC breeding programs are unique in the geographical breadth of their target environments, which in many cases cover the world tropics The wide adoption and wide success of improved rice and wheat cultivars is due largely to the fact that they were bred for production environments that existed or could be created on a large scale across the tropics, i e , high productivity environments involving soil moisture and soil fertility modification

While breeding successes have been documented for other IARC commodities, these have not had the impact across the tropics that was realized with wheat and rice This can be attributed in part to the very different target environments for other IARC commodities Most of these crops are grown under a great diversity of production situations, and this heterogeneity of the target area must in turn profoundly influence the strategy of a plant breeding program Under such conditions, a single genotype has a minimal chance of being optimally adapted over many regions, which leads to the conclusion that some degree of decentralization of evaluation and selection is necessary

We present a background on the implications of genotype-environment interactions in crop breeding, and the implications specifically for the tropical pastures, bean, cassava, and upland rice programs as related to target area subdivisions and decentralization of breeding activities Finally, we consider in the discussion section the comparative research capabilities of an IARC versus the national programs, as influenced by a decentralized breeding strategy

The Concept of Genotype by Environment Interactions

A major obstacle to success in many plant breeding programs arises from the fact that the relative performance of different genotypes is often not the same under different environmental conditions An example is that of traditional vs improved dwarf rice genotypes in high vs low yielding environments In a low management, low fertility environment, the traditional varieties commonly out-yield the improved varieties However, in a high fertility environment the ranking of genotype value is completely reversed, here, the dwarf varieties greatly out-yield the traditional, tall varieties This phenomenon is referred to as genotype-environment (G-E) interaction

The detection of a G-E interaction, if it exists, and the quantification of its magnitude can be achieved by applying various statistical procedures to performance data obtained from appropriately designed experiments A minimum requirement for detecting G-E interaction effects is the testing of a least two different genotypes in two or more environments The evaluation of a single genotype in different environments can determine whether some difference between the environments affects the mean performance of that genotype, but reveals nothing about the existence or magnitude of G-E interaction Likewise, the testing of two or more genotypes in a single environment allows detection of genetic differences (in that environment) but, again, tells us nothing about G-E interaction

If no one genotype is best across the range of conditions encountered in a set of environments, then which genotype is to be selected? There is no obvious, single answer to this question, since selection of any one genotype automatically implies accepting something less than the optimum performance possible in one or more of the particular environments in question Several alternative solutions to this dilemma come to mind Where environmental variation is largely or entirely unpredictable and uncontrallable (e g , year to year differences in rainfall, temperature, insect or disease intensity) selection could be on highest mean performance over this range of environmental variation However, it must be clearly recognized that a one ton per year yield obtained every year is quite different from a five ton yield obtained one year in five Given that security of obtaining some minimum yield is of prime importance to the small farmer (who is not able to absorb a crop failure) a better criterion of selection than mean yield would be some measure of the minimum yield in poor years

Where environmental variation is more predictable and/or controllable (e g , climate, cropping system, or fertilizer use) a third selection strategy is possible -- namely, to subdivide the range of variation in the target environment and select a set of genotypes, each of which gives optimum performance in one or more of the specific sub-environments That is, we subdivide the target environment and breed separately for specific adaptation to each sub-environment

Target Area Subdivision for Breeding Objectives

The definition of the target environment for a plant breeding program is therefore of fundamental importance for setting the objectives of the program The nature of the target environment and particularly the nature of the variability occuring within it will importantly influence all genetic objectives Definition of the target environment can be made rationally only on the basis of some description of the range of existing or expected variability, as well as some information regarding the reaction of genotypes to these environmental variables

In recognition of this fact, all the CIAT commodity programs have made explicit decisions to subdivide the overall set of environments into several, more uniform target environments Any delimitation which creates more uniform conditions automatically decreases the potential magnitude of G-E interaction and thus increases the efficiency and effectiveness of genotype selection within any particular environment

Each division into more uniform sub-environments will improve the efficiency of selection and increase the potential for genetic gains within sub-environments, assuming equal resources available for each However, a point is soon reached at which we either begin to exclude important production environments or we have so many concurrent breeding programs that they exceed the resources available for such activities Further, excessive subdivision can be counterproductive in terms of selection of characteristics required across several environments The products of a plant breeding program must, without doubt, be adaptable over a certain range of environmental diversity Fundamental questions are how broadly adaptable ought varieties be and at what cost is adaptability obtained in terms of maximum genetic performance in any specific environment?

Until now we have considered "environment" in an overall, global sense However, this overall "environment" may be broken down into any number of more precisely defined component factors Any one or more of these environmental factors may be responsible for giving rise to a G-E interaction for a particular set of genotypes In many cases these factors can be clearly identified and analyzed, particularly in experimental situations in which specific environmental factors can be controlled In such situations it is possible to apply different levels of these factors to a set of genotypes, holding all other environmental factors constant Examples would include soil fertility, soil moisture, photoperiod, planting density, and cropping system In other cases, unequivocal identification of the specific factor(s) causing a G-E interaction is more difficult or impossible Where "environments" are represented by different locations, for example, the environments may differ by numerous, uncontrollable factors such as temperature, rainfall, soil characteristics, and presence of pathogens or insects In such cases, it is often not possible to specify with any certainty the factor or factors which are causing the interaction

Environmental factors can be classified as to whether they are part of the physical, the biological or the socio-economic environment i e , the climate and soil, diseases and pests, rhizobia (for legumes), grazing animals (for pastures), costs of agricultural inputs and products, and consumer preferences

It is perhaps even more useful to consider specific environmental factors in terms of the degree to which they are economically controllable, and the degree to which their variation in the environment is predictable If a given factor can economically be controlled in the commercial production system, that factor ceases to be of any practical importance as a source of G-E interaction Logically, the extent to which the environment can practically be modified depends on the crop species, and the economic environment in which it is being produced Insect and disease control by pesticides is routine practice for bean producers in developed countries but not as commonly used by small farmers in less developed areas Pesticides are not commonly used on forage species for grazing in any part of the world

Given that complete environmental control is theoretically possible, but that any such modification incurs some cost, the implications of environmental modification on breeding strategy are largely socio-economic Most CIAT breeding programs are presented with a fundamental dilemma Should we concentrate research resources on the relatively simple problems of developing germplasm for the more uniform, modified production environments (e g irrigated rice), where short term payoffs are great and breeding programs can be simplified by centralization of testing operations? Or, should we tackle the much more formidable problems of developing germplasm to solve the production constraints in less modified (and therefore more heterogeneous, less predictable) environments?

Many environmental factors are, of course, practically uncontrollable by the farmer, but even these may be predictable, at least within limits For example, average climatic conditions at a site can be predicted on the basis of previous climatic data and native soil characteristics can be determined rather precisely for a particular site The probable presence of certain insect pests and pathogens may be predictable While socio-economic environmental factors are man-made, they are largely beyond the control of the farmer Many of these, however, are highly predictable (e g consumer preferences)

It is not generally possible, though, when a farmer plants his crop to predict the exact amount and distribution of rainfall, precise ambient temperatures, or the presence and abundance of specific pathogen races to which the crop will be exposed during its production cycle Precise input and production costs are, in many cases, difficult to predict For such factors, over the range that they are impossible to predict, we must take a breeding approach seeking greater yield stability (lower variation across seasons), as well as broad adaptability (lower variation across locations)

The problem, then, faced by IARC breeders for rainfed crops is not generally as simple as the choice between broad adaptability or specific adaptation, but rather a balance between the two extremes which optimizes the possibility for success with available resources The way in which this balance is being sought is discussed for each of the CIAT commodities

TROPICAL PASTURES

The Tropical Pastures Program (TPP) is unique among the CIAT commodity programs in that germplasm development activities are presently concentrated on exploiting naturally occurring genetic variability (both intra- as well as interspecific) rather than genetic variation generated by hybridization Sustained activities in plant breeding *per se* in the TPP are of only relatively recent development, though it is anticipated that plant breeding will become increasingly important in the directed genetic adaptation of the naturally occurring germplasm to the more intense agricultural environment The strategies of plant breeding in tropical forage species have been, and will continue to be, influenced by results obtained from the study of naturally occurring genetic variation and its interactions with environmental factors It therefore seems appropriate, in considering tropical pasture species, to deal broadly with germplasm development strategies which include primarily the evaluation of naturally occurring intraspecific, interspecific, and even intergeneric genetic variation generated by plant collection and introduction rather than by hybridization Nevertheless, the principles of genotype evaluation, and the implications of target environment variability and resulting G-E interactions are largely the same whether the genetic variation arises from a plant breeding program or from germplasm collection and introduction

Forage plants are unique among crop species with respect to the magnitude of the range of environmental variation over which selected cultivars must be adapted Since these species are perennials (or at least are expected to persist over several years) they are exposed to the entire within- and among-years variation in environmental conditions at any given site Due to their extremely low, direct per hectare value, environmental modification for forage production is minimal in present agricultural practice, particularly for the extensive cattle production systems of interest to CIAT's TPP Fertilizers, if applied at all, are used generally at low levels for establishment with no maintenance applications Chemical control of disease and insect pests is non-existent Thus the potential physical and biological diversity of the target environment is tremendous Management systems for livestock production in Latin America are likewise extremely diverse, ranging from highly intensive "cut and carry" operations with confined animals, to extensive, largely uncontrolled grazing of natural vegetation

Evidence for G-E Interactions

Experiences at CIAT and elsewhere within the tropics have shown strong G-E interactions (mostly, but not exclusively, on the species level) in the tropical forage species For example, Desmodium ovalifolium and Brachiaria humidicola are considered to be highly valuable species at Carimagua and at sites in the tropical forest regions These species have given distinctly inferior performance at CPAC, near Brasilia The performance of Stylosanthes capitata has been so outstanding at Carimagua that a cultivar of this species has recently been released commercially in Colombia In the tropical forest regions of Latin America, as well as under Australian conditions, other species of Stylosanthes are much more successful than S capitata At the accession level, strong interactions are observed among S capitata accessions between CPAC and Carimagua In S guianensis, "common" accessions have given outstanding performance at a number of sites in the tropical forest regions of eastern Peru and in Colombia while these same accessions fail completely at Carimagua and CPAC

Factors Responsible for G-E Interactions

These observations suggest that site differences within the tropics, and particularly within the lowland Latin American tropics, strongly and differentially affect germplasm performance We may consider some of the more important environmental factors which are known (or suspected) to give rise to such differential species and accession performance across sites

Physical factors

Among the physical environmental factors known to affect forage plant performance several specific climatic variables can be identified Mean temperature, which primarily varies with altitude within the tropics, strongly limits species adaptation Towards the limits of the tropics, minimum temperatures may strictly limit the distribution of non-frost-tolerant species Total annual precipitation and its distribution through the year is known to influence species performance Andropogon gayanus, for example, is considered to be a strongly drought tolerant species and can be planted successfully in regions with long, intense dry seasons where other grass species (e g , Panicum maximum and B humidicola) perform less well Soil drainage characteristics likewise affect moisture availability Some species (e g , A gayanus and S capitata) perform well only on well drained soils while others (e g , B humidicola and D ovalifolium) are better adapted to poorly drained situations Photoperiod variation through the year is known to affect flowering response in some important species (e g , S guianensis) Accessions which flower profusely at high latitudes in the tropics may flower only sporadically or not at all at low latitudes and this can severely limit commercial seed yield (a very important trait for cultivar adoption) as well as sharply decrease the opportunity for regeneration from self-sown seed in the grazed pasture

Soil characteristics are known to be of utmost importance in determining species adaptation of tropical forage plants Species interact very strongly with levels of soil fertility, pH, and Al saturation levels Many species (e g , P maximum, C pubescens, L leucocephala) are known to be demanding in terms of soil fertility Others (e g , A gayanus and S capitata) adapt well to very acid, low fertility soils In fact, performance of S capitata is severely reduced on soils of higher pH and under these conditions other legume species give superior performance

Biological factors

Biological factors have proven to be of great importance in limiting performance of many tropical pastures species Distribution of many parasites and races of parasites (e g , Colletotrichum gloeosporioides, causal agent of Stylosanthes anthracnose), is highly variable across tropical Latin America The present distribution is not likely determined by physical environmental factors, but probably depends on the patterns of natural distribution of the host species and the history of their use as introductions in areas where they are not native Colletotrichum races highly pathogenic on many accessions of S capitata appear to be widely distributed in Brazil (where S capitata is native) while most S capitata accessions appear "resistant" to anthracnose in Colombia, where native S capitata is not found While spittle bug appears to be widely distributed across tropical Latin America, different species occur in different locations and grass species preferences of these differ Stemborer of Stylosanthes is encountered at high levels at testing sites in Colombia but does not appear to be a severe problem at present at CPAC

Socio-economic factors

Socio-economic factors may also strongly affect species performance in a differential manner The economic feasibility of fertilizer use in pasture establishment and/or maintenance can be definitive in the selection of pasture species Pasture establishment is generally considered a pioneer agricultural activity in which species adapted to low fertility are established with only minimal modification of the native soil Government policy (e g , restrictions on fertilizer importation, fertilizer price subsidies, cost and availability of credit, etc) can affect the economic feasibility of fertilizer use in pasture establishment Agricultural policies in some countries make attractive the practice of opening new land with one or two highly fertilized, annual crops rather than with pastures Fertilizer use is compensated by the annual crop production Subsequent establishment of pastures takes advantage of residual crop fertility This practice of following highly fertilized crops with pastures permits the use of a set of forage species which would not be considered for establishment in newly opened agricultural areas

Systems of forage utilization (e g , cut vs grazed, legume association with a grass vs pure legume "protein banks", continuous vs rotational grazing, and intensity of grazing) can differentially influence the performance of a particular species or species association

Target Area Subdivisions

Due to the vast diversity of the environment across the Latin American tropics where livestock production occurs and the magnitude of the G-E interactions known to arise therefrom, the focus of TPP germplasm development activities was considerably limited, within the Latin American tropics, basically to the more difficult conditions represented by the very acid, infertile Oxisol-Ultisol regions of the tropical lowlands This restriction of the global target area reduces the environmental diversity in terms of soil chemical properties, but even this target area encompasses extensive diversity in climatic conditions, biological factors, and socioeconomic conditions

A target area survey conducted during 1978 and 1979 accumulated voluminous data on a number of physical attributes of this target area including radiant energy received, temperature, potential evapotranspiration, water balance, and other climatic factors, landform, hydrology, and vegetation, and soil physical and chemical characteristics A single, derived environmental variable--potential wet season evapotranspiration (PWSE)--was found to correlate well with natural vegetation types and was used to divide the overall target area into three broad ecosystems savanna, seasonal forests, and tropical rainforests Based on soil drainage, the savanna ecosystem was further subdivided into well- and poorly-drained savannas, and the well-drained savanna regions were divided still further on the basis of mean wet season temperature (MWST)

The resulting five ecosystems (Table 1) are considered to reflect natural vegetation types and it is assumed that they will aid in orienting pasture germplasm distribution and evaluation They form the present basis for subdividing the germplasm evaluation and selection activities of the TPP as well as for the organization of the program's regional trials network

Adequacy of the Present Divisions

We cannot presume, on the basis of available germplasm performance data, to have definitively confirmed the validity and utility of the present ecosystem classification in terms of the environmental response of the forage germplasm itself A detailed evaluation, in controlled experiments, of the response of germplasm accessions to different environmental variables (coupled with a detailed characterization of the variation in these factors within the global target environment) would aid in validating or refining a subdivision of the target area for purposes of germplasm testing The confirmation of the validity of a particular subdivision of the target area would require extensive testing of a large set of germplasm accessions at a large number of sites with a common performance criterion measured at each site A useful ecosystem subdivision of the global target area would be reflected by small G-E interactions within subdivisions and large G-E interactions between subdivisions We simply do not yet have sufficient data either on germplasm response to defined environmental variables nor from multilocational trials for drawing definitive conclusions on the present ecosystem subdivision of the target area Some tentative conclusions do, however, appear warranted at this stage regarding germplasm adaptation within and across the five defined ecosystems, where "adaptation" is measured by performance (principally dry matter yield under cutting) in monoculture, agronomic plot trials

Among the grasses, some species (e g , *A gayanus* and *B decumbens*) seem to be remarkably broadly adapted within and across the present ecosystems (Table 2), suggesting that the present ecosystem divisions may be largely irrelevant to comparisons among grass species Large site differences in grass species performance have been recorded but these cannot generally be attributed to the variables upon which the present ecosystems are defined The determining factors for grass species adaptation appear to be related primarily to soil fertility (which is not contemplated in the present ecosystem subdivisions) and the length and intensity of the dry season (only indirectly contemplated in PWSE)

In fertilizer trials, large grass species-fertilizer level interactions are commonly observed (e g , CIAT Annual Report 1979, Tropical Pastures Program, p 63) Strikingly different results were obtained in grass evaluation plots between two sites on sharply different soil types within the CPAC experimental station

Table 1 Tropical Pastures Program major ecosystem definitions

Ecosystem	Potential Wet Season Evapotranspiration	Mean Wet Season Temperature	Drainage
Well drained, hyperthermic, tropical savannas (Carimagua)	910-1060	> 23 5°C	Good
Well drained, thermic tropical savannas	910-1060	< 23 5°C	Good
Poorly drained tropical savannas	Variable	Variable	Poor
Tropical, semi-evergreen seasonal forests	1061-1300	Variable	Variable
Tropical rainforests	> 1300	Variable	Variable

Table 2 Adaptation of key forage species by major ecosystem (as of December, 1981)*

SPECIES	PROMISING FOR		
	Well-drained Savannas		Tropical Forests[c]
	Isohyperthermic[a]	Isothermic[b]	
Grasses			
Andropogon gayanus	yes	yes	(yes)
Brachiaria decumbens	yes	yes	(yes)
B dictyoneura	yes	?	?
B humidicola	yes	no	(yes)
Legumes			
Centrosema brasilianum	yes	yes	(no)
C macrocarpum	yes	yes	(yes)
Desmodium ovalifolium	yes	no	(yes)
Pueraria phaseoloides	yes	no	(yes)
Stylosanthes guianensis ('tardío)	yes	yes	(yes)
S guianensis ('common')	no	no	(yes)
S capitata	yes	yes	(no)
S macrocephala	yes	yes	?
Zornia brasiliensis	yes	yes	?

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a Llanos

b Cerrados

c Includes both types of tropical forests

Parenthesis indicate estimate is from preliminary trials only

Question mark indicates no data available

*Taken from CIAT Report, 1982, p 74

Brachiaria humidicola performs well both at Carimagua (representative of the well-drained, hyperthermic savanna ecosystem) and at sites in the tropical forest ecosystems, in contrast to its poor performance at CPAC (representative of the well-drained, thermic savanna ecosystem) (Table 2) It seems unlikely that the difference in performance of this species between Carimagua and CPAC is due to differences in MWST (the criterion upon which the two well-drained savanna ecosystems are separated) It is more probably related to differences between the two sites in the duration and intensity of the dry season (four months with less than 100 mm rainfall at Carimagua vs six months at CPAC), a factor not directly contemplated in the distinction between the ecosystems represented by these two sites Perhaps PWSE could explain this difference in germplasm performance between CPAC and Carimagua, but if so, the present definition of the well-drained savanna ecosystem is insufficiently precise

Many more forage legume accessions have been widely tested than the grasses so that patterns of species adaptation are somewhat clearer (Table 2) In some cases species performance does appear to conform to the present ecosystems However, for most species the differences between the two well drained savanna ecosystems (represented by Carimagua and CPAC) are more probably related to differences in the duration and intensity of the dry season than to the defined difference between these two ecosystems (MWST) As for grasses, many of the known cases of strong G-E interaction (at the species level) in the legumes arise from variability in soil fertility

In at least one case (S guianensis, common) the differential response between the savanna ecosystems and the tropical forests is determined only indirectly (if at all) by contrasting environmental conditions The poor performance in the well-drained savannas is known to be due to biological pressures (anthracnose, primarily), and whether this difference in intensity of anthracnose is dependent on differences in PWSE or simply is due to the present distribution of races of the pathogen is not yet known with certainty

An attempt is being made within the present system of regional trials to relate species and accession performance to more detailed descriptors of the test sites such as soil chemical factors, detailed meteorological data, and pest and disease presence [Annual Report, 1981, (mimeo edition) Vol 1, p 4-20] This information, if combined with reliable performance data, should allow more precise definition of the environmental factors which affect performance of the germplasm and may lead to better definition of the target area ecosystems

Thus, while it does appear that important G-E interactions may arise from the environmental factors used to define the present ecosystems, it is not entirely clear whether the present subdivision is precise enough really to be useful or whether addition of other environmental variables (e g , some measure of the duration and intensity of the dry season) might permit subdivision of the global target area into an equal number of ecosystems which would allow more accurate prediction of germplasm performance That many species are broadly adapted across ecosystems and that several striking instances of sharp differences in performance of particular species within ecosystems occur (usually attributable to disease factors) suggest that there is considerable room for improvement of the definition of ecosystems

Future Research Needs

Specific information which would help determine the utility of the present ecosystems and to define better the ecosystems include the following

1 Definition of what factor(s) cause the strikingly different reaction of some species (i e , *B humidicola* and *D ovalifolium*) between CPAC and Carimagua If this does not involve MUST then the present division of the savanna ecosystems is inadequate since it fails to predict this important site differences in species performance

2 It would be extremely helpful to have a detailed disease-insect potential inventory of the target area which would permit prediction of accession response to location While the preparation of such an inventory may be difficult in the short term, it ought to be possible to relate longer term observations on disease incidence to some one or more physical environmental factors

3 Soil fertility levels appear to be extremely important in determining species potential at a particular site Since the TPP philosophy dictates "minimum input" and since common commercial practice of pasture establishment and particularly maintenance is "zero input", an inclusion of native soil fertility characteristics in the ecosystem classification might greatly improve its utility in predicting species performance Significant variation in soil characteristics does occur even within the broad "acid, infertile soils" target area While such localized variation in soil characteristics may be extremely difficult to map precisely, it certainly could be clearly defined

4 While socioeconomic environmental factors (e g , pasture management systems) are known strongly to affect pasture plant performance, these factors are not, at present, formally contemplated in the ecosystem subdivisions of the global target area These management systems (including primarily soil fertility modification and system of forage use) require more precise definition and "prioritization" They should be rationally used to define appropriate conditions of germplasm evaluation in particular situations

BEANS

Field beans (*Phaseolus vulgaris*) are the most important grain legume in the Americas, where 47% of world bean production occurs, and also probably in Eastern Africa, where 16% of production occurs They are produced mainly for consumption of the dry grain, with an average consumption of 15 kg/capita/annum in Latin America, and 12 kg/capita/annum in Eastern Africa They are also locally consumed as immature seeds, and the immature pod is one of the most widely eaten green vegetables in the world The leaves are used as spinach in some parts of Africa

Different consumption patterns, and especially of different grain types, impose a natural division of the target area in terms of the objectives of the breeding program It is assumed that it is more difficult to change consumer preferences, particularly among rural populations, than it is to breed improved varieties with certain grain types It is not possible, of course, to breed for every type, but insofar as these can be grouped into major classes this provides a restriction to the germplasm base available to any particular region and reduces the need for extremely broad adaptability

Beans differ from some of the major cereal crops in a number of important ways they are a legume with capacity for fixing nitrogen, they are frequently intercropped, particularly with maize (up to 70% of the total area), and they are generally grown with low technology (e g low planting density without irrigation) These factors together indicate the need for a different approach to bean breeding from that which has been successfully used for wheat and rice Most plant breeding has been carried out in the past in favorable environments, and its benefits have been severely reduced when improved varieties were planted in poor environments Part of the cause of this is that the process of selection was not carried out in a poor environment, but in addition, the particular stresses involved in creating a poor environment differ from one place to another, and this reduces greatly the probability that any one variety will adapt to all locations

On the other hand, certain characteristics of the bean plant can be identified which could contribute to a broader adaptability, such as insensitivity to photoperiod Vigor, or competitive ability, is also likely to be important, whereas the partitioning of biomass to grain (harvest index) is not likely to be as important as in some other crops Competitive vigor is something which natural selection will have been acting on in farmers' fields for centuries However, the percentage of natural hybridization in beans is low (up to 1%), and the genetic variability present in a farmer's land race would not be comparable with the CIAT germplasm collection By evaluating the total variability of the species, and suitably recombining it by hybridization and selection, we are able to achieve, in collaboration with national programs, what could not be done by natural selection, or by national programs acting on their own This depends, however, on setting appropriate breeding objectives, based on an understanding of G-E interactions Evidence for the need to divide the target area for the purpose of defining breeding objectives is presented in the following sections

Evidence for G-E Interactions

Genotypes x geographical location

The international bean yield and adaptation nursery (IBYAN) was uniform over all locations in 1976, after which it was split into progressively more groups (Table 3) An analysis of adaptability and stability of performance for the IBYAN 1976 was presented by Laing (1978), where broad adaptability was indicated by a high relative performance of a particular genotype when grown in a range of locations, and stability referred to the response of a genotype to changing environmental factors over time Whereas broad adaptability is important to the breeder, stability is clearly more important to the individual bean producer Whilst some factors involved in determining adaptability will be the same as those determing stability (i e , water availability and disease and pest incidence), others are more especially important in determining adaptability among different locations (i e , photoperiod, temperature and soil nutrient status)

In the 1976 IBYAN and those that followed, there was a highly significant G x locations interaction (Table 4) and this was analyzed by regression analysis for 20 varieties over 39 locations (Figure 1) The most contrasting varieties are encircled in three groups firstly, those that had high yields, especially in favorable environments, characterized by G 1820 (P I 309 804) and G 3645 (Jamapa), both type II's, those that had high yields, especially in relatively poor environments, characterized by G 4525 (ICA Pijao) and G 4495 (Porrillo Sintético), also type II's, and those that had low yields, but which did relatively better in poor environments, characterized by G 0076 (Red Kloud), G 4460 (Pompadour 2), G 4494 (Diacol Calima) and G 4523 (Línea 17), all large grain type I's

In the 1979 IBYAN the superiority of black grained experimental lines from CIAT (e g , BAT 58, BAT 304, BAT 450, BAT 518) was more significant in the poor environments, reflecting the low input breeding strategy of the bean program Broad adaptability has been identified more frequently in bush bean lines than in climbers, which show a much higher frequency of photoperiod sensitivity, more specific temperature adaptation, and tend to show growth habit instability Of CIAT bush bean lines tested internationally BAT 304 (black), BAT 85 and BAT 561 (cream) have demonstrated exceptionally broad adaptability

Genotypes x cropping system

The principal cropping systems in which beans are grown are intercropping with maize and monoculture The intercropping systems can be further divided into row intercropping, which consists of simultaneous or nearly simultaneous planting of the associated crops, relay intercropping, where the second crop (usually beans) is planted near to physiological maturity of the first crop, and mixed intercropping, which frequently involves more than one other companion crop planted simultaneously, and not arranged in rows Intercropping

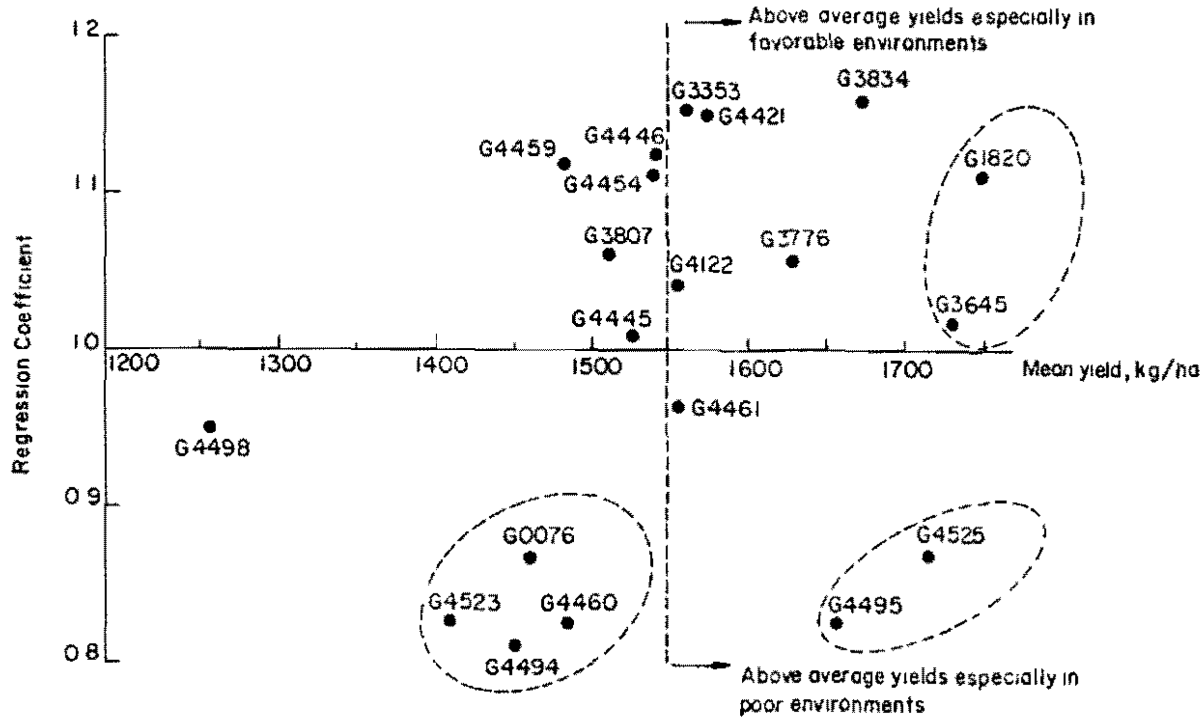
TABLE 3 THE GROUPS OF VARIETIES IN THE IBYAN FROM 1976

	1976	1977	1978	1979	1980	1981	1982
BUSH	All colors	Black	Black	Black	Black	Black	Black
		Non-black	Non-black	Non-black	Small red	Small red	Small red
					Large red	Large red	Large red
					White	White	White
					Coffee/cream	Coffee/cream	Coffee/cream
CLIMBING			Black	Black	Black	Black	Black
			Red	Small red	Small red	Small red	Small red
			Other colors	Large grains	Large grains	Large grains	Large red
							Large cream/ yellow

TABLE 4 THE GENOTYPE x LOCATION INTERACTION IN IBYAN TRIALS OF BLACK BEANS FROM 1976 TO 1979 (from Voysest, 1982)

Year	Source of variation	d f	Variance Ratio (F)
1976	Interaction	393	3 33***
	Error	1150	
1977	Interaction	512	2 56***
	Error	1042	
1978	Interaction	494	2 52***
	Error	1024	
1979	Interaction	390	3 78***
	Error	865	

*** $P \leqslant 0\ 001$



Variety Identification

G 0076 - Red Kloud
G1820 = PI309804
G3353 = Puebla152
G3645 = Jamapa
G3776 = Venezuela 2
G3807 = Brasil 2
G3834 = 51051
G4122 = S 166-A-N
G4421 = S-630 B
G4523 - Linea 17

G 4445 - Ex-Rico23
G4446 - Ex-Puebla 152
G4454 - ICA-Tui
G4459 - NEP 2
G4460 = Pompadour 2
G4461 - Porrillo1
G4494 = Diacol Calima
G4495 = Porrillo sintetico
G4498 - Sanilac
G4525 - ICA-Pijao

Figure 1 Genotype x Geographical Location Interactions for 20 bean varieties in the 1976 IBYAN (Modified from Laing 1978) predominates among small farmers and is probably at least as important as monoculture in terms of bean production in the developing world

Competitive ability of the bean plant is crucial for most intercropping systems, and is generally defined by the early vigor of the plant, final plant height and climbing ability Strong interactions of genotypes by cropping systems have been found, but when materials are divided according to their growth habit, much of the interaction disappears, especially in bush bean materials Nevertheless, intercropping can be regarded as a stress situation, involving competition for light, nutrients and water, and as such requires deliberate selection of breeding populations for adaptability to these stresses

In general terms, type I beans (determinate bush) are the least competitive, and give the poorest yields when intercropped, although some varieties with large leaves can be exceptionally competitive with certain genotypes of maize in the early stages of growth Type IV climbing beans compete well, and types II and III (indeterminate bush and semi-climbing) are intermediate Types I and II are most frequently used where there is little competition from other crops, whereas types III and IV are most commonly used for intercropping For the latter types, correlations between monoculture yields of varieties and their yield when intercropped with maize are generally low (Table 5) On the other hand, correlations among intercropping systems with different maize cultivars are usually high This indicates that selection of beans can be carried out with one maize cultivar, although a selection experiment is currently underway, with breeding populations of all growth habits, to test this hypothesis For relay cropping, differences in climbing ability are largely responsible for the genotype x cropping systems interactions that are observed (CIAT, 1981a)

Genotypes x levels of technology

Levels of technology may include differences in plant population density, fertilization, disease and pest control, and irrigation Factorial trials combining different levels of these factors with different varieties are being carried out by the bean program in on-farm trials, and preliminary results from Nariño, Colombia, have indicated an interaction between a local variety (Limoneño) and an improved line (BAT 1235) The latter performs relatively better with higher levels of density and fertilization The same applies to an improved climbing bean line, E 1056, tested on farms in Antioquia The improved lines which are selected for disease resistance, on the other hand, tend to do relatively better than the controls without disease and pest control (Table 6)

In general, semi-climbing and climbing beans (Types III and IV) have a lower optimum plant population density than Type I and II bush beans (CIAT, 1978) The heavy branching of the TYPE III allows a high degree of canopy compensation, making it particularly suitable for unmechanized small farm monoculture or relay cropping systems The climbing ability of the Type IV makes it particularly suitable for intercropping

TABLE 5 CORRELATION MATRIX (8 d f) FOR BEAN YIELDS IN MONOCULTURE AND INTERCROPPED WITH 3 DIFFERENT MAIZE CULTIVARS

		Monoculture	Intercropped with maize	
			ICA H-210	Suwan-1
Intercropped with maize	ICA H-210	0 6079	-	-
	Suwan-1	0 2367	0 6710*	-
	La Posta	0 4088	0 8952***	0 8902***

* P ⩽ 0 05

*** P ⩽ 0 001

TABLE 6 COMPARISON OF E 1056 (RECENTLY NAMED ICA-LLANOGRANDE IN COLOMBIA) WITH TRADITIONAL VARIETY CARGAMANTO WITH AND WITHOUT BENOMYL FUNGICIDE, AVERAGED OVER 13 FARM TRIALS IN ANTIOQUIA (EL CARMEN DE VIBORAL), 1981

	Yield (kg/ha)	
	With Benomyl[1]	Without Benomyl
E 1056	1959	2063
Cargamanto	1638	1013
LSD	383	

[1] Benomyl was sprayed three times during the growing season

Levels of fertilization and disease and pest control are tested routinely in the EP yield trials in CIAT-Palmira and Popayán (Figure 2). Although a generally positive correlation between variety yields at the two levels of technology has been found, there are also clear cases of varieties which do relatively better under one or the other situation. The most desirable types are those which do well under both situations. The reason for the generally positive relationship in variety response between the two levels of technology is that a number of factors enter at once in Popayan (i e , nutrient availability, and several diseases, especially powdery mildew, <u>Ascochyta</u> and anthracnose). Different levels of tolerance to these factors in the materials tend to balance each other out on average. On the other hand, it does seem that the lines that do best at low levels of technology have more of the relevant disease resistances.

Factors Responsible for G-E Interactions

The factors responsible for the interactions described above can be divided into those related to the physical environment (photoperiod and temperature), the biological environment (diseases and pests), and a combination of physical and socio-economic environment (water availability and soil nutrient status).

Photoperiod

A much higher percentage of bush bean materials has been found to be insensitive to photoperiod than of climbing beans. The most extreme response to photoperiod (complete lack of flowering in long days) is found mostly in climbers. In short days, varieties exhibit variability for the temperature at which they flower in the shortest time and yield best. Below this temperature, in photoperiod sensitive varieties, the photoperiod response is progressively reduced in most materials, and above this optimum temperature the response increases. Cargamanto, for example, has an optimum temperature of about 17°C, whereas Diacol Calima is at its optimum at about 24°C.

Sub-tropical environments with a short growing season require photoperiod insensitive early genotypes of beans for optimum yield. Where an extended growing season is available, particularly with irrigation, an intermediate response to photoperiod may extend the period of vegetative growth and increase yield, as has been proved for the variety Porrillo Sintético (CIAT, 1978).

The ability of photoperiod response as measured in CIAT to predict the field response of varieties around the world was tested by Jones (CIAT, 1980a), using the data for 20 varieties in the 1976 IBYAN (Table 7). The coefficient of photoperiod reaction (B_1) was estimated from the flowering time IBYAN data, using information on the daylength expected at each location during the cropping season (Figure 3). The larger the coefficient, the greater was the response to increasing daylength in the field. All materials with a B_1 value of 0 had been classified as 1N (insensitive) or 2N (slightly sensitive) in the photoperiod lot of CIAT, indicating a close correspondence between observed response and the predicted response. The data also allowed a division of the varieties

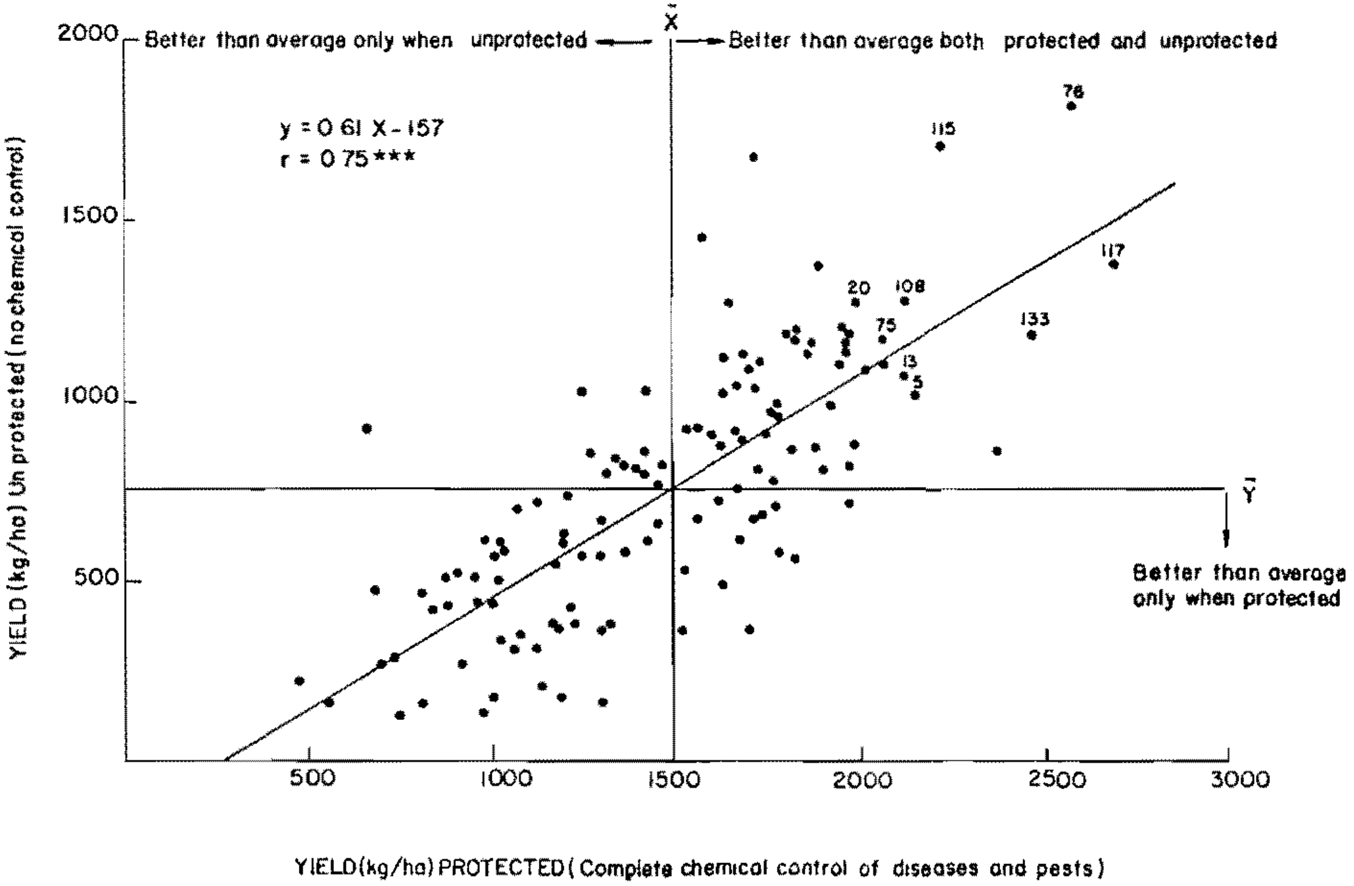


Figure 2 Effect of levels of chemical control of diseases and pests on advanced breeding lines in the EP 1981, CIAT-Popayán Numbers adjacent to points refer to EP 81 entry number

TABLE 7 CORRESPONDENCE BETWEEN PHOTOPERIOD RESPONSE AS MEASURED IN 39 INTERNATIONAL TRIALS ($\beta_1 > 0$ is photoperiod sensitive) COMPARED WITH PHOTOPERIOD REACTION EVALUATED UNDER LIGHTS IN CIAT (Scale 1-5, where 1 is insensitive, N = normal flowering, A = abnormal), IBYAN 1976 DATA

Variety	Growth habit	Temperature response	Photoperiod coefficient β_1 %	Photoperiod reaction in CIAT
G 4495	II	Normal	0 8	3N
G 3834	II	Normal	2 7	3N
G 4451	II	Normal	1 1	3N
G 4454	II	Normal	3 0	3N
G 3645	II	Normal	0 0	1N
G 4525	II	Normal	0 0	1N
G 1820	II	Normal	0 0	1N
G 4122	II	Normal	1 4	2N
G 4421	II	Normal	0 0	2N
G 4459	II	Intermediate	0 0	1N
G 3776	II	Intermediate	2 7	2N
G 3353	III	Intermediate	0 1	2N
G 4446	III	Intermediate	1 9	2N
G 4523	I	Intermediate	12 7	4A
G 3807	I	Intermediate	2 8	3N
G 4445	I	Broad	0 0	1N
G 4498	I	Broad	0 0	2N
G 4494	I	Broad	7 3	4A
G 4460	I	Broad	5 6	4A
G 0076	I	Broad	0 0	1N

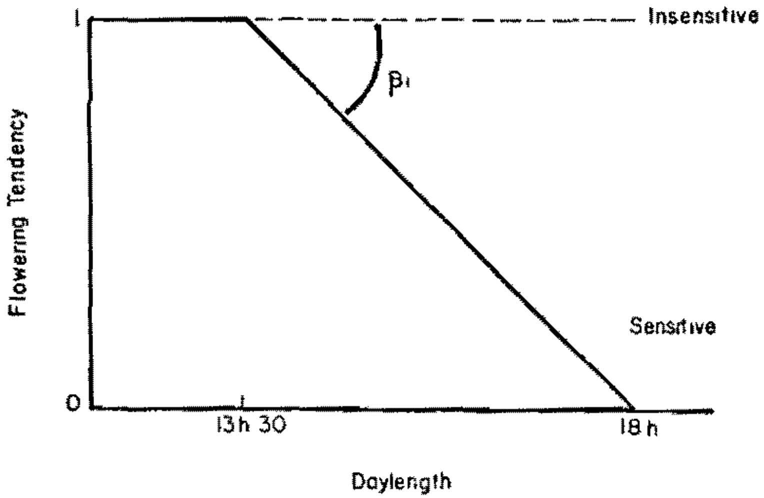


Figure 3   Method for estimating photoperiod response from International Trials data, using coefficient β_1 Flowering tendency = 1 signifies flowering in minimum time, whereas zero indicates that plants will never flower

according to the effect of temperature on the time to flowering (Table 7) Those with a broad response were all Type I varieties, whereas those with a normal response (greater effect of temperature on flowering) were all Type II varieties Broad adaptability to photoperiod and temperature was evident in G 4445 (Ex-Rico 23) and G 0076 (Red Kloud) These varieties did not do especially well in terms of yield (Fig 1) On the other hand, the highest yielding varieties (C 1820 and G 3645) were insensitive to photoperiod with a normal response to temperature, and growth habit II

The relationship between photoperiod response and yield across the major bean production regions of the world, however, is still far from being completely understood For this purpose, a special international nursery is being developed in collaboration with Cornell University to study this relationship and enable breeding objectives for photoperiod response to be established for each production region The ultimate answer on the adaptation of a new material has to come from the production region, and for this purpose it may be more efficient to send segregating materials for local selection, especially when suitable photoperiod information is available for the parents

Temperature

Temperature adaptation as such is most readily observed in the tropics without the interfering influence of photoperiod Much of the variability in temperature adaptation in beans remains to be adequately exploited, especially in selection programs for broader temperature adaptability

In a first study (CIAT, 1979a) considerable variation was demonstrated in temperature response among a set of 250 varieties of all growth habits grown at 6 locations in Colombia, differing mainly in temperature as regulated by altitude In a second study, the whole germplasm bank of semi-climbing and climbing types was evaluated at four locations, and the best at each location were selected and put into a yield trial (CIAT, 1980a) Greater variability for temperature response was found in this second set (Figure 4) The best materials for a cool climate (Pasto) barely flowered or set seed in a warm climate (Palmira), and the reverse phenomenon ocurred in the best materials for a warm climate There was also a set of intermediate materials It is probable that there is continuous variation available for temperature adaptation, and its genetic control is not expected to be linked to that of photoperiod sensitivity, although no materials have yet been found that are insensitive to photoperiod and adapted to cool temperatures These are being actively sought, as are materials with a broader adaptability to temperature

Absolute yields of adapted materials (Figure 4) appear to be slightly higher in a cool climate than a warm one, but the growing season in the cool climate is much longer At any rate, there is no evidence that a narrow range of temperature is optimum for yield in the species as a whole, as has been suggested on many occasions (e g , CIAT, 1979) There is enormous variability available which largely remains to be exploited, offering possibilities for area expansion

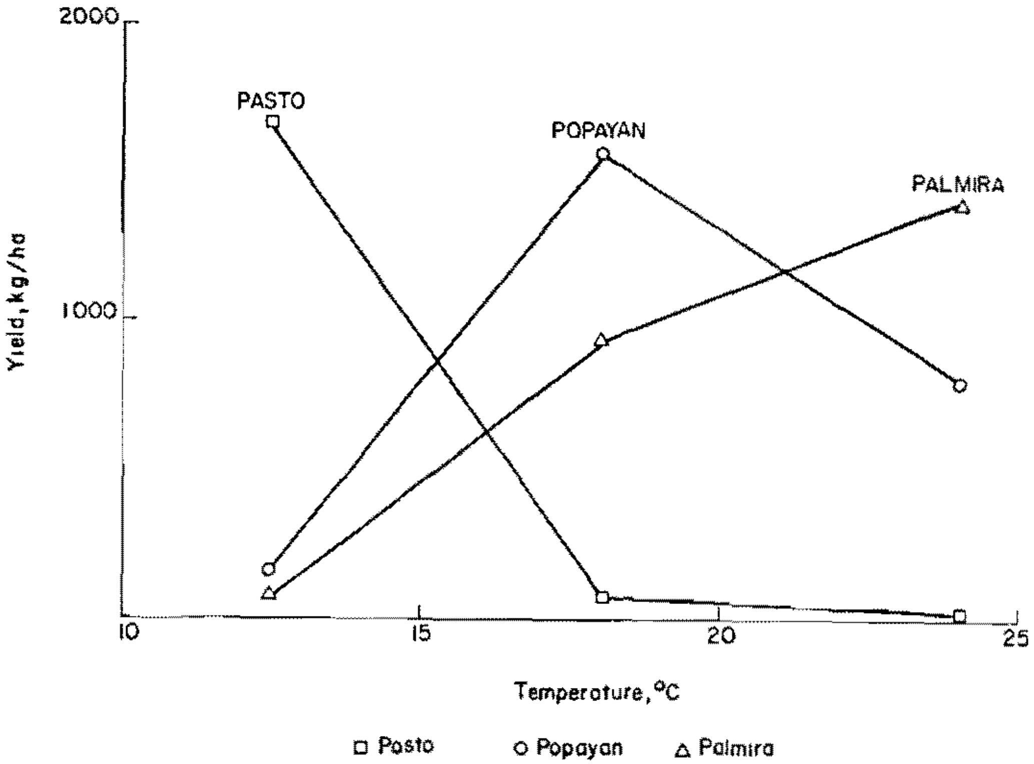


Figure 4 Mean yield of the five highest yielding bean varieties among 180 sown at three altitudes in Colombia, and plotted against the mean growing season temperature The place names refer to the curve for the mean of the five best varieties at that location Altitudes Pasto 2,710 m, Popayán 1,750 m, Palmira 1,000 m

Diseases and pests

Resistance to diseases and pests contributes both to broad adaptability and to yield stability, but since any given material can only be resistant to a few diseases and pests, this resistance is more likely to contribute to stability, in good years versus bad years, than to broad adaptability From one location to another, not only the spectrum of diseases may change, but also the races of the diseases For the purpose of measuring these effects, the bean program has established some international disease resistance nurseries, particularly for rust (since 1973) and anthracnose (since 1978) Materials have been identified with a wide spectrum of resistance to different races of these diseases, e g , Ecuador 299 for rust, and BAT 841 and V 7917 for antracnose When intermediate, or tolerant, reactions are present these may interact with cultural practices Intercropping and low plant density tend to reduce the severity and incidence of many diseases and pests, though not all For small farmers, who frequently intercrop and plant at low densities, intermediate reactions may be more stable over time and sufficient to control the problem

Water availability

Irrigation is only available in a small proportion of the total area for bean production Bean farmers, as a general rule, do not have adequate control over the supply of water to their crop Tolerance of drought stress, particularly from flowering onwards, will contribute greatly to yield stability Drought screening of advanced bean lines has been underway in CIAT since 1978 As with all stress selection, it is desirable that materials should yield well both with and without the stress Many regions employ cropping seasons that require a short-season cultivar to minimize the risk of end-of-season stress In other areas, rainfall is unreliable and Type III and IV varieties, capable of recuperating from a stress period by producing a second flush of pods, may be used This behavior is associated with delayed and uneven maturity, and would not be convenient to large farmers, but is no problem to small farmers, for example in subtropical areas where relay intercropping is common

Soil nutrient status

Variability is available in beans to tolerate different levels of Al saturation and P availability, as well as variation for the ability to fix N Varieties such as Carioca, from Brazil, are particularly tolerant to acid soil conditions Routine screening of advanced lines for tolerance to acid soils has been underway since 1979, and materials like BAT 26, BAT 28, EMP 28 and BAT 458, have shown to be promising for tolerance to low P and high Al saturation An attempt has been made to select materials that not only yield relatively well under P stress, but also respond well to fertilization with P

Agroclimatological Divisions of the Target Area

Bean production in Latin America and the Caribbean was characterized by Jones (CIAT 1979a, 1980a), using a cluster analysis to group the different regions according to temperature at flowering and water balance during the vegetative, flowering and pod-filling phases Seven climate types were described, and these are shown in Table 8, in order of descending temperature By far the most bean production occurs in climate type E, with a mean temperature of 20°C, and possible late season water stress This classification only includes two of the five factors already mentioned as being responsible for G-E interactions, and it could be made more comprenhensive by including information on soil, daylength during the growing season, biological factors including diseases and pests, and socio-economic factors including cropping systems Such information, however, is not yet sufficiently available Other important areas, such as Eastern Africa, have not been included in survey work of this kind The information to date indicates the importance of selecting materials adapted to temperatures somewhere between CIAT-Popayan and those at CIAT-Palmira and with some tolerance to water stress after flowering

This information has helped divide up bean production geographically, though more weight has been given to consumer preferences for particular grain types More detailed studies are needed of the agroclimatic variation within pre-defined geographical regions, for the purposes of identifying suitable locations for testing materials, and for setting priorities in the breeding program for particular adaptation characters The way in which the available information has been used to divide up the target area for breeding purposes is described in the following sections

Structure of CIAT's Bean Breeding Program

The trend which began in 1977, by dividing the IBYAN into two sets, has continued to penetrate the organization of the whole program (Table 9) This is still an evolving scheme, which has undergone a number of changes It serves to divide responsibilities among breeders, and to define more clearly the breeding objectives and the collaborative ties with national programs each breeder needs to establish Each breeder has the responsibility for cultivar improvement within the groups assigned to him In addition, he works with the relevant disciplines to increase the level of expression of particular traits, such as improved or more stable resistance to bean common mosaic virus (BCMV), anthracnose, or halo blight, or improved capacity to fix nitrogen, improved drought tolerance, or tolerance of temperature extremes (Table 9)

All advanced materials, when the breeding program considers they are uniform, pass through a series of nurseries for the purpose of evaluation and selection The first stage is the VEF (Vivero del Equipo de Fríjol) nursery, which has been carried out only in Colombia Selected materials pass on to the EP (Ensayos Preliminares) At this stage, since 1981, limited numbers of sets of materials have been available for testing internationally, normally by regional programs or

TABLE 8 A SIMPLIFIED DESCRIPTION OF THE CLIMATE TYPES FOR BEAN PRODUCTION IN LATIN AMERICA AND THE CARIBBEAN, FROM CIAT 1979

Climate type	Mean Temp °C at flowering	Water balance	Production x 1000 tons	Example sites
D	26°	Late season stress	262	Veracruz, Mexico
A	23°	Adequate	661	Huila, Colombia
B	23°	Slight excess water	118	Turrialba, Costa Rica
C	23°	Very dry, irrigated	538	Culiacan, Mexico
E	20°	Possible late season stress	1672	Durango, Mexico
F	16°	Moderate deficits	451	Rio Grande do Sul, Brasil
G	13°	Adequate	45	High altitude Andean Region

Table 9 The Structure of CIAT's Bean Breeding Program

CLIMATE		TROPICAL				TEMPERATE				TROPICAL			
		WARM		MODERATE						MODERATE	COOL		
GROWTH HABIT		BUSH AND CLIMBING			BUSH	BUSH AND CLIMBING	BUSH			BUSH	CLIMBING		BUSH
SEED SIZE		SMALL AND MEDIUM			LARGE	MEDIUM	SMALL	MEDIUM	LARGE	MEDIUM & LARGE	LARGE		
SEED COLOR		BLACK	RED	WHITE	YELLOW CREAM LIGHT BROWN	LIGHT BROWN CREAM	CREAM (MOT) L BROWN (MOT) PURPLE	CREAM (MOT) L BROWN (MOT) PINK (MOT)	WHITE	RED (MOT) PINK (MOT) PURPLE (MOT)	RED (MOT)	YELLOW CREAM LIGHT BROWN WHITE	RED (MOT) YELLOW CREAM
BREEDER		I				II				III			
COUNTRIES / REGIONS		LOWLAND MEXICO C AMERICA CUBA VENEZUELA	C AMERICA CARIBBEAN	COASTAL ECUADOR PERU CHILE	COASTAL ECUADOR PERU MEXICO	HIGHLAND MEXICO	BRAZIL	HIGHLAND MEXICO	ARGENTINA MID EAST	ANDEAN REGION AND EASTERN AFRICA			
BREEDER	PROJECT	IMPORTANCE WITHIN EACH GROUP 1 = very important, 2 = important, 3 = occasionally important - not important											
I	BCMV	1	1	1	1	3	1	1	1	2	-	-	3
I	BGMV	1	3	-	-	-	3	-	2	-	-	-	-
I	RUST	2	2	1	1	2	2	1	3	2	2	2	2
I	WEB BLIGHT	2	2	-	-	-	-	-	-	3	-	-	-
I	BACTERIAL BLIGHT	2	1	-	-	-	2	3	2	2	-	-	-
II	ANTHRACNOSE	1	2	-	-	1	1	1	1	1	1	1	1
II	ANGULAR LEAF SPOT	2	3	-	-	2	2	2	2	2	3	3	2
III	HALO BLIGHT	-	-	-	-	-	-	-	-	3	2	2	2
III	ASCOCHYTA	-	-	-	-	-	-	-	-	3	2	2	2
III	POWDERY MILDEW	-	-	2	2	2	3	3	-	3	2	2	2
I	EMPOASCA	3	3	2	2	3	2	2	3	2	3	3	3
I	APION	2	3	-	-	2	-	2	-	-	-	-	-
II	EPILACHNA	3	-	-	-	3	-	3	-	-	-	-	-
III	BEAN FLY	-	-	-	-	-	-	-	-	2	3	3	3
III	BRUCHIDS	3	3	1	3	3	3	3	1	2	3	3	2
I	N-FIXATION	2	2	2	2	2	2	2	2	2	2	2	2
II	DROUGHT	3	3	1	1	3	1	1	3	2	3	3	3
II	LOW P	1	-	-	-	-	1	3	-	3	3	3	3
II	EARLY MATURITY	-	2	-	3	-	3	1	-	-	3	3	-
II	ARCHITECTURE	2	2	2	2	-	2	2	1	1	2	2	1
III	LOW TEMPERATURE	-	-	-	-	2	-	2	-	-	1	1	1
III	PHOTOPERIOD	3	2	3	3	1	2	2	1	3	2	2	3
EP / IBYAN SERIES		1-0000	2-0000	3-0000	4-0000	5-0000	6-0000	7-0000	8-0000	9-0000	10-0000	11-0000	12-0000

specially selected collaborators, seed being in short supply Since the material in the EP is grouped in the same way as the IBYAN, it can be sent for testing in the relevant regions Lines selected out of the EP pass on to the IBYAN international yield trials, which are again distributed according to the region of interest (e g IBYAN series 90000 goes mainly to the Andean Region and Eastern Africa)

Segregating materials have so far only been selected in the regions where a regional program has been operating (e g , for Golden Mosaic resistance in Central America), or where special collaboration exists A trend towards earlier generation selection in the regions of interest is likely as more regional programs get under way, especially in Brazil, the Andean Region, Eastern Africa and the Middle East Although many adaptation factors can be tested for in Colombia, as previously demonstrated, the complex interactions of these, and the occurrence of diseases and pests not present in Colombia, make it essential to select for local adaptation as early as possible Characteristics contributing to wide adaptability, for use primarily in parents, can be selected for in Colombia It is envisaged that all locally selected materials would find their way back to the VEF-EP-IBYAN scheme, which would continue to provide an opportunity for testing materials uniformly, and comparing them with materials from other regions The scheme would begin to lose its present value as a vehicle for distributing advanced lines internationally

A Breeding Strategy

Beans in the developing world are grown mainly by small farmers, and selection procedures should take into account the special needs of these farmers, who are normally in less favorable environments (steep slopes, poor soils, inadequate control of water, etc) It is not enough to suppose that disease and pest resistances alone will resolve these problems Diseases and pests may indeed be more readily controlled in small plots than in extensive plantings, especially when intercropping is used Plant characters related to competitive ability, efficient use of P and tolerance of drought should be emphasized, as these factors are particularly relevant to the problems of small farmers Alternative sources of resistance need to be actively sought, and more emphasis given to intermediate or tolerant reactions, which may be more stable over time The pressure on pathogens to mutate in some tropical areas, where beans may be grown almost all year round, is much greater than in temperate countries, where major gene resistance to certain diseases of beans (e g , anthracnose and BCMV) has held up for considerable periods of time There is evidence to indicate that these same genes do not hold up for long in the tropics

Broad adaptability <u>within</u> each of the 12 major groups, as defined by the bean program, is desirable for the sake of making a wider impact with new materials Intermediate sensitivity or insensitivity to photoperiod needs to be incorporated into more semi-climbing and climbing varieties (Types III and IV) Evidence exists that broader temperature adaptability exists, and could be selected for

For the farmer, local adaptation and yield stability are of first importance A breeding method to select for these is proposed in Figure 5, modified from the F_2 progeny method of Lupton and Whitehouse (1957) It involves F_2 single plant selection in Colombia, followed by F_3 progeny testing, particularly for BCMV resistance, and parallel clean seed production F_4 populations are tested in the region of interest in a yield trial, followed by another yield trial in F_5 giving the opportunity to test temporal stability, and select the best from the two seasons in bulk in the F_5 Single plants are again selected in the F_6 in the region, and from there on the normal procedure for testing advanced lines is followed Other schemes could be developed, but it is important that the concept of temporal stability should be incorporated

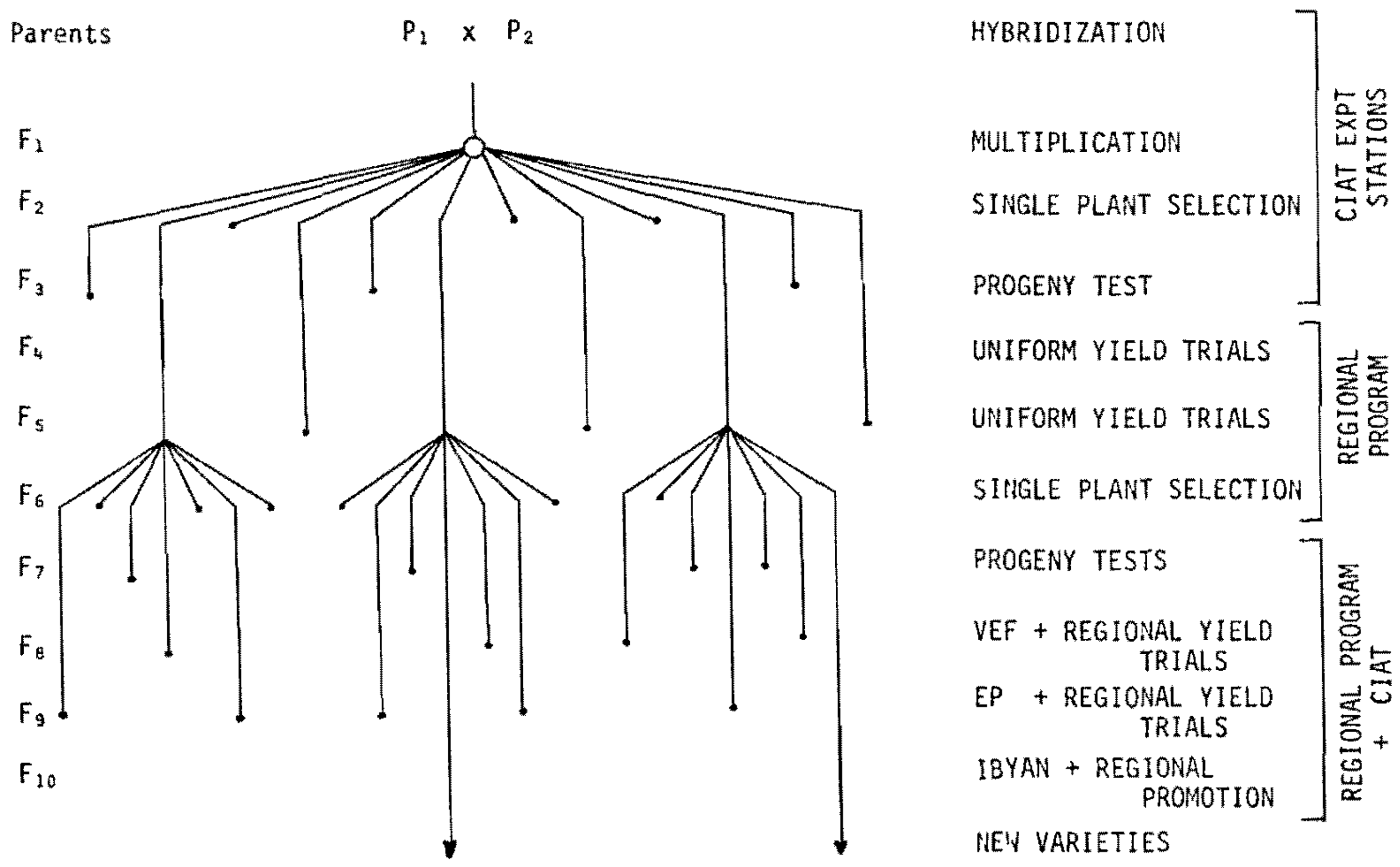
Yield trials and selection nurseries should be carried out in the predominant cropping system of the region It has often been stated that large yield advances are only achieved by breeding under high input technology in monoculture, and exploiting improved partitioning of photosynthate to economic yield Nevertheless, much variability exists in beans for characters that contribute to biomass production, and being a self-pollinating species, this variability has not had sufficient opportunity to recombine Evidence exists that considerable progress can be made by selecting under stress conditions, such as intercropping, or drought In absolute terms, the yield advances cannot be as great, but in relative terms they can be just as significant

The success of such a strategy depends on the stresses applied being relevant to local adaptation, and for this purpose, more information is needed, region by region, on the principal stresses and key locations for testing materials As regional programs are further developed, the collecting of such information will be facilitated Broad adaptability and yield stability should be sought within such regional programs, and CIAT's program in Colombia can be instrumental in identifying sources of material, as well as providing hybrid populations with a uniquely broad genetic base The present VLF-EP IBYAN scheme may in the future cease to be a vehicle for distributing CIAT materials internationally, but become a means of comparing progress for specific characters, and facilitating the interchange of new materials between regions

CASSAVA

Cassava is extremely efficient in producing carbohydrates under more marginal agricultural conditions Because of its relatively high labor requirements, adaptability to intercropping systems and flexible harvest period, it is ideally suited to small farm production systems The intensification of production will be based largely on the diversification of alternative end uses of cassava, such as starch and animal feed The cassava program has three principal thrusts a) development of low-cost, yield-increasing technology, particularly directed at small farmers, b) research on developing cassava as a crop for expansion into the frontier, and c) research on more efficient processing and utilization technologies

FIGURE 5 A BREEDING METHOD TO SELECT FOR YIELD STABILITY IN BEANS, MODIFIED FROM THE F_2 PROGENY METHOD OF LUPTON AND WHITEHOUSE (1957)



Evidence for G-E Interactions and Factors Responsible

Differential genotype performance is common for cassava grown in distinct environments Information on G-E interactions from CIAT breeding and agronomy trials and international trials, plus experiments designed to detect specific factors causing G-E interactions provide the basis of our discussion Cock (1981) has reviewed in detail factors contributing to G-E interactions, and conversely, to genotype stability for cassava

Temperature

As a result of early studies in cassava physiology (Irikura, et al 1979), it was concluded that very different genotypes would be required for areas with mean temperatures below 22°C as compared to above 22°C Agronomy, pathology and breeding trials strongly confirm this hypothesis (Figure 6) Selections from higher temperature sites are consistently poor performers in Popayan (18°C), and vice versa It is not yet clear if a significant interaction exists for temperatures of approximately 23-25° compared to 26-28° If an interaction does exist, it is certainly less marked than for the high versus low temperature comparisons Selections at CIAT (intermediate temperature) commonly do well on the north coast (high temperature), and vice versa

There is also little known about interaction effects of large annual fluctuations in temperature such as in the subtropics Genotypes of subtropical origin, e g , southern Brazil and Cuba, commonly do very well in regions of constant temperature Movement of germplasm in the other direction has been too limited to draw solid conclusions Low latitude-selected material evaluated in Florida and Cuba have generally not performed well, but this cannot be specifically attributed to temperature effects

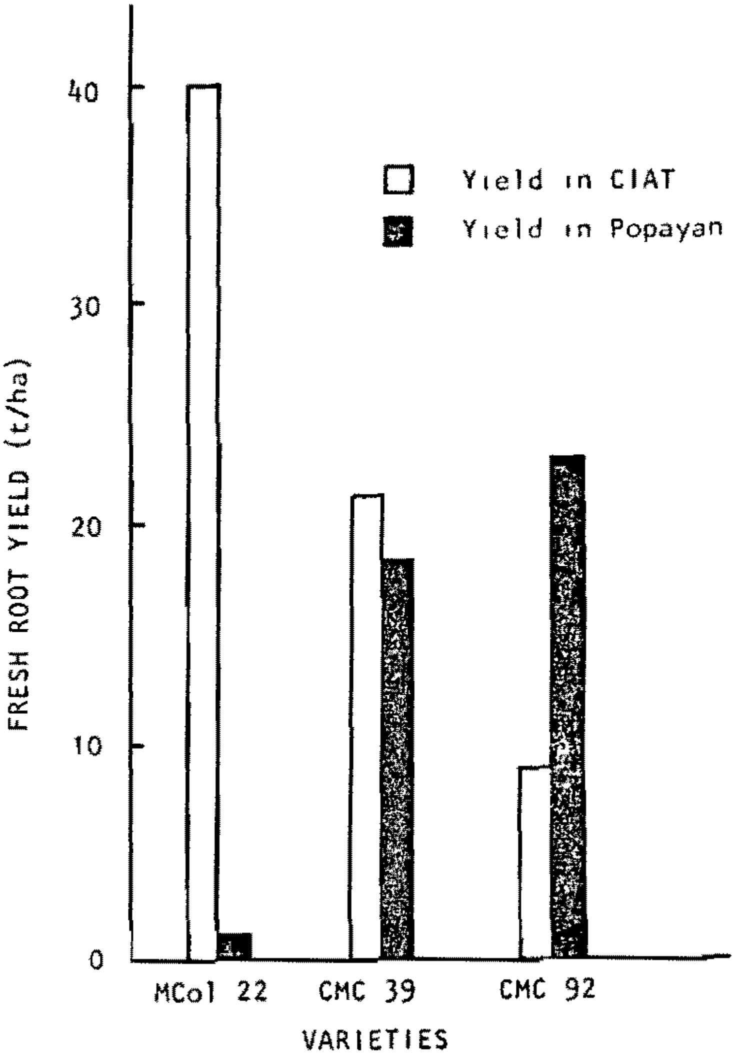
The physiological basis of varietal response to different temperature regimes is not known The photosynthetic rates of low temperature-adapted and high temperature-adapted clones are apparently similar across a wide temperature range (Figure 7)

As a species, cassava is basically adapted to the higher temperature lowland tropics The frequency of genotypes adapted to highland conditions is very low

Photoperiod

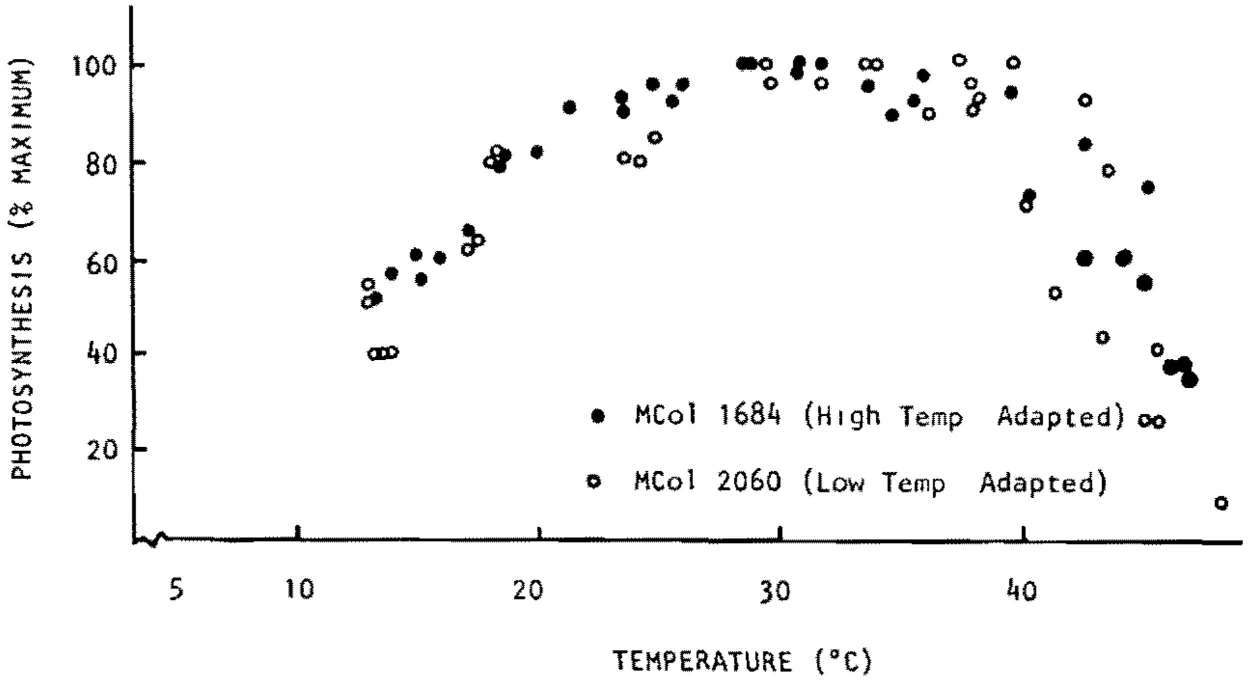
Photoperiod response in cassava is now well documented, and there is some evidence for genotype - photoperiod interactions (CIAT, 1981b) The importance of the interactions cannot yet be estimated with the preliminary data available As mentioned previously, genotypes from the subtropics, with fluctuating photoperiods, commonly do well under constant daylength conditions Little is known about genetic variability for response to photoperiod, though preliminary data show less sensitivity of some clones (Table 10)

Figure 6 Yields of three varieties of cassava in CIAT - Palmira and Popayan



Source CIAT Cassava Pathology Section

Figure 7 Photosynthetic rate as percentage of maximun rate for two cassava clones at different leaf temperatures



SOURCE CIAT Annual Report, 1981, Physiology Section

Table 10 The Effect of Long Days on the Yield of Cassava Nine Months After Planting

Clone	Yield (t Dry Matter/ha) Long Days	Yield (t Dry Matter/ha) Short Days	% Reduction
M Col 22	8.3	9 5	13
M Col 1684	4 6	8 7	47
M PTR 26	4 9	8 1	40

SOURCE J H Cock, Background Documents for Cassava Program Review, 1981 (Unpublished internal CIAT document)

Ambient relative humidity

Cassava is highly responsive to changes in vapor pressure deficit, through stomatal closure and consequently reduced photosynthetic rate (CIAT, 1981) It appears that significant varietal differences exist in response to vapor pressure deficit, but it is not known whether this is translated to differences in yield at the field level (Figure 8) Cassava growing environments are highly variable with respect to ambient relative humidity during different periods of the year, and this potentially could be one of the most important environmental factors responsible for G-E interactions

Soil water availability

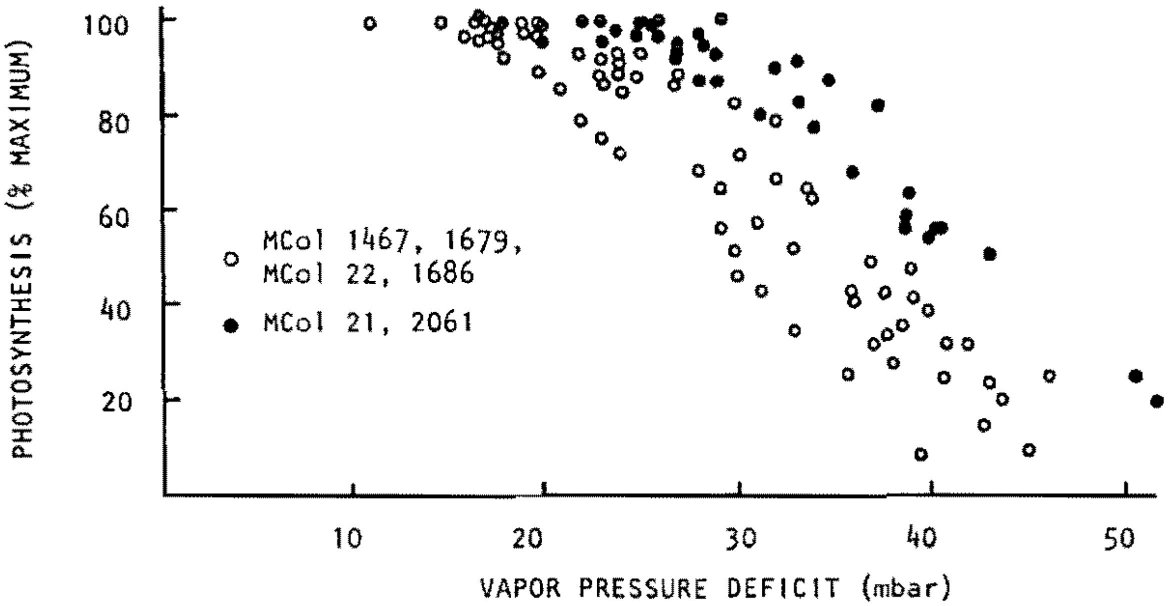
Controlled environment studies have shown a significant genotype x drought stress interaction both for potted plants and in the field at CIAT-Quilichao (CIAT, 1980b) Data are available for such a narrow range of genotypes that no generalizations can be made at this stage Irrigation experiments have often shown a lack of response, which may be in part due to a generalized high drought tolerance in cassava, and in part to a lack of response to irrigation if relative humidity of the air is very low From regional trial data there is no clear distinction between genotype performance in high rainfall compared to low rainfall sites which can be attributed directly to soil moisture availability Clones like M Col 1684 and CMC 40 have done well in such diverse sites as Santa Clara, Costa Rica, with nearly 4000 mm of rainfall a year, and in Media Luna with about 1000 mm Perhaps a higher level of stress is required to distinguish differential varietal response

Soil nutrient status

Results from studies on G-E interaction caused by soil fertility differences are inconsistent, and analysis of data from regional trials in varying fertility conditions do not clarify the picture very much Studies in plant nutrition have demonstrated significant interaction for effects of soil acidity and soil phosphorous levels (CIAT, 1980b, 1981b) In CIAT-Quilichao the ranking of varietal performance between fertilized and non-fertilized plots in the 1981-82 trial was distinct (Figure 9) While the regional variety, Valluna, was one of the poorest performers under higher fertility, it was the best under no fertilizer application On the contrary, trials during two years by the varietal improvement section have shown no genotype x fertility level interaction (CIAT, 1981b, 1982) Trials by the Economics section have shown no interaction in comparing improved and local varieties in Media Luna and San Martin (CIAT, 1981, 1982)

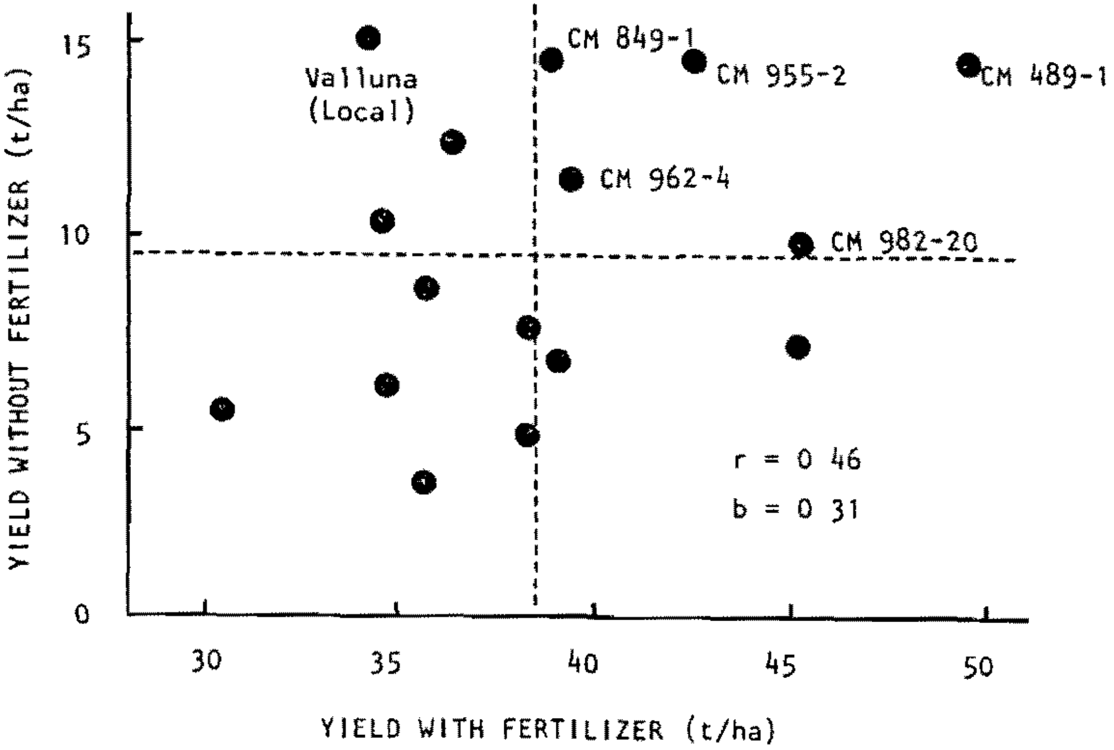
At this stage it is difficult to generalize, but it does appear possible to develop genotypes with good relative performance across a broad range of fertility conditions, perhaps with the exception of extreme stress conditions To achieve this broad adaptation, selection should probably be done under both low and moderate to high fertility conditions

Figure 8 Photosynthesis of different clones as related to vapor pressure deficit between leaf and air



SOURCE CIAT Annual Report 1981, Physiology Section

Figure 9 Comparison of fresh root yields of cassava in Santander de Quilichao with and without fertilizer application



SOURCE CIAT Cassava Agronomy Section, 1981/82 Regional Trials

Cropping system

Data available on genotype-cropping system interaction are limited Research emphasis has been on factors other than cassava genotype In the case of intercropping with short season grain legumes, the same cassava genotype appears to be appropriate for either monocropping or intercropping systems (CIAT, 1979b) Since about 40% of cassava is intercropped on a world basis, the possible existence of G-E interactions is not irrelevant

Diseases and pests

The contribution of pests and diseases to G-E interactions is perhaps the best understood of all the environmental factors Where the following three criteria are met, we can assume G-E interaction should be considered in defining breeding objectives 1) significant yield loss occurs under the attack of the disease or pest, 2) genetic variability for resistance exists, 3) other control measures are not readily available or cannot be economically applied This information has been fairly well documented for many pests and diseases of cassava, and continues to be studied There is also a rather good understanding of the environmental conditions which favor disease or pest buildups, and their geographic distribution

A dramatic example of G-E interactions caused by diseases and pests seems to be illustrated by the comparison of clones in regional trials in CIAT and Carimagua over years (Table 11) In the first years of the regional trials, loss to diseases in Carimagua could largely be avoided by isolation, and insects were not yield limiting in CIAT Correlations for yield performance between the two sites were high However, over time, insects, mites, and diseases built up in Carimagua, and mites and insects in CIAT, and correlations dropped rapidly to non-significant levels

Summary

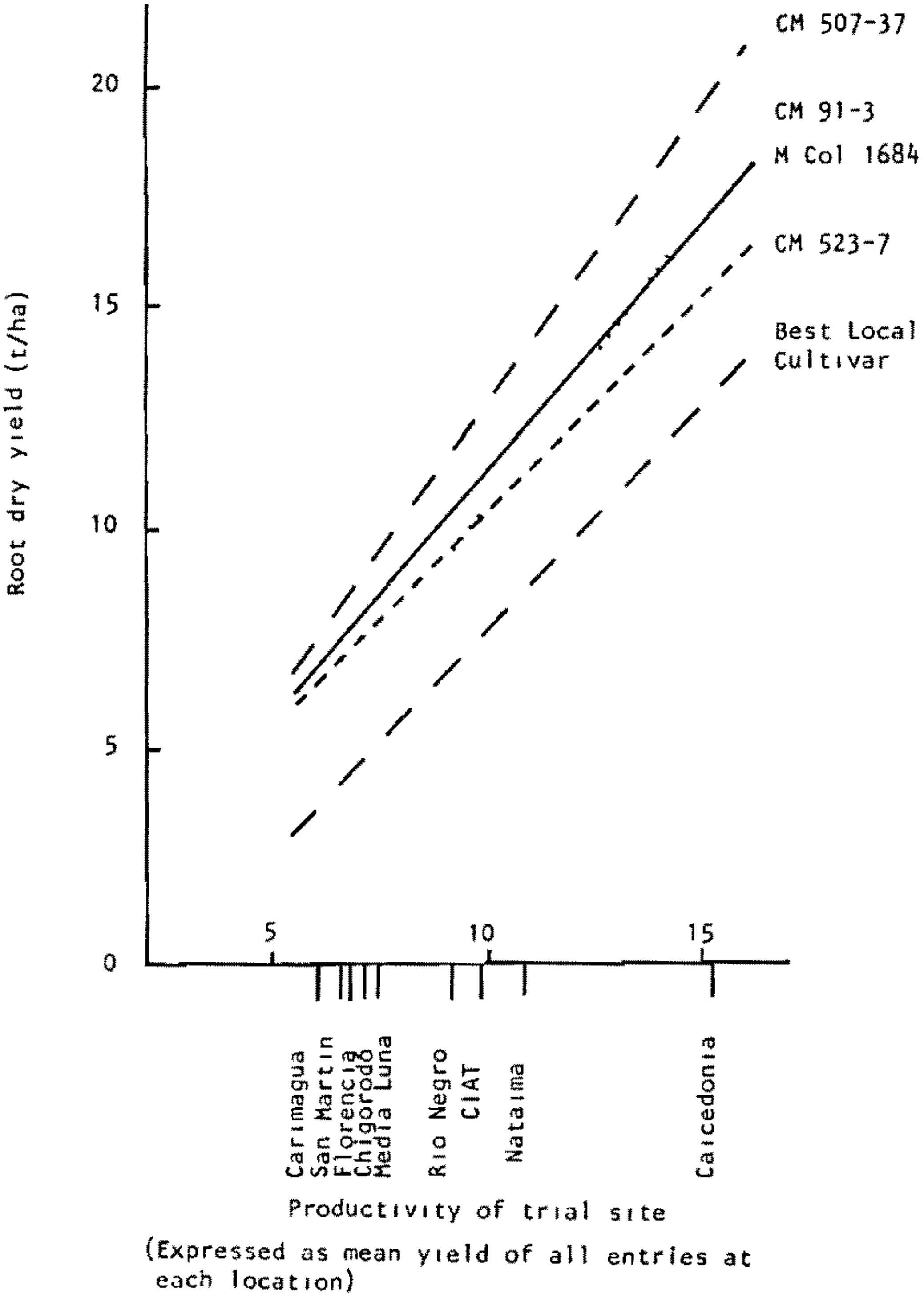
Except for adaptation to high versus low temperatures, there is no strong evidence to suggest that breeding for broad adaptability in cassava is not theoretically possible Colombian regional trials and international trials in the lowland tropics show some clones to be broadly adapted across physical environments, when diseases and pests are not limiting (Figures 10 and 11) Pests and diseases provide the strongest evidence for other causes of G-E interactions, however it should theoretically be possible to combine resistance to a very wide range of biological problems The question then is not what is theoretically feasible, but to structure breeding activities to make the most rapid advances possible for overall genetic improvement to meet individual needs of many national programs Although interactions may not be strong for individual factors like soil fertility, soil water availability, photoperiod or cropping systems, the combined effects of these, plus major interaction effects of diseases and insects, temperature, and possibly others, indicate that some subdivision of the target area for breeding objectives is necessary

Table 11 Summary of linear correlations between sites for fresh root yield

Year	Locations compared		
	CIAT-Media Luna	CIAT-Carimagua	Media Luna-Carimagua
1976/77	0 22	0 82	0 84**
1977/78	- 0 15	0 72	0 37
1978/79	- 0 26	- 0 48	0 38
1979/80	0 04	0 09	- 0 14
1980/81	- 0 67	0 18	0 15
1981/82	- 0 16	0 16	- 0 15

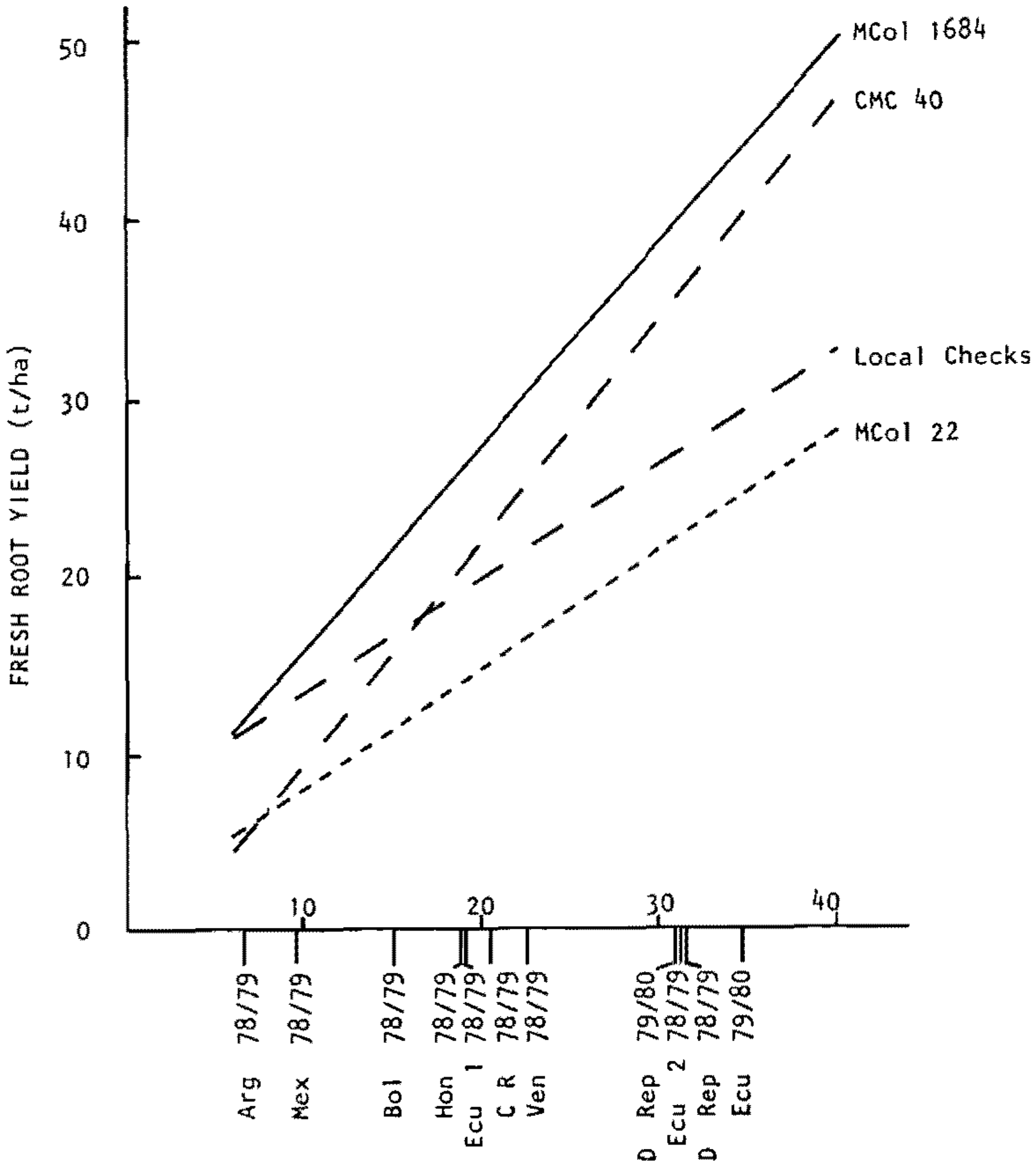
SOURCE CIAT Annual Report, Cassava, Agronomy Section

Figure 10 Regression of selected CIAT clones and local cultivars on productivity level of trial site in Colombian Regional Trials



SOURCE CIAT Annual Report, 1981, Agronomy Section

Figure 11 Regression of yields of selected CIAT clones and best local cultivars on productivity level of trial site in international yield trials of cassava



PRODUCTIVITY OF TRIAL SITE
(Expressed as mean yield of all the entries at each location)

Source CIAT Annual Reports 1979 and 1980, Agronomy Section

Target Area Subdivisions

Historial perspective

In the first years of the CIAT Cassava Program, a principal breeding objective was for wide adaptability - to develop cultivars which could be successful across the three principal selection sites in Colombia CIAT-Palmira, Carimagua, and Caribia In the regional trials network, most clones were planted in all sites Emphasis later shifted toward selection under moderate to high stress conditions for yield stability New selection sites were added in the north coast (Media Luna and the Guajira region) where low soil fertility, drought stress and mite attack are principal constraints to productivity A small evaluation and selection program was added in Popayan, for selection of clones adapted to low temperatures

In addition to selection in new, high stress sites, disease and insect pressures continued to increase in intensity in Carimagua, and insect pressures in CIAT-Palmira This natural phenomenon also partially accounted for increased emphasis on selection for stress tolerance Work in entomology has permitted artificial screening for insects not found in sufficiently high or uniform populations under field conditions in Colombia, such as mealybug and lacebug

By the end of the seventies a great deal of information had been accumulated on effects of various factors on varietal adaptation and G-E interactions Based on this information the cassava team made a subdivision of cassava-growing regions into six edapho-climatic zones[1] (Table 12) This subdivision is based principally on differences in mean temperature, rainfall distribution, photoperiod, and soil characteristics These physical factors in turn largely determine the pest and disease complexes which are potentially or actually important, and a description of predominant pest complexes was developed to accompany the edapho-climatic zone description (Table 13) The choice of six zones was made based on an intuitive balance between the number of separate breeding projects which could be managed by CIAT, and the number of resistance and adaptation factors which could be combined in a single genotype

Quality factors do not enter into the subdivision Clearly, different quality characteristics will be required for different markets, but it appears possible to maintain variability for these characteristics within each of the breeding projects for the different zones Indeed, except for fresh consumption of cassava, quality requirements appear to be less stringent than for many crops

The definition of edapho-climatic zones has further influenced breeding strategy Selection is now highly decentralized from the earliest stages, with each zone being basically a separate breeding

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[1] Originally described as "ecosystems" but later changed to "edapho-climatic zones" to more accurately reflect the actual basis of the subdivision

Table 12 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 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	Amazon 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, India, Indonesia, Viet Nam
5	Cool, tropical highland areas, with mean temperatures of approx 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

13 Description uf factors related to genoyte adaptatl)n In ca sava a d genotype environment interactions 1/

Factor	Importance in G E Interactions 2/	Predictability 3/	Controllability Other Than by Genotype 4/	Potential for Adaptation Through Breeding 5/	Reliability of Present Information on Importance in G E Interactions 6/	Importance in Determination of Target Area Subdivision	Probability of Stress Effects in Each Edapho Climatic Zone 7/ I	II	III	IV	V	VI
al Env Factors												
perature	+ + +	+ + +	0	+ +	+ + +	+ + +	0	0	0	+	+ + +	+ + +
ient R H	+ +	+ + +	0	+ +	+ +	+ +	+ + +	+ + +	+	+ +	+	+
toperiod	+ +	+ + +	0	+ +	+ +	+ + +	+	+	+	+	+	+ + +
l Water	+ +	+ +	+	+ +	+ +	+ + +	+ + +	+ + +	+	+	+	+
l Acidity	+ +	+ + +	+ +	+ +	+ +	+ +	+	+ + +	+ +	+	+ +	+ +
l Phosphorus	+ +	+ + +	+ +	+ +	+ +	+	+ +	+ + +	+ +	+ +	+ +	+ + /
ical Env Factors												
terial Blight	+ + +	+ +	+	+ + +	+ + +		+ +	+ + +	+	+ +	+	+ + +
cospora Leaf Spots	+ +	+ +	+	+ + +	+ +		+ +	+ +	+ +	+ +	+	+ +
ma	+ + +	+ +	+	+ + +	+ + +		0	0	0	+	+ + +	+ +
relongation	+ + +	+ +	+	+ + +	+ + +		+ +	+ + +	+ +	+ +	+	+ + +
hracnose	+ + +	+ +	+	+ +	+ +		+ + +	+ + +	+ +	+ +	+ +	+ + +
t Rots	+ +	+ +	+ +	+	+ +		+	+	+ +	+ + +	+ +	+ + +
en Cassava Mite	+ +	+ +	+ +	+ + +	+ + +		+ + +	+ + +	+	+ +	+	+
Spider Mite	+ +	+ +	+ +	+ +	+ +		+ + +	+ +	+	+ +	+	+
ips	+ + +	+ + +	+	+ + +	+ + +		+ + +	+ + +	+	+ + +	+	+
te Fly	+ +	+ +	+ +	+ +	+ +		+ +	+ +	+ +	+ +	+	+
worm	+	+	+ + +	+	+		+ +	+ +	+ +	+ +	+	+ +
ot Fly	+ +	+ +	+ +	+	+		+ +	+	+ +	+ +	+	+ +
c Bug	+ +	+ +	+	+ +	+ +		+ +	+ + +	+	+ +	+	+
lybug	+ + +	+ +	+ +	+ +	+		+ + +	+ + +	+ +	+ +	+	+
le Insects	+	+	+ + +	+	+		+ +	+ +	+ +	+ +	+ +	+ +
ds	+	+ + +	+ + +	+	+ +		+ + +	+ + +	+ + +	+ + +	+ + +	+ + +

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his is not intended as an exhaustive list but is believed to include the principal presently known factors of importance particularly in atin America The evaluations are highly subjective and based in many cases on limited and scattered data

0 = Zero or near zero
\+ = Low
\+ + = Moderate
\+ + + = High

ot necessarily indicative of importance in comparison of all zones but assuming comparison of zones with a wide difference in presence absence intens ty etc of the factor under consid ration Based on estimated effects on yield

h degree to which a given factor can be expected to be present and/or at what level

he degree to which the factor can be modified in its effect on the plant other than modification genetically of the genotype objective There is no longer much emphasis on breeding for broad adaptability across zones, but rather on adaptability across the variability existing within zones The regional trials network moved toward more selective placement of clones in particular sites based on their performance in different zones in the earlier stages of selection

CIAT-designed international trials are non-existent in cassava Individual countries request germplasm, and CIAT or the requesting institute matches the edapho-climatic and pest conditions of the region with appropriate germplasm There has not yet been a systematic attempt to evaluate the efficacy of selection in Colombian edapho-climatic zones for adaptation in other countries This topic will be discussed in some detail in a later section

Adequacy of the present division and research needs for the future

CIAT's Agroecology Unit made a preliminary refinement of the target area subdivision in 1981, using agro-climatic and production data from Brazil Zones were differentiated on the basis of data from physiology studies showing cassava's expected responses to temperature, soil water stress, vapor pressure deficit, and daylength differences Further testing of the biological validity of this subdivision is required, both through continuation of physiology studies and by testing of genotypes in the distinct zones

Testing of these hypotheses at the field level will be no simple matter The restrictions on international movement of cassava clones, and the modest level of resources available to CIAT and to most national programs diminish the possibility for rapidly obtaining this type of basic information Various alternatives are possible for further study of the biological validity of the present target area subdivisions

We could, theoretically, design a large regional trial program, with a broad range of genotypes fitting all the known edapho-climatic conditions where cassava is grown--a sort of "super ecosystems trial" of the type now being carried out in Colombia This uniform trial would ideally be planted in many locations in each of many countries, a traditional design for a G-E interactions study Planting under both protected and non-protected conditions would provide additional capability of separating effects of the biological and physical environmental factors
Uniform regional trials have been used in various crops,(e g , wheat, rice, beans, and maize), to aid in definition of environments

The drawbacks of this strategy applied to cassava are rather severe First, there is the very real question about whether national programs would be willing to process and multiply large numbers of clones (most of which would be unacceptable to an individual program), and evaluate them over several years The present resources of virtually all cassava programs are such that they would not look very favorably on this plan Overall it is not a viable option for cassava at the present time

The concept of uniform regional trials to detect G-E interactions has other serious drawbacks Unless carried out over a long time period, these trials do not take into account the potential changes in an ecosystem brought about by the introduction of new varieties and new cultural practices in a region This may be particularly true for non-traditional areas of production for the crop in question A case in point is the buildup of pests and diseases over years for Carimagua and CIAT-Palmira, mentioned earlier If a breeding strategy had been designed only based on the early data, we would have made a grave error Similar experiences are likely in many areas, and consequently more creative investigative approaches are required in determining target area subdivisions

Another alternative would be to compare well-known varieties from many countries in the CIAT-selected Colombian sites, a sort of "reverse regional trial" concept The site in which the material most closely conforms to performance in its area of origin would be the site where CIAT could presumably do preliminary selection for a given region of another country A drawback of this plan is the lack of uniformity of data available for local clones from most countries Nor would it be easy to take into account either the potentially dynamic nature of the ecosystem in which the local variety originates, or factors such as pests and diseases which may be present in the country of interest, but not in Colombia There would need to be a careful compilation of information on major problems of each region to accompany the data on performance in Colombia sites The cassava program is to a limited extent pursuing this strategy already

A third alternative would be to evaluate the usefulness of Colombia sites for selection of parents, by evaluations of progeny by national programs across a range of edapho-climatic, disease and pest conditions Data on half-sib or full-sib progeny performance could potentially provide information on G-E interactions and the definition of target area subdivision The assumption of additivity for most traits of agronomic importance allows us to compare performance of parents in Colombian sites with expected performance of progeny in similar conditions in other countries If progeny performance is different from our predictions, it may them be necessary to reclassify the environment relative to similar conditions in Colombia Critical to this alternative would be a means of data standardization from evaluation of segregating populations, and rapid feedback of information to CIAT In the past, the quantity and quality of data being received by CIAT on performance of F_1 populations sent out as cassava true seed has been variable and generally low

Complementary to any of these approaches would be extension of agroecological surveys to other cassava-growing regions outside of Brazil, and continued physiology work on cassava's response to various environmental factors

Possibly the most important input of all is the first-hand observation by CIAT and national program scientists of cassava under the widest possible range of conditions Often, close observation combined with a common sense, problem-solving mentality by crop scientists can contribute more to an appropriate breeding strategy than a series of sophisticated experiments

In summary, the further refinement of the definition of the subdivisions of cassava-growing regions for purposes of germplasm development should follow a multifaceted approach From the outset we can discard the possibility of a standard uniform international trial network The following steps are suggested as a feasible strategy

1) Physiology studies should be continued to study effects on cassava of principal physical environmental variables, particularly photoperiod, soil water availability, ambient relative humidity and temperature

2) With careful planning, selected local varieties from national programs can be planted in diverse sites in Colombia, repeated over years, to indicate some of the characteristics required for particular regions, as well as identify the site(s) in Colombia where selection can most appropriately be done This strategy however should take into account that some traits may need to be dramatically changed in certain local varieties, to adapt to new cultural practices or new forms of utilization

3) A systematic international progeny testing system should be further developed to provide rapid information feedback This in turn would allow CIAT to make adjustments in parental selection by knowing some of the limitations and successes of crosses sent, compared to performance of these parents in Colombian sites

This combination of strategies, though perhaps not giving a neat package of answers to the question of G-E interaction in cassava nor the optimum target area subdivision, would be a practical approach to getting basic information while simultaneously allowing national programs to make progress in selection for locally adapted materials

A Breeding Strategy

Selection by CIAT in Colombia

Principal characteristics of present breeding strategy as carried out by CIAT in Colombia can be summarized as follows

1) Evaluation of the germplasm collection in regions which most closely approximate the edapho-climatic conditions and combine the various pest problems of the globally defined zones

2) Evaluation of the germplasm collection under controlled conditions for pests, diseases and other factors when they cannot be evaluated adequately under field conditions in Colombia

3) Selection of parental clones based on the above evaluations Basically separate gene pools are maintained for each zone, but broadly adapted parents are also used extensively

4) Hybridization and production of segregating populations

5) Planting of all progeny in CIAT-Palmira, where the required careful supervision of the F_1 plants can be assured

6) Low selection intensity in CIAT-Palmira, elimination of only those plants of obviously inferior genetic potential

7) Continued evaluation and selection in the edapho-climatic zone for which the cross was originally made in order to select for temporal stability

8) At the intermediate stages of selection, planting in a wide range of sites to evaluate for broad adaptability, and to have a complete description of genotype performance

9) Recommendation for testing by national programs in regions where the clone has a reasonable probability of adaptation and aceptability

This strategy has the objective of creating genotypes with adaptability across the conditions _within_ each of the major edapho-climatic zones, but not necessarily _across_ zones Diverse specific needs of national programs are met by maintaining a broad genetic base for each of the edapho-climatic zones, and by including broadly adapted parents in many crosses

Evaluation of finished varieties

The definition of a "finished" variety in cassava is necessarily rather arbitrary, since the genotype is already fixed by vegetative propagation at the F_1 stage For purposes of clarification, in this section a finished variety is defined as a clone which has advanced through the final stages of selection by CIAT in Colombia, after being evaluated over years and locations in replicated yield trials At this stage, clones are ready to enter regional trials in Colombia and internationally

To understand the possibilities for international trials in cassava, based on clones sent from CIAT, it is necessary first to understand some of the limitations on the international movement of vegetative propagative material CIAT has decided to send cassava vegetative material internationally only by _in vitro_ culture This has implications particularly in terms of which programs are capable of receiving material, and time required to multiply and distribute material for regional trials There are an increasing number of countries which can receive _in vitro_ cultures, and therefore this limitation on movement, within Latin America, is in fact disappearing Regeneration multiplication and distribution of materials originating from meristems can take two years or more from time of introduction to time of planting of a trial, and then another year until harvest The implications of this system for the design of the international trials are several First, because each individual clone requires so much attention and time to get it to the point of being incorporated into a regional trial, national programs are in general interested only in introducing material that has some reasonable probability of being adapted and useful in the region Furthermore, clones with obvious deficiencies would be eliminated during the multiplication phase The concept of uniform regional trials is untenable in cassava under the present circumstances What are the alternatives? One very logical approach seems to be for CIAT to make known in detail to national programs what is available, and for them to choose which clones to introduce In such case, CIAT does not make set packages of international trials, and the way in which each country organizes their regional trial network is completely their own decision Nevertheless, CIAT can aid in the standardization of the design of trials and of data-taking, by calling periodic workshops at CIAT, and maintaining close contacts with national programs

This system makes it difficult or impossible to collect the wide range of information on G-E interactions and varietal adaptation that might be desirable Nevertheless, data from national program organized trials can still be used to advantage to determine the adequacy of CIAT selections in Colombia, and to make adjustments in that selection for individual programs

Sending segregating populations to national programs

For cassava, for all practical purposes, the discussion of at what stages of selection it is most appropriate to send germplasm for testing by national programs can be divided into two possibilities unselected populations of F_1 seed, or clones having passed through selection by CIAT to the advanced stages Since the F_1 generation is the only seed-propagated generation, it is the only stage at which large numbers of genotypes can reasonably be expected to be moved internationally For movement of vegetative material (by <u>in vitro</u> culture) the number of genotypes sent must be drastically reduced, such as the number entering final stages of selection by CIAT Movement of the amount of materials passing the intermediate stages of selection would be prohibitive

The shipment of segregating cassava populations to national programs is a highly attractive option for several reasons 1) the amount of genetic diversity that can be sent, and the relative ease with which it can be sent are far greater than for vegetative material, 2) because of the rather long period required for regeneration and multiplication of <u>in vitro</u> cultures, there is little difference in amount of time required to reach an equivalent stage of selection for either of the two systems of introduction, 3) finally, there is a highly increased probability for selection for good local adaptability due to the large number of genotypes, while at the same time taking advantage of gains made in CIAT through selected parents

A major concern in sending out segregating populations is to have a rapid and effective information feedback system which will allow CIAT to assess and adjust the methodology for parental selection The cassava program has initiated on a trial basis a suggested standardization of information feedback for F_1 families to allow us to more effectively select parents for specific regions

Summary

In general terms, the CIAT cassava program seeks broad adaptation to the extent required for stable performance across the conditions within the six previously described edapho-climatic zones Adaptation across zones in not stressed, and is viewed as a difficult option in view of the complex combination of resistance, adaptation and other characteristics which would have to be combined in a single genotype

Wide adaptation within zones is sought by 1) analysis of the range of edapho-climatic conditions and pest complexes for each zone, 2) selection of sites in Colombia which most closely resemble the definition of zones in other countries, and, 3) selection of parents and progeny primarily for performance within specific zones, but with evaluation across zones in later selection stages

UPLAND RICE[1]

Of the estimated 14 4 mt of rough rice produced in tropical America in 1980, 53% was produced under upland conditions Although, the bulk of upland rice is found in Brazil, it is also important elsewhere Mexico adopted a policy of shifting from irrigated rice to upland production in the humid southeast Essentially all production in Central America, excepting that of Nicaragua, is from upland rice Upland culture occupies significant areas in Venezuela, Colombia, and Ecuador Peru is increasing its production through emphasis on the upland sector Bolivian production is essentially all from upland rice

Average yields for the upland systems in the region contrast sharply with the yields obtained under irrigated conditions For the more favored upland systems regional average yield in 1980 is estimated at 1 7 t/ha while the unfavored system yielded approximately 1 0 t/ha Estimated average national yields for the more favored upland systems vary considerably from country to country with a range from 1 1 to 3 5 t/ha reflecting a wide variation in production conditions and constraints Approximately 94% of the total area in the unfavored system in the region was grown in Brazil where considerable fluctuations in productivity and production occur from year to year as a result of variation in rainfall and disease incidence

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[1] The section on upland rice has been, almost in its entirety, extracted from two documents kindly made available by P R Jennings and D R Laing (Jennings, et al , 1981, Laing, et al , 1982)

Although the Colombian rice program has had a successful tradition of rice research, its activities until recently have been restricted to irrigated rice Several Colombian varieties and lines have been successful for upland production in specific countries but these contributions were unexpected spin-offs from breeding under irrigated conditions

Evidence for Genotype-Environment Interactions and Factors Responsible

Tables 14, 15, and 16 show the performance of several varieties and breeding lines under different upland conditions Not a single entry does well under all these conditions, especially when the drought stress is too severe like in Campinas and Minas Gerais These data clearly indicate G-E interactions in upland rice

Physical and biological constraints lead to lower productivity and greater instability of production over time at any particular location and across regions This is partly the result of the absence of irrigation water, the presence of which increases soil fertility, reduces soil acidity, eliminates drought stress, aids in weed control, and reduces disease and insect attack Possible factors causing interaction can be categorized as part of either the physical or biological environment

Physical factors

Laing et al (1982) presented a study of eight locations representative of the range of upland rice growing environments in the Americas A description of the terrain and soil of each sample area was made and the relevant meteorological station identified Table 17 lists the sample locations and selected environmental descriptors Of the eight locations, three are considered favored upland, three moderately favored, and two unfavored upland sites A description of these sites gives a reasonable idea of the environmental variability under which upland rice is grown

In general, soils at the favored upland sites are all deep and heavy textured The sites have soils with a high base status and moderately high fertility Moisture holding potentials are high at all favored sites and since hydromorphic features are present, access to a water table within 50 cm is common

At two of the moderately favored sites soils have high fertility, high base status and good working properties and are not inferior to the best favored sites The vitric andasol in Panama has a deep profile but is inherently quite acid and low in fertility

Both selected unfavored sites in Brazil are on a deep, loamy, well-drained acric ferralsol These soils are highly acid and infertile with high aluminum saturation (> 70%) in most areas although at Goiania areas of relatively low aluminum saturation do occur Phosphorus is very low at both locations and soil water available to plants is limited due to restricted root development in the highly acid subsoil

TABLE 14 Performances (kg/ha) of several lines and varieties under upland conditions in Brazil VIRAL-S 1979

Line/Var	EPAMIG[a] Minas Gerais	IAC[b] Campinas
KN361-1-8-6	0 3	0 5
IR 36	0 2	-
IR1529-430-3	0 2	0 4
IR2035-242-1	0 2	-
CICA 8	0 5	-
CR 1113	0 3	-
Local Check	0 5	1 7

a= Upland favored, b= Unfavored upland
—= Not yield at all

TABLE 15 Performance (ton/ha) of several lines and varieties under upland conditions in Brazil VIRAL-S 1978

Line/Var	LOCATIONS				
	UEPAE[a] Bacabal	CNPAF[b] Goiania	IAC[b] Campinas	EPAMIG[b] Uberaba	UEPAE[a] Rio Branco
KN361-1-8-6	4 9	2 6	0 5	0 7	4 0
IR 36	5 4	2 2	0 2	0 6	3 9
IR1529-430-3	5 6	1 7	0 2	0 1	4 3
IR2035-242-1	6 3	0 5	-	0 2	3 8
CICA 8	6 3	0 8	-	2 0	3 3
CR 1113	5 3	0 1	-	3 5	3 0
Local Check	4 9	3 2	0 8	1 7	3 3

a = Favored upland, b = Unfavored upland

Local check = IAC 1246, IAC 47, IAC 25

TABLE 16 Yields (kg/ha) of four promising lines under favored upland conditions in Colombia Regional trials 1979 B - 1980 A

Entry No	North Coast		Eastern Plains	
	1979 B 1/	1980 A 2/	1979 B	1980 A
5685	3200	5900	5913	5209
5709	2650	6262	5188	5525
5715	2040	-	4310	-
5738	2510	7843	4744	4561
CICA 8	2730	6693	5200	5236
CICA 4	2660	4725	2560	4547

1/ Low rainfall

2/ Good rainfall

Table 17 Environmental descriptors for eight selected locations representing typical sites within each of three upland rice ecosystems/production systems in Latin America

No	Site	Country	Mean Annual Rainfall mm	Mean growing temperature °C	Principal soil type classification USDA[1]	FAO[2]	Base Status	Al toxicity	Est Pot Water mm
Favored-upland									
1	Villavicencio	Colombia	4096	25 6	Tropoquept	Eutric gleysol	Mod	Mod	150
2	Uraba	Colombia	4805	25 9	Tropofluvent	Eutric fluvisol	High	Low	250
3	Puerto Cortes	Costa Rica	4809	26 7	Hapludoll	Mollic gleysol	High	Low	250
Moderately favored upland									
1	Juquilisco	El Salvador	1842	26 3	Tropofluvent	Eutric fluvial	High	Low	200
2	Liberia	Costa Rica	1887	28 2	Pellustert	Mollic gleysol	High	Low	200
3	David	Panama	2364	26 9	Vitrandept	Vitric andosol	Low	High	150
Unfavored upland									
1	Campina Verde	Brazil	1489	23 3	Haplorthox	Acric feralsol	Low	High	75
2	Goiania	Brazil	1399	23 1	Haplorthox	Acric feralsol	Low	High	75

[1] Soil taxonomy A basic system of soil classification for making and interpreting soil surveys Soil Conservation Service USDA Handbook 436 Washington D C 754 pp 1975

[2] FAO-UNESCO Soil Survey May of the World

All locations described above are on level or gently rolling terrain with slopes generally less than 8% in cultivated areas. The unfavored sites in Goias and Minas Gerais are on soils very similar to many other unfavored sites in Brazil One of the main characteristics of the two selected locations is the relatively level terrain which facilitates mechanized cultivation

All locations appear to have adequate growing season length (minimum 154 days) of contiguous days when soil water available was greater than 1/3 of potential under mean climatic conditions Temperature and radiation are also adequate for rice at all locations, even though mean growing season rainfall decreases from the favored to the unfavored sites (Tables 17 and 18), calculations of water balances (using long-term mean rainfall) suggest that water supply would be in surplus over potential evapotranspiration even at the unfavored sites Rainfall variability, however, is quite high at the lower rainfall sites and thus there is a high probability of stress during the growing season at the more unfavored sites At almost all moderately favored sites a considerable number of mild stress days was experienced Stress was predicted to be quite severe at the unfavored sites (Table 19)

One factor which is of particular importance in the above analysis is the critical importance of rooting-depth of upland rice in relation to climate At the drier unfavored locations the inability of rice roots to penetrate aluminum saturated subsoils is a very important constraint on production and is partly responsible for the lower yields and high yield variability in unfavored rice areas, particularly in Brazil The occurrence of "veranicos" or dry spells during the rainy season in Brazil is a well known limitation to increased rice production in the unfavored areas

Biological factors

Upland rice in Latin America is affected more severely by biological constraints than is irrigated rice Biological constraints vary quantitatively and qualitatively across the upland ecosystems Soil, climate, and cultural practices interact resulting in complexes of insect, disease, and weed problems Some of these, which are invariably more pronounced in the unfavored upland ecosystem, are described in the following sections

Insects *Elasmopalpus lignosellus*, *Blissus leucopterus* and *Phyllophaga* spp , are widespread but sporadic insects found only in upland rice Damage by the first two is appreciable when the crop is subject to prolonged drought stress during the early growth stages They generally do not cause yield reductions in higher rainfall ecosystems *Phyllophaga* (white grubs) cause losses in rice fields rich in organic matter particularly in converted pasture areas The *Sogatodes* planthopper is a serious pest in both irrigated and upland conditions because of direct feeding damage and as the vector of the hoja blanca virus The insect is most serious in areas of high relative humidity and moderately high rainfall *Sogatodes* is thus a particular problem in favored upland rice ecosystems in Colombia, Venezuela, and Central America

Table 18 Range[1] of agroclimatic parameters for typical selected upland sites

Growing season	Favored		Mod-favored		Unfavored	
Length days[2]	287	365	154	210	154	182
Mean temperature °C	25 6	26 7	26 3	28 0	22 7	23 3
Mean E_t mm day^{-1}	3 8	4 8	4 4	5 9	5 2	5 8
Radiation $MJm^2 day^{-1}$	15 9	19 3	19 6	21 0	20 5	21 6

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[1] Range noted in sample meteorological station data

[2] Length of growing season calculated from estimated daily soil water budgets as the number of contiguous days when available soil water is greater than 0 33 of potential available

[3] Potential evapotranspiration (E_t)

Table 19 Effects of rainfall variability (simulated rainfall reduction by 50% mid season for one month) at selected upland rice sites

	Reduced[1] GSD	Mild[2] Stress day	Days to[3] stress	Probability of[4] dry period	Yield[5] t ha^{-1}
Favored upland					
Site 1	0	0	23	Highly unlikely	4 50
Site 2	0	0	39	Nill	4 40
Site 3	0	0	34	Nill	3 50
Moderalety favored-upland					
Site 1	0-35	28-35	22	Possible	3 00^{i}
Site 2	0	21-35	26	Possible	1 92^{c}
Site 3	0	0-14	22	Unlikely	2 59^{c}
Unfavored-upland					
Site 1	98	14	9	Highly likely	1 10^{c}
Site 2	64-98	14	9	Highly likely	1 20^{c}

[1] Reduction in growing season (GSD) days (days with soil moisture available greater than 1/3 soil moisture holding potential) due to one mid-season month with half of normal mean rainfall

[2] Mild stress days, days with soil water availability between 2/3 and 1/3 capacity, as induced by reduction in rainfall by 50% for one month

[3] Days of growth available before 2/3 of available soil water is exhausted if no rain falls as in foot note 1

[4] Subjective estimate of the probability of a dry spell as least as long as the figure in preceeding column

[5] From census data where available (c) or from CIAT estimates from informed sources (i), yield estimates not including traditional subsistence areas

Diseases Two ecological factors and their interactions play a predominant role in the Americas in the development of the major fungal diseases of upland rice, i e , blast (*Pyricularia oryzae*), brown spot (*Helminthosporium oryzae*), leaf scald (*Rhynchosporium oryzae*), and eye spot (*Drechslera gigantea*) Prior drought stress preconditions plants toward susceptibility and the longer the stress period the greater is the degree of leaf disease incidence High spots in upland fields and sandy soils provoke heavier disease pressures The interaction with water stress is particularly noteworthy in the case of blast but is also significant with the other diseases mentioned

The second critical factor is that of soil conditions Crops on some soils appear particularly disease prone while crops on other soils have a remarkable absence of infection under similar climatic conditions One general class of soils which favors the development of leaf blast and other fungal diseases are the ultisols and oxisols that predominate in the savannas of South America These highly acid soils, particularly under upland rice, appear to contribute to stronger disease epidemics Other problem soils associated with enhanced leaf diseases, especially eye spot and brown spot, include soils with high organic matter content

Apart from this association with soil type, diseases are also enhanced under conditions of high relative humidity, excessive nitrogen fertilization and heavy seeding rates, particularly in favored upland conditions

Weeds The major difficulty in control of weeds in upland rice is related to the prevailing soil moisture conditions Excessive moisture, when weeds are most sensitive to herbicides, makes entry into fields with ground equipment very difficult The resulting delay in application requires heavier herbicide dosage and results in less effective weed control On the other hand drought stress, when weeds should be controlled to save water reserves, reduces the effectiveness of herbicides considerably Application must be delayed until rainfall results in weed development past the period of greatest susceptibility to herbicide control

Target Area Subdivision

A quantitative agroecological study of upland rice growing areas in Latin America is now underway by the Agroecological Section at CIAT in collaboration with the Rice Program The aim of this study is a quantitative characterization and classification of upland environments, both to elucidate the present status of the crop and to aid in the estimation of future potentials within each environment The unit of study will be at the level of a microregion Soils, landscape, climate, and agronomic conditions are being defined for each microregion These are relatively small production areas with relatively uniform production conditions and consisting of statistical subdivisions at the municipal level These data are not yet at a stage where a quantitative classification can be undertaken

From the previous brief description of the soils and terrain characteristics of various sample locations it is clear that no one set of conditions uniquely classifies sites as favored upland There is a greater preponderance of good soils at the more favored end of the upland spectrum However, fertile soils are not necessarily indicative of a favored upland ecosystem, because of possible climatic limitations On the other hand, there is a definite tendency towards low fertility and highly acid soils in unfavored rice situations Soil classification alone, however, will not be sufficient to develop a useful quantitative classification of upland environments Another difficulty encountered in classifying rice environments is illustrated by an analysis of data of crop climate for these locations

It was concluded from the climatic data and from the demonstration of the effects of reduced midseason rainfall, that it is not possible to produce a useful quantitative classification of upland rice environments in Latin America based only on soil quality characteristics and estimates of growing season length (from water balances) under mean climatic conditions It is equally difficult to estimate relative suitability of different microregions based on these parameters alone Without rainfall variability data further progress towards a quantitative classification of rice environments in the region cannot usefully be carried out Data collection is now proceeding in order that a complete analysis including all of the above factors will be available

In the meantime, a working classification of rice environments has been developed and three categories of upland rice ecosystems/production systems have been defined, i e , subsistence upland, moderate to highly favored upland, and unfavored upland rice

Subsistence upland rice

This system utilizes no mechanization and no purchased inputs Forest or scrub is cut and burned and rice is planted in widely separated holes with pointed sticks The crop is shifted to new land after one or two harvests Farm size is roughly 1 ha/family Varieties are unimproved land races The system is moderately stable but productivity averages less than 1 t/ha The harvest is consumed by the farm family The system is located in remote areas and at the agricultural frontier Total area of production is unknown but considered negligible

The major constraint is total dependence on family labor This limits farm size, obliges wide spacing, demands native varieties and prohibits use of purchased inputs Farm production is defined by the consumption demand of the family Other factors including soil fertility, variety, weeds and pests are of secondary importance

CIAT, at least initially, will not research this ecosystem given its minor contribution to regional production

Moderate to highly favored upland rice

Highly favored upland rice is confined to relatively flat areas having rainfall over 2000 mm during 6 to 8 months There is no marked dry period during the rainy season Soils are normally alluvial, slightly to moderately acid and well drained Modern dwarf varieties and purchased inputs are suitable Yields average about 2 5 t/ha but better farms consistently produce 4 or more tons The system is found in most of Central America, parts of Colombia and sub-Amazonian Brazil Major yield constraints are grassy weeds, the blast disease and lodging in the case of CICA 8, the most productive variety for this system available in Colombia

Moderately favored upland areas differ from the highly favored ecosystem in having a shorter wet season, less rainfall and normally a dry period during the growing season Additionally, soils may be infertile as in Pará and Maranhao Dwarf varieties are grown in Central America and tall ones in Brazil Yields in these two areas average about 2 and 1 5 t, respectively Yield variances around these averages are very high due to irregularity in rainfall The constraints are several interrelated factors triggered by mild to moderate drought stress, including mineral deficiencies, diseases, insects, and weeds Drought alone reduces yields and complicates land preparation, seeding and timing of herbicide and fertilizer applications

Unfavored upland rice

This system is characterized by irregular and low total rainfall Planting density is very low (60 cm between rows compared to 17 cm in favored environments) because of water stress, all varieties are tall Yields average about 1 t/ha and are highly unstable The primary constraint is inadequate soil moisture Drought stress can occur repeatedly during the growing season and normally is severe In much of the area a second constraint is highly acid, infertile soil with aluminum toxicity and/or phosphorus deficiency

This extremely important category of upland rice, characteristic of much of Central Brazil, is not found in Colombia This restricts CIAT's ability to address the problem Our lack of experience with unfavored upland rice indicates that CIAT must depend heavily on the experience and knowledge of Brazilian scientists to help define what, if any, attention CIAT should give to the system

Breeding Strategy

Experience has been accumulated in Colombia where the north coast and the eastern Llanos represent two highly favored upland areas of fertile soils (alluvial deposits in the case of the Llanos) and heavy, well distributed rainfall CIAT's first generation dwarf irrigated varieties out-yielded and replaced old, tall cultivars However, they quickly lost their resistance to blast CICA 8 now covers most of the upland area in the Llanos and is increasing on the north coast Its success is attributed to exceptional yields and blast resistance, presumably of the "slow blasting" type, since leaf blast is found in fields temporarily stressed by drought or excessive nitrogen fertilizer Most affected fields to date have recovered and produced high yields

Data also indicate that several breeding lines coming out of both IRRI and the Colombian rice program do reasonably well under highly to moderately favored upland conditions Dwarf varieties from the Colombian irrigated rice breeding program have contributed to increased yields in this ecosystem in Central America However, most advanced lines from Colombia are ill-adapted to these upland conditions The current practice is to select dwarf segregants from the F_2 onwards under the environmental soil and biological stresses of the Central American upland system CIAT contributes F_2 seed of crosses estimated to have utility for these conditions

Nevertheless, the outlook is quite different for the unfavored upland and genetic variability appears to be narrow Searching for more suitable donors should have a high priority Progress in this area is going to be difficult and slow

The Rice Program considers that breeding objectives for highly favored upland conditions are similar to those for irrigated rice These include

a) Vigorous dwarf plant types
b) Lodging resistance
c) Maturity of 110 to 130 days
d) Moderate threshability for mechanized harvest
e) Durable blast resistance, either through gene pyramiding or of the slow blasting type
f) Tolerance to other foliar/panicle pathogens (Rhynchosporium, Helminsthosporium, Thanatephorus)
g) Resistance to Sogatodes and hoja blanca virus disease
h) Tolerance to upland soil stresses
i) Long grain, heavy grain (26-30 g/1000), clear endosperm, intermediate amylose and gelatinization temperatures

Since the objectives are similar to those from the irrigated program, parents from crosses will be similar but with greater use of upland varieties from the Americas, Africa, and Asia Routine breeding procedures will include high volume crossing, with emphasis on top crosses, large F_2 populations, modified bulk selection from the F_2 through F_5

Breeding for favored upland rice will be conducted on upland soils, without supplemental irrigation, to expose populations to upland soil stresses Fungal disease pressures will be induced

In recent years, CIAT has diversified its germplasm through crosses with IRAT, Brazilian, African, and Asian upland varieties and with Surinam materials combining excellent grain and slow blasting characters Some of these parents unexpectedly combine well in crosses with high yielding dwarfs Furthermore, CIAT has selected, following irradiation, dwarf versions of IAC 25, Moroberakan, Tetep, Tadukan, Tapuripa, OS 6 and other upland varieties for the crossing program

CIAT's favored upland program will also concentrate on a potentially important subsystem that combines excellent rainfall with strongly acid infertile soils CIAT has no prior experience with this environment found in the Colombian and Venezuelan savannas, the jungle areas of Peru and perhaps in northern Brazil Existing varieties in these areas are tall land races that tolerate aluminum toxicity, phosphorus deficiency and fungal diseases at low input levels

Approaches to breeding upland varieties for infertile soils where drought is not a major constraint will depend upon answers to three questions

a) To what level can we increase and stabilize productivity? Is a 3 t yield objective overly optimistic?
b) Will the disease and soil problem tolerances of land races be maintained with increased seed density and fertilizer levels?
c) What is the ideal plant type to achieve moderately high yields in this ecosystem?

An initial step for improvement for unfavored mechanized upland conditions could be from a comprehensive set of land races, upland varieties and upland breeding lines from IRAT materials, IITA improved lines, old African and Asian varieties, Brazilian varieties and lines and native varieties such as Monolaya from Colombia These would be evaluated in four locations

a) Colombian Llanos, high rainfall, alluvial soil
b) Colombian Llanos, high rainfall, infertile savanna
c) Goiania, low rainfall, moderately acid soil
d) Peru, high rainfall, acid soils, rainforest

DISCUSSION

The distinction between breeding for broad adaptability versus site specificity has important implications for the optimum division of responsibilities between an International Center and national research programs In the past, most IARC breeding programs have been based on the centralized production of varieties for distribution to national programs Under this scheme, the division of research responsibilities is based on the supposition that the IARC has 1) an advantage in the diversity of the available germplasm base, 2) greater possibilities for creating diversity through hybridization or other means, 3) an advantage in selection by organizing nurseries which avoid duplication of efforts among national programs

This structure was developed for irrigated, high input crops, where centralized breeding activities can be very effective It is difficult to imagine on the other hand that an IARC would have a comparative advantage in selecting for local adaptation for crops grown across a wide diversity of environmental conditions A decision to work toward increased production under more variable conditions leads to a different balance of research responsibilities CIAT has already taken this decision for all its commodities, and we will explore some of the broader implications of that decision

In a decentralized structure of genetic improvement, regional and national program cooperative activities become all-important Research at headquarters should be directed toward broadly applicable aspects of the new technology, while more location - specific research is left to regional and national programs

Strong participation by national programs in technology development is obviously not a new concept, it has always been, in one form or another, part of the IARC philosophy However, when national program interests or capabilities do not conform to the IARC definition of the ideal, there is a temptation for the IARC to take over direct responsibility for activities which should logically be those of the national program Long term progress will require the more difficult approach of aiding national programs develop research capability, by scientist training and by influencing decision makers to reallocate resources to agricultural research

Centralized breeding by the IARC's can especially be cause for frustration in the collaborative relationships with stronger national programs Such programs are usually found in countries where a commodity is particularly important to the national economy, and therefore it is these same countries which are given high priority by the IARC's Strong national programs, however, may feel less need of the services of an IARC than less developed ones They do not necessarily want finished varieties from an outside source National pride, as well as the fact that these broadly adapted varieties may not meet their precise needs, can result in a lack of interest in collaboration when the IARC offers no alternative Consequently a centralized breeding philosophy can lead to having least impact in some of the most important production areas

The tendency for centers to opt for centralized breeding strategies has been for various motives The economic need to make new technology rather broadly relevant has already been discussed Decentralized breeding largely limits the opportunity for an IARC or an individual scientist to be widely recognized for developing improved varieties With a decentralized strategy we cannot be satisfied with less progress, but we probably must be willing to accept less recognition for it IARC's are in the peculiar position of trying to prove to donor agencies that they in fact have primary responsibility for positive results, while simultaneously giving full credit to national programs While the political expedience of this dichotomy may be unavoidable, at the practical level we must continue to work toward collaborative relationships with national programs which optimize the research advantages of each organization

In the following sections we discuss several priority research areas related to germplasm development where CIAT can be expected to have a comparative advantage in the medium to long term future

The Germplasm Base

International Centers have an overriding responsibility to collect, maintain, and make available a broad germplasm base in the commodity programs These functions are the backbone of crop improvement efforts The CIAT programs already maintain large germplasm collections in all the commodities, and in the case of beans and cassava, CIAT has world responsibility for germplasm maintenance

How does CIAT make optimum use of the wide diversity it has available? The temptation of many breeders is to select intensively toward some predetermined, rather narrowly defined goal, such as a given plant type, disease or insect resistance, or high yield potential The pressure to produce quick results may lead to over-dependence on a narrow range of parental materials having maximum or near maximum expression of the traits of interest This strategy can lead to impressive short-term gains for the characters being selected, but it is an unwise strategy for an international center interested in maintaining long-term genetic advance, and with a diverse range of breeding objectives being dictated by national programs Breeding for short-term gains involves the risk of creating a very narrow set of improved materials on one hand, and on the other hand an immense, static set of germplasm in the form of a "bank"

There is no straightforward answer to the question of how wide a germplasm base should be maintained in the active breeding populations for an international center In rainfed crops in the tropics this genetic base will need to be much more diverse than for an irrigated, high-input crop where environmental variability is inherently limited or artificially controlled In a general sense, the appropriate level could be described as a germplasm base which is broad enough to include genes in moderate to high frequency for meeting the requirements for adaptation (and all its broad implications), yield potential, resistance and quality, in collaborating countries For the TPP such genetic variability can be maintained both within and among species For other commodities, variability must be eventually combined within a single species, though other species may contribute genes

CIAT programs in general have probably been more successful than most in maintaining a broad germplasm base, because of early recognition of the diversity of needs of national programs

The maintenance, evaluation, and utilization of large germplasm collections is probably the single most important set of activities of IARC's in terms of long-term potential contributions to increased crop production These activities could not be efficiently taken over by national programs, as there is considerable advantage to a centralized, apolitical management of the germplasm base for crop improvement

Large-scale Hybridization

Though hybridization in most crops is not particularly difficult, arguments can be made for some degree of centralization of F_1 seed production in the IARC's Most importantly, the centers have immediately available a broad range of potential parents with which to make crosses, national programs generally have a narrower range of germplasm Secondly, crossing programs should have continuity, a characteristic lacking in many national programs Finally, hybridization is a largely non-location-specific activity that an IARC can provide as a service to national programs This may be especially important for small national programs, which can then concentrate their activities on the more site-specific selection in breeding populations

Studies of Pest and Pathogen Distributions, Population Dynamics, and Management Methods

Because pests and pathogens can move across international boundaries, and because distribution patterns and population levels change in ways which are not fully predictable, there is considerable advantage in having an international organization monitor these changes The centers can play a key role in monitoring pest and pathogen population dynamics, searching for new sources of resistance and developing improved management techniques

Breeding Methodology

CIAT has accumulated considerable experience in breeding methodology for crops and conditions which had previously received little attention Much of this information is empirical in nature Few studies have been conducted with the specific objective of providing information on the inheritance of particular traits, on correlations between traits, on optimum conditions for the evaluation of certain traits, or on the relative effectiveness and efficiency of alternative breeding schemes In many cases such information can be generated in an on-going breeding project at little or no additional cost except for some careful design, planning, and data collection For example, encouraging thesis students to do their practical work at CIAT achieves the dual aim of training and providing information on breeding methodology

Such information, which will allow improvements in the efficiency of future breeding activities in CIAT commodities (both at CIAT and elsewhere), ought to be one of the products the center has to offer This information often is broadly applicable, and may be directly adopted, or adapted and modified by national programs Solid background data on alternatives for breeding methodology will become increasingly important as more national programs develop a capacity for varietal selection programs, or increase their level of plant breeding sophistication More basic research by CIAT can help reduce expensive preliminary investigations in this area

CIAT studies of breeding methodology should take into account various levels of ability of national programs and provide bases for strategy decisions at all levels, including (from lowest to highest level of development) a) introduction of finished varieties from CIAT, b) introduction of segregating populations, c) hybridization among local cultivars, and d) introduction of basic germplasm for use in hybridization These are not mutually exclusive options, but for each, different sets of background information and technical expertise are required

CONCLUSIONS

The existence of G-E interactions is a universal phenomenon for crops under low levels of environmental modification and across broad geographical areas A number of physical, biological and socioeconomic factors are responsible for the differential performance of genotypes under different conditions Several important similarities and distinctions can be made in terms of how environment interacts with each of the CIAT commodities and the implications for genetic improvement

The four CIAT commodities are very different in evolutionary background, input from modern breeding, and their biological nature Cassava and pastures are long season annual and perennial crops, respectively This means they are exposed to the entire range of environmental conditions over the entire year, and for pastures across years However, neither has a highly sensitive growth period during which a passing environmental stress is likely to cause crop failure Those factors most important in G-E interactions are likely to be expressed over relatively long time periods

Rice and beans, on the other hand, are particularly sensitive to environmental stress near flowering Due to a shorter growing season, the within-years environmental variability is less than that experienced by long season crops The shorter growing season of beans and rice and their higher direct economic value make chemical control of pests and diseases a more feasible option than for pastures or cassava For all the commodities, however, breeding for resistance has high priority

Temperature is not a principal variable in the CIAT target area for pastures or rice, but is important for beans and cassava This relative importance of temperature is basically the result of delimitation of the target area in which CIAT has decided to work rather than inherent differences among the commodities for temperature response

Soil fertility level and soil water availability have major effects on productivity of all the commodities, but their importance as determinants of G-E interactions appear to vary considerably, depending primarily on the possible degree of modification of the crop environment

Socio-economic factors influence breeding objectives for each of the commodities, but consumer preferences have an overriding priority in the subdivision of breeding objectives for beans Performance of tropical pastures is influenced by the complicating factor of variable grazing management Cassava has various market alternatives and quality characteristics required for each vary somewhat

The CIAT commodity programs have delimited and/or divided the target environment on the basis of quite different criteria For the TPP the target area was delimited by soil type, and a derived variable (potential wet season evapotranspiration) divides the major ecosystems within this target area The Bean Program pays little attention to physical environmental variables apart from temperature in target area subdivision, grain type, cropping system, and temperature are the principal discriminant variables The target area subdivision of the Cassava Program is based on temperature, rainfall distribution, photoperiod, and soil type The Rice Program separates upland from irrigated rice, and subdivides upland breeding objectives by overall productivity of a region, based principally on soil water availability and soil fertility

The choice of criteria for the present subdivisions has been based not so much on actual data on the sources of G-E interaction, as on intuitive estimates based on experience and observation Overall, available data are too limited to determine the adequacy or utility of the present target area divisions Grain type preference in beans is a logical discriminant variable The most convincing environmental subdivisions are those based on temperature extremes in the Bean and Cassava Programs For all the other variables considered, results do not clearly indicate higher C-E interactions across than within subdivisions For tropical pastures, soil fertility has been tentatively identified as a useful discriminant variable, and for upland rice, soil water availability

Within the physical environmental subdivisions, each program has described typical disease and pest complexes Though pests and diseases are among the principal yield constraints in all the CIAT commodities, and genotypes clearly react differentially to these stresses, they have not been used as principal discriminant variables for sub-environment definition In general, pathogen and pest establishment and potential importance are regulated by rather predictable edapho-climatic environmental factors, thus it may be inappropriate to consider pests and diseases <u>per se</u> as descriptors

One of the most difficult aspects of describing the importance of pests and diseases in a region is their dynamic nature A changed agroecosystem brought about by change of genotype or change of cultural practices can dramatically change disease and insect balances and severity Pest and disease potential inventories should be developed and superimposed over any agroclimatic target area definition Any discrepancies in the area definition by the two procedures would need to be taken into consideration in a breeding program

For the Tropical Pastures, Bean and Cassava Programs, agroclimatological survey data have been used to subdivide target areas, but only in the TPP is this division actually being utilized to subdivide germplasm evaluation activities Agroclimatic data have been correlated with overall productivity of different regions, but generally have not been related to differential varietal performance, which is the key to [illegible] subdivision of breeding objectives Until the commodity programs can provide solid data on the importance of a range of environmental factors in G-F interactions, the utility of agroclimatic survey data in target area subdivision cannot be determined The Cassava Program has come closest to linking physiological data and G-E interactions with an agroclimatic target area subdivision, but adjustments still need to be made

It is axiomatic that there can never be fully discrete, neatly divided breeding objectives for each subdivision of the target area The variables providing the basis for subdivision are normally continuous and not discrete Likewise genotype reaction to any given state of a variable is most often continuous Consequently, though mapping and other categorization may imply a reassuring simplicity, the real-world situation more often requires intelligent judgements among several not-so-clear options The programs should recognize the target area subdivisions as general but somewhat fluid guidelines

Priority areas for future development area

1) More detailed studies of international trial data to relate genotype performance to environmental variables of the trial sites

2) Studies designed specifically to determine the importance of individual environmental factors in G-E interactions

3) Studies of CIAT's ability to extrapolate results from Colombian selection sites to national program needs

4) Inclusion in the target area surveys of more or different factors known to be important in contributing to G-E interaction

5) Development of inventories of disease and insect potential for each commodity for the target production areas

6) For beans, cassava and upland rice, development of procedures for routinely sending segregating populations to national programs, and for effective selection and information feedback

7) Continued development of regional programs to expedite collaboration between national programs and CIAT

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