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TROPICAL CROP BREEDING - ACHIEVEMENTS AND CHALLENGES[1/]

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CIAT BIBLIOTECA
10 FEB 1981

1/ A paper to be presented at Session I-5 Breeding of the symposium on Potential Productivity of Field Crops under Different Environments to be held at IRRI, September, 1980.

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One of man's greatest achievements was the domestication of crop species. The domestication of nearly all the major food crops occurred in the tropics or adjacent areas. Numerous pathogens, pests and cultural practices co-evolved with each crop species in its center(s) of origin. Consequently, the great bulk of variability in crop germplasm, pests, and cultural practices is found in the tropics. Agricultural advance in the temperate countries constitutes a recent and small chapter in the history of the domestication and evolution of crop production. Yet, modern theory related to crop breeding and production largely developed in the temperate countries and resulting technology tended to be imported to the tropics without appropriate modification. While some of the imported technologies were useful, it is now generally recognized that crop improvement in the tropics is more difficult and complex than originally thought.

The basic difficulty of tropical crop breeding derives from the tremendous variability in crop germplasm, pests and the cultural systems for crop production and the highly complex interactions among these factors.

We present several underlying factors about crop breeding in the tropics which may be important in defining the basic strategy for specific crop breeding programs. Many of these are not emphasized in the textbooks prepared from the temperate experience.

I. Physiological factors under different environments in different crops.

Genetic improvement for yield of food crop has been achieved through the improvement of total dry matter production, or of harvest index, or both. Harvest index is the proportion of economic yield to

the total biological yield of a plant. In cereal crops, it is the proportion of grain weight to the total plant weight. In root and tuber crops, it is the proportion of root or tuber weight to the total plant weight. Total biological yield represents the effectiveness of photosynthetic exploitation by the crop while harvest index represents the efficiency of the crop to convert photosynthesized products into an economically valuable form.

We evaluated the relative importance of harvest index and of total plant weight to yield at different levels of environmental productivity in rice (Table 1) and cassava (Table 2), using yield data of wide germplasm variability under a range of environments. Two statistics are compared to assess the relative importance. One is the simple correlation coefficient between yield and harvest index or total plant weight and the other is the relative size of variance of harvest index or total plant weight compared to that of grain or root yield. Environmental productivity is given by the total average yield of each yield trial.

In rice grown in high yield environments the importance of harvest index to grain yield was much more significant than of the total plant weight. Under low yielding environments, the importance of total plant weight to rice yield was overwhelming (Table 1).

In cassava, on the other hand, harvest index was important across all the yield levels. The relative importance of total plant weight tended to be greater in the lower than in the higher yield environments (Table 2).

Tropical food crops may be grouped according to the relative importance of harvest index and of total biological yield to economic

yield. The first, exemplified by cassava, includes crops where the harvest index is universally important to economic yield over a wide range of environmental productivity. The second group includes crops in which the harvest index is more important under high yielding environments while total biological yield is more important under low yielding environments. This is represented by rice.

In crops such as wheat (Syme, 1970, McEwan, 1973, Donald and Hamblin, 1976), barley (Singh and Stoskopf, 1971), oats (Simš, 1963), and peanut (Duncan et al, 1978), harvest index is more important under high yielding environments. It is at present difficult to analyze which factor is more important under low yielding conditions with these crops because very limited attention has been given to the genetic aspect of yield factors under less productive conditions. However, these crops may fall into the same category as rice.

In field bean, total plant weight is highly correlated with grain yield while harvest index is not correlated (CIAT, 1975, 1978). Similarly, in soybean, harvest index is not an important factor to grain yield (Buzzell and Buttery, 1977). In tropical maize, total plant weight is highly correlated with grain yield throughout a wide range of planting densities, while harvest index is equally important only at a high planting density (Yamaguchi, 1974).

These field bean, soybean and maize studies were conducted in comparatively well managed fields, receiving adequate fertilizer, irrigation, and weed and pest control. Thus, they represent relatively high yielding environments.

In these crops also, very limited research has been conducted under low yielding environments. Since the relative importance of

total plant weight to grain yield tends to be greater under low yield environments in rice and cassava, it appears that total plant weight is important to grain yield also under low yielding environments in these crops. Thus, field bean, soybean, and maize represent a third group where total biological yield is important over a wide range of environmental productivity.

We conclude that the crucial physiological factors related to yield differ drastically according to the crops and to the potential productivity of the environment.

II. Competition and evolution of cultivars.

Twenty-five genotypes of rice and 20 of cassava of different growth habits were mix-planted in alternative rows with a tester genotype in separate experiments conducted under high yielding environments. The yield data of each genotype were compared with those of the same genotype grown in monoculture. Competitive ability of each genotype was given as: yield in mixture/yield in monoculture.

In rice, competitive ability of each genotype was positively correlated with straw weight of the same genotype in monoculture ($r = 0.615^{**}$) and negatively with harvest index ($r = -0.690^{**}$). Those genotypes that performed well in mixtures (defined as strong competitors) had large straw weight and low harvest index. Grain yield of each genotype in mixture was highly correlated with grain yield of the same genotype in monoculture under low yielding environment ($r = 0.762^{**}$); but it was not correlated with grain yield under high yielding environment ($r = -0.034$, Fig. 1). On the contrary, harvest index of each genotype in mixture was highly correlated with grain yield of the same genotype in monoculture under a high yielding environment ($r = 0.809^{**}$)

but it was not correlated with grain yield under a low yielding environment (r = -0.042, Fig. 2). Thus, selection for harvest index is much more efficient than selection for grain yield itself if the selection target is high grain yield under a high yielding environment. When the objective is improved grain yield under a low yielding environment, selection for grain yield is efficient.

In cassava, competitive ability was highly correlated with stem and leaf weight of the same genotype in monoculture (r = 0.806**) and it was negatively correlated with harvest index of the same genotype in monoculture (r = -0.859**). Since harvest index is highly important to root yield, competitive ability was negatively correlated with root yield in monoculture (r = -0.703**). Stem and leaf weight, which is a good indicator for the quantity of stem cuttings for propagation, in mixture was negatively correlated with root yield in monoculture (r = -0.539*). Root yield in mixture was correlated with root yield of the same genotype in monoculture (r = 0.568**). However, harvest index in mixture was most closely correlated with root yield in monoculture (r = 0.905**, Fig. 3). Thus, selection for harvest index is more efficient than for root yield itself when the selection objective is higher root yield. If plantings from genetically mixed cassava populations are made at random from available stem cuttings, genotypes with high competitive ability, but low yielding ability, would dominate after several cycles of plantings.

Since the essential part of intergenotypic competition occurs through competition for light interception by different rice genotypes (Kawano and Tanaka, 1967, Jennings and Aquino, 1968), those genotypes with high harvest index are expected to be weak competitors because of

the relatively fewer resources allocated for stem and leaf expansion. We generalize that genotypes with high harvest index are weak competitors and those with large total plant weight are strong competitors.

In cassava and its wild relatives, roots are not an indispensable organ for reproduction because seeds and stems are the means of propagation. The evolution of cassava cultivars for higher productivity must have occured mainly through the improvement in harvest index because the species must have started from a harvest index near zero: The gain in productivity was attained at the expense of competitive ability.

In grain crops seeds are the essential organ for reproduction even in their wild forms. Evolution of grain cultivars must have started from a harvest index higher than zero. Evolution of such crops as rice, wheat, oats, and peanuts for higher productivity under high yielding environments must have occured mainly through the improvement in harvest index at the expense of competitive ability.

In field bean, competitive ability is positively correlated with yielding ability in monoculture (CIAT, 1977). The same is true for maize (Kannenberg and Hunter, 1972). Evolution of yield in field bean and maize must have occured through a delicate balance between the improvement in harvest index and in competitive ability. Evolution of other grain crop yield for low yielding environments must have been attained in a similar manner.

The bulk population method of crop improvement is characterized by exposing genetically mixed populations to natural selection. From the available data we speculate that the bulk population method would result in rice genotypes which yield reasonably well under low productivity environments, cassava genotypes which yield poorly under medium

to high productivity environment, and field beans which may yield satisfactorily under low or high yielding environments. Farmers' selection and propagation over thousands of years constitute a large-scale bulk population breeding program. Many old land varieties cultivated traditionally in the tropics resulted from this process and they perform quite respectably in their accustomed environments.

The competition studies cited were conducted in high productivity environments. The present discussion may not be extended to intraspecific competition under low productivity conditions. Thus, interaction of competition factors with the adverse yield factors of low productivity environments merits further attention to establish breeding methodology for these stress environments.

III. Disease and pest factors

Among the factors which influence the productivity level of environments, biological restraints, especially diseases and pests, contribute to low productivity. California, New South Wales in Australia, and the northern coast of Peru are known for extremely high yields of rice and the sub-tropical elevations of Colombia (Caicedonia) produce high yields of cassava. These areas are characterized by such factors as fertile soil, excellent water management or favorable rainfall patterns, and good agronomic practice. They also are remarkable in having very few disease or insect problems.

The rainfed rice area of Asia shows stagnant, low yields. Tropical American savannas are extremely difficult for successful cassava production. While physical factors contribute to the low productivity of these areas, multiple disease and insect problems abound in each. Biological factors are most numerous and severe in low productivity

environments and they are most accentuated within centers of crop origin. Under low productivity environments, the number of major biological yield restraints is seldom less than half a dozen and the interactions of crop genotypes with these biological factors is extremely complex. The reduction of one or two pests through breeding would not result in successful cultivars for these difficult conditions. New strategies for multiple and stable pest resistance are needed for low productivity environments and particularly for those falling within centers of crop origin.

Reviewing numerous cases of crop vs. disease interaction, Robinson (1976) carefully distinguished between vertical and horizontal pathosystems. He concluded that vertical (non-rate reducing, monogenic) resistance frequently characterizes sexually propagated annual species, often as a result of disturbance by plant breeders of evolutionarily balanced systems. Nature, and less meddling by man, favored the development of horizontal (rate reducing, polygenic) resistance in vegetatively propagated perennials. This suggests that vegetatively propagated perennial crops such as sugarcane and cassava are more easily bred for durable disease resistance. Durable, multiple resistance in sexually propagated annuals such as rice and field bean in less favored environments must come from exploitation of the rate reducing resistance remaining in land varieties. Alternative strategies include the pyramiding of "major" genes of the development of genotypically diverse cultivars.

IV. Traditional cultivars

Traditional cultivars are genotypes that have been selected and grown for many years by farmers of a given region. They are characterized by stable performance and are in balance with their total

physical and biological environment.

The relative productivity of traditional strains of rice and cassava was analysed under different levels of environmental productivity. Minabir 2 is a local rice cultivar of the northern coast of Peru. Its grain yield was compared with the total average yield of 25 genotypes including many modern selections in 11 different environments. The relative yield of Minabir 2 was higher in low yielding environments than in high yielding environments (Fig. 4).

Valluna is a traditional cassava cultivar of the Valle region of Colombia while Manteca and Montero are traditional cultivars from the northern coast of Colombia. Llanera and Chirosa Yema de Huevo are traditional cultivars from the Llanos Orientales region of Colombia. Twenty-eight varietal yield trials, including the local cultivars, were conducted in these regions. The root yield of these traditional cultivars was compared with the total average yield of all the varietal entries in each trial. The relative root yield of the traditional cultivars was highest in the low yielding environments (Fig. 5).

Traditional cultivars of rice and cassava (and perhaps all other crops) are successful under less productive conditions. Most farm conditions in the past had low productivity by modern standards and the ancient practice of bulk population selection favored adaptation to low productivity environments. Natural selection favored the accumulation of genetic resistance to diseases and pests and an array of other physical stresses including soil, weeds, drought, flooding, and so forth. Thus, we confirm the direct usefulness of traditional strains under low productivity environments and we view them as elite sources of resistances for more modern varietal types designed for high productivity

environments.

V. Center of origin and productivity

Man has domesticated plants and transferred them from their centers of origin to other continents, so that now many crops are cultivated on a worldwide basis. Purseglove (1968) and Jennings and Cock (1977) have shown that the principal production areas for many major economic crops are distant from the regions in which they originated. The average yield figures for some important food and industrial crops show that in general crops yield better outside their centers of origin (Table 3).

Crops extensively cultivated in the more developed temperate countries such as maize, soybean, barley, and potato show the largest yield increases outside their centers of origin. All of our major crops have their centers of origin in less developed areas of the world. Hence, the yield increase when a crop is grown outside its centers of origin can be ascribed in many cases to the greater technology available in the developed countries. Yet those crops grown only in the underdeveloped tropical areas including cassava, banana, and several tree crops, all yield better outside their centers of origin (Table 3).

Remarkable success in tropical crop production are exemplified by sugarcane in South America, rubber in Malaysia, rice in Colombia and Peru, and cassava in Thailand. All of these involve crops transferred to places distant from their centers of origin. These successes, however, are limited to medium to high productivity environments with medium to high technology. In the areas where the physical environment is extremely unfavorable or where the production technology is very poor, crop production is very low even the crop is carried far away

from its center of origin. Upland rice production in central Brasil is an example for the former case and rice in West Africa exemplifies the latter.

On the contrary, importation into centers of origin of specific crop technology developed outside the center of origin is normally unsuccessful. Maize hybrids to the Andean zone and Japanese or United States rice cultivars to tropical Asia are clear examples.

Crop species, including their weedy progenitors, existed within centers of origin for thousands of years before man developed agriculture and directed crop improvement towards his ends. The evolution of parasites followed a course parallel to crop evolution. Just as centers of crop origin are distinguished by their wealth of varietal diversity, they are also centers of variability of pathogens and pests. Jennings and Cock (1977) deduced that the major reason why the principal areas of production of many important crops are located outside their centers of origin is that losses in crop yields due to insect and disease damage are greatest within centers of crop origin.

Although crop productivity suffers greater biological restraints within centers of origin, crops outside centers of origin are not free from insect and disease damage, but the causal agents are fewer and the overall damage is easier to contain. Nevertheless, there are several cases of massive disease and pest losses of crops outside their centers of origin including coffee rust in Sri Lanka, the Panama disease of bananas in Central America, stem rust of wheat in North America, late blight of potato in Europe, Sogatodes feeding and hoja blanca virus on rice in the American tropics, and the Southern corn leaf blight epiphytotic in the United States (Jennings and Cock, 1977). Most of these

epidemics, however, were induced by genetic crop uniformity including the Gros Michel banana, the Lumper potato, a few resistance genes in wheat, the rice cultivar Bluebonnet 50, and the Texas cytoplasm in maize. These examples of genetic vulberability outside centers of origin resulted from human miscalculations and emphasize the importance of genetic diversity wherever crops are produced.

The massive biological, physical, and social restraints to productivity within centers of origin demand a comprehensive research program to achieve progress. These restraints, the inadequacy of investment capital for infrastructure improvements, and the frequently limited research capability in these areas render difficult the overcoming of stagnancy in food production within centers of origin.

Incomplete technological packages inadequate within centers of origin may dramatically increase food production outside centers of origin. This point is well illustrated by the new rice and wheat technology based on dwarfed cultivars which yield only about 0.5 additional ton/ha in tropical Asia and the Middle East, respectively, whereas a portion of this technology adds 2.0 additional ton/ha of rice in tropical America or wheat in Mexico. Although a technology related to improved yielding ability can be tested outside centers of origin with possible success, a simple technological change is unlikely to achieve change within centers of origin.

VI. Experiment stations vs. farmers' fields

One of the greatest difficulties in tropical agricultural research is the transfer of experiment station results to farm production. This difficulty exists also in temperate areas, but to a lesser degree.

In Japan, for example, there are eight national agriculture ex-

1 periment stations and forty seven prefectural agriculture experiment
2 stations. Each of these stations has sub-stations. This network covers
3 most of the environmental variation found on farms. Scientists in deve-
4 loped temperate countries can pursue the objective of maximum crop pro-
5 ductivity for most farmers. The technology thus generated often invol-
6 ves high input levels. Most farmers can apply the new technology and
7 many surpass the experiment station yields. Well developed educational,
8 social and credit systems permit the farmers to respond to the recommen-
9 dations by the experiment station. A yield increase of 10% is consi-
10 dered as a significant technical advance for extension to farmers. Ja-
11 pan may be an overly specific case, yet the basic goal of research in
12 temperate countries is the generation of maximum yield technology for
13 each environment.
14 Brasil has about 23 times the area of Japan but there are fewer
15 experiment stations than in Japan. Yet, among the tropical countries,
16 Brasil has one of the most developed experiment station networks. The
17 typical situation in the tropics involves a scattering of experiment
18 stations over a great area and enormous environmental variability. Ex-
19 periment stations tend to be located on the more fertile soils in the
20 more favorable rainfall areas and they usually have irrigation facili-
21 ties. The clients for research are the minority of influential farmes
22 who produce high value cash crops in favored environments. The majority
23 of the farmers grow traditional crops such as upland rice, beans, maize,
24 or cassava in mixed associations on less fertile soils. These farmers
25 benefit little from research aimed at productive environments. Agricul-
26 tural production infrastructure is normally insufficient to reach the
27 majority of the farmers.

We suggest two reasons why experiment station technology is often ineffective. The first one is that the experiment station is not located in the representative environment for the majority of the farmers. The second is that the technology developed on experiment stations is unsuited to the needs of most of the farmers because it is generated with cultural practices atypical of most farms. The cultivars developed with high fertilizer application and good water and weed control are inappropriate for low productivity environments (Table 1) characterized by low soil fertility, irregular water and weed control and by complex disease and pest problems. The genotypes selected under chemical disease and pest protection are biologically unfit for low productivity environments.

The CIAT cassava program, in awareness of these factors, conducts genotype evaluation and selection in three different environments: The Cauca Valley is characterized by fertile soil and favorable rainfall and the environment is considered as highly productive for cassava. The tropical northern coast, a center of cassava production in Colombia that resembles many other cassava production areas, is characterized by a wide range of cultural practices. The Llanos Orientales characterized by infertile oxisols, represents a vast area of Latin American Savannas. In each of these areas, trials involving varieties and agronomic practices are conducted on experiment stations and farms.

The remarkable progress made by breeding in the Cauca Valley is indicated by the large difference between the average yield of CIAT lines and that of local traditional cultivars (Table 4). This difference narrows considerably when the trials are conducted on farmers' fields but the superiority of CIAT lines is maintained. The decrease

in the superiority of CIAT lines on farms is partly due to the excellent production systems developed for local cultivars on large farms. The newest CIAT lines now average 50 ton/ha on farms indicating that breeding is successful for this highly productive environment which represents, however, a tiny portion of cassava production in the tropics.

On the northern coast, progress was achieved in cassava breeding on the local experiment station since the CIAT lines consistently outyield the local traditional cultivars (Table 5). The superiority of CIAT lines is maintained on farmers' fields with improved cultural practices (good land preparation, good preparation of planting stakes, and good weeding). However, it disappears totally on farms that employ no improved cultural practices. There the traditional cultivars are best.

In the Llanos Orientales progress was made in breeding and selection at the experiment station The superiority of CIAT lines over traditional cultivars is greater with high input technology (heavier lime application and irrigation) than with medium input technology. The soils in this area are so poor that no meaningful yield can be obtained either from traditional strains or CIAT lines without soil amendments. In this low yield environment breeding advance is not possible if fertilizer is not applied.

These data, although scanty, do permit a generalization that agrees with our observation of plant breeding in the tropics. That is: the superiority of newly selected genotypes is greatest on experiment stations utilizing high input technology while the improved genotypes are useless in traditional farmers' fields without any attendent improvement in technology.

The data also suggest that the genotypes selected at experiment

stations can be highly effective a) If the selection conditions resemble those of the target area farms and, b) If the farmers are able to upgrade their cultural practices to permit expression of genotype potential. Thus, to plant breeders, the crucial issue is the capability of farmers to improve their level of cultural practices. In the case of cassava, this includes land preparation, selection of planting stakes, weeding, and fertilization for poor oxisols as the basic requirements for the expression of higher productivity in new cultivars.

The data also question whether crop breeders cam improve yield in low yielding environments of traditional farms where the farmers are unable or unwilling to improve to change their cultural practices. Other studies demonstrate that the evolution of cultivars was accompanied by improvemnt in cultural practices, suggesting the difficulty of changing cultivars without changing crop agronomy (Oka and Chang, 1964, Kawano et al 1974). Traditional strains resulted from natural and bulk selection over thousands of years. It is understandable that traditional cultivars have remained superbly adapted to their total environment for long periods of time without major change. No viable strategy is available for the genetic improvement of traditional agriculture. Substantial change in cultivar type would require equivalent change in crop husbandry. Minor change at minimum yield levels would be invisible both to the scientist and to the farmer.

Traditional farmers produce their crops for their own subsistence. They are more concerned about crop failure than a modest yield increase. Consequently, subsistence farmers are the most conservative farmers. To convince them to adopt new cultivars, it would be necessary to demonstrate the large yield advantage of modern cultivars under their farm

conditions. While new cassava materials may demonstrate a 50 to 100% yield increase on farms of medium to high level technology, it would be extremely difficult to show a yield gain on traditional farms. The paradox is that we can produce a quantum yield advance for rich farmers where only a small increase would suffice, while we cannot create small improvement for poor farmers who theoretically would benefit most from great yield increases.

Very little scientific attention has been given to the improvement of traditional farms. Our understanding is too scanty to abandon the possibility of productivity advance through plant breeding. Nevertheless, improvement in the traditional low yield agriculture in the tropics is more logically a task for production agronomists.

Large interactions between genotypes and geographical areas introduce an additional complication in tropical crop breeding. This type of interaction has been the subject of much study and is relatively easy to understand. Careful characterization of the target area and location of experimental sites, are the best response to the problem. However, the interaction between genotype and technology level is more difficult to quantify, less attractive scientifically, and more dependent on socio-economic factors. The present level of understanding of this type of interaction is inadequate to allow us to define a comprehensive strategy of breeding and selection particularly for low yielding environments in the traditional agricultural sector.

VII. Success and failure

A review of modern crop breeding would indicate unquestionable success in some areas and failure in others.

The early rice breeding work at IRRI is one of the few notable

successes in tropical crop breeding. The success stemmed from the strategy to seek maximum and rapid progress by concentrating research on high yielding environments largely defined by good water control, nitrogen fertilizer application and the selection for high harvest index types having short stems, erect leaves, and photoperiod non-sensitivity (Jennings, 1964, 1974; Tanaka et al, 1967; Chandler, 1969). Rice genotypes with a high harvest index are productive under high yielding environments but not under low yielding environments (Table 1). Human and natural selection evolved many venerable strains well adapted to traditional low input technology. These rices are tall, vigorously growing, low harvest index types. Selection for harvest index was not practiced by farmers. Similarly the bulk population breeding method would discriminate against genotypes with a high harvest index because of their low competitive ability. Thus, advance in rice breeding depended upon finding a plant character productive in the target area but which had not been uncovered in the farmers' practice of bulk selection. The character employed was a simply inherited diwarfism of stems and leaves.

The great success of the wheat breeding program in Mexico may be interpreted in the same manner. These small grain achievements, however, are largely confined to areas having good water control and high fertilizer application. Yield increases have been higher outside the center of origin than inside. Their inability to increase the yield under low yielding environments is readily explained by the fact that physiological factors related to high yield are completely different between high and low yielding environments (Table 1). A distinct breeding strategy for low yielding rice and wheat areas requires an assessment of these different yield restraints and a search for distinct genotypes

to overcome them.

In cassava, harvest index is the critical trait for high yield in medium to high productivity environments where medium to high technology is available. Improved harvest index did not usually result from long term natural and farmer selection. Thus, progress in modern cassava breeding in favored environments should result from attention to harvest index (Kawano et al 1978a, 1978b). The process, however would be lengthy because the crop is propagated vegetatively, its multiplication rate is low, and it has a low economic value.

Since harvest index is also important for cassava production under low yielding environments, there should be scope for breeders to make some progress in these areas although it appears to be extremely difficult for farms having no improvement in cultural practices.

The case of tropical maize is confounded by the added complexities of genetic manipulation of populations. Increased economic yield in maize is related to an increase in total biological yield. In temperate favored environments maize is successful as a result of vigorous single and double cross hybrids. These genetically uniform populations were unknown during the domestication of maize. The reasons why this success cannot be repeated on small farms in the tropics may involve the following factors: (a) precise husbandry of genetic populations is difficult on small farms; (b) the yield restraints and agronomy in maize growing areas differ from the cultural conditions of maize research stations; (c) open-pollinated maize in low productivity environments was milked dry by farmers during thousands of years of bulk selection leaving little scope for modern breeders; (d) hybrids lack the genetic variability to tolerate the multiple stresses of low yield

environments.

Field beans were domesticated in the Andean zone and have been a major component of the human diet there for thousands of years. Variability, and adaptability to diverse local environments is evident in the collections of traditional cultivars found from Mexico to Chile. In this crop total biological yield is highly correlated with competitive ability and with grain yield under a wide range of environments. This suggests that breeders must work fundamentally in the same path of natural and farmer selection. Hence, modern efforts to improve the yield level may represent only a fraction of what has been achieved during thousands of years. Consequently, a quantum jump in yielding ability is not likely.

Apart from these major food crops, we cite sugarcane as a superb example of breeding success. This crop is among the highest in dry matter production per unit area per unit time. Especially in the American tropics highly efficient dry matter production is achieved on millions of hectares largely in the absence of major disease or pest problems. Sugarcane is managed as a plantation crop on highly fertile lands with good water control, heavy fertilizer application and good cultural practices. It would appear that intelligent plant breeding successfully managed the relatively uncomplicated physical and biological yield restraints in this high value cash crop whose main production areas are now concentrated remote from the center of origin.

Progress in tropical crop breeding has been confined to medium to high productivity environments with medium to high technological investment levels. No crop breeding program has made a significant contribution to the traditional farming situations in low productivity

environments. Attempts to extend technology developed in high productivity environments to low productivity environments have failed.

VIII. Easy and difficult cases

Apart from those factors already described which control the degree of difficulty of plant breeding in the tropics, there are others that are more generally understood. In terms of ease of handling genetic materials, vegetatively propagated crops are the easiest, sexually propagated crops are more complicated, and outcrossing crops are the most difficult. In terms of physiological yield formation, root and tuber crops are the simpliest because the sink-source relationship is fairly straight forward and there is no danger of lodging caused by overfilling the sink. In this connection crops such as sugarcane or oil palm have the same advantage. Cereal crops are more complex because the time factor complicates the sink - source relationship and yield components are more numerous. Grain legumes are among the most difficult because of the added factor of the balance between protein and carbohydrate synthesis. Table 7 summarizes these factors according to their contributions to the difficulty of plant breeding.

IX. The challenge

The major research efforts in tropical crop breeding have concerned development of high yielding cultivars for high yielding environments with high technology levels partly because of the tradition of agronomic research in temperate areas and also because it is easier to expect measurable research results in a short period of time. In several instances, this strategy has been successful. Wherever such opportunity remains it should be exploited without hesitation. Examples of potential success would include high technology cassava pro-

duction for animal feed in Asia or cassava farming with massive inputs in Brasil for alcohol production.

In some instances research for high productivity environments has fulfilled its primary mission and a continuing strategy of research priority for these environments is debatable. The majority of arable land area in the tropics is characterized by infertile soils and irregular water supply. The underlying philosophy in agronomic research in temperate areas has been to convert unfavored environments into highly productive ones. Low productivity environments in the tropics may be upgraded but only with immense investment for irrigation, drainage, and fertilizer application. Such capital investment is rarely available. Hence, more research attention is needed for moderate and stable yield levels under less favorable environments. Important examples include Asian rainfed rice, Andean maize and field beans and acid infertile soils for cassava.

The first requirement is a careful analysis and definition of target areas in climatic, soil, biological and socio-economic terms. The most critical determination is the level of cultural practices or technology falling within the reach of the majority of the farmers in each target area. Experiment sites are required within each target area. The research organization that assumes world responsibility for the crops should be located in the principal center of origin.

Experimental plot management cannot exceed the cultural practices within the reach of average farmers. Impractical and cosmetic plot protection including pesticides and excessive water or weed control should be eliminated. The major selection criterion should be overall performance within a given environment. Selection for individual

traits is used to reinforce general adaptability. Extensive use of land cultivars from each target area is a necessary component of the broad germplasm variation in hybridization programs.

The pedigree method of selection is falling into disfavor largely because it requires prohibitive costs to accommodate a desired volume of segregants. Renewed interest in modified bulk population breeding for specific environmental complexes is emerging as a substitute for pedigree selection.

We take issue with the belief that a widely adapted cultivar confers stable yield. A farmer is not interested in wide adaptability. His concern is stable yield on his farm. More important is stability of performance over seasons within each target area. Multilocational testing identifies tolerance to important disease and pest problems that are sporadic in any single location. The physical rotation of segregating populations among relatively similar environments may permit identification of tolerances to subtle but cumulatively massive physical and biological yield restraints.

Finally, we are confronted with the most difficult question of whether the breeder can serve those traditional farmers who cannot improve their cultural practices. This is primarily a socio-economic issue and even for agriculturalists it is primarily a concern of agronomists. Observations suggest that it is extremely difficult for breeders to contribute to this situation since most of the possible improvement might have been done by farmers already. Yet, one approach that farmers may not have exhausted is wide and multiple crosses among varied germplasm sources. Thousands of multiple crosses in one year at one location may be equivalent to natural crossing over many years at

many locations. This, combined with modified bulk selection, may be our only realistic approach to the lowest yielding situations.

X. Conclusions

All the major food crops were domesticated in the tropics or its adjacent areas. Diseases, pests, and cultural practices co-evolved over ages with the crop species. Profound richness in the variability of crop germplasm, pests, environments, and cultural practices complicate tropical crop breeding. Yet, the major difficulty in breeding is the need to grapple with the bulk of farming situations that have partial or no access to modern cultural practice technology.

Breeding may be relatively easy for the areas of high environmental productivity with high cultural technology outside the center of origin of the species. When the crop is a vegetatively propagated perennial, disease resistance may be obtained with relative ease. Where the harvest index is the yield limiting factor, a quantum yield increase by selection is possible.

In contrast, breeding becomes extremely difficult for the areas of low environmental productivity with low cultural technology inside the center of origin of the crop. If the crop is a sexually propagated annual it will be a challenge to obtain stable disease resistance. If the total biological yield is the yield limiting factor, substantial yield increase by breeding may not be expected.

Earlier research emphasis given to the tractable farming situations of high input technology is shifting to the bulk of tropical farms having low to medium technology possibilities where yields are stagnant.

These target areas for research must be identified in terms of

biological, climatic, soil and socio-economic factors. A critical issue is identification of cultural practices within the reach of the farmers in each target area. Research plots for varietal selection should be managed at a level within the reach of the average farm. A maximum use of land cultivars within each target area combined with broad based and high volume hybridization is critical. The major selection criterion should be the overall performance of a population and secondarily selection for individual single traits. The final selection should be made on the basis of moderate and stable yield over years within a given environment.

XI. Acknowledgement

We wish to thank J. Hernandez, H. Gonzalez, and M. Lucena, Ministry of Agriculture, Chiclayo, Peru, for their valuable help in the rice experiments; M. Rios, ICA, Colombia and P. Daza, Edgar Salazar, Luis Fernando Calle, and Julio Holguin, CIAT, for their help in the cassava experiments; and J.C. Toro, R. Howeler, J. Lynam, and R.O. Diaz for permitting to use their data.

XI. Literature cited

Buzzell, R.I. and B.R. Buttery. 1977. Soybean harvest index in hill-plots. Crop Sci. 17: 968-970.

Chandler Jr., R.F. 1969. Plant morphology and stand geometry in relation to nitrogen. p 265-285. In J.D. Eastin, F.A. Haskins, C.Y. Sullivan, C.H.M. van Bavel, and R.C. Dinaver (eds). Physiological aspects of crop yield. Am. Soc. Agron. Madison, Wis.

CIAT, 1975. Annual report. Centro Internacional de Agricultura Tropical, Cali, Colombia.

____, 1976. Annual report. Centro Internacional de Agricultura Tropical, Cali, Colombia.

____, 1977. Annual report. Centro Internacional de Agricultura Tropical, Cali, Colombia.

____, 1978. Annual report. Centro Internacional de Agricultura Tropical, Cali, Colombia.

____, 1979. Annual report. Centro Internacional de Agricultura Tropical, Cali, Colombia.

____, 1980. Annual report. Centro Internacional de Agricultura Tropical, Cali, Colombia.

Donald, C.M. and J. Hamblin. 1976. The biological yield and harvest index of cereals as agronomic and plant breeding criteria. Adv. Agr. 28: 361-403.

Duncan, W.G., D.E. McCloud, R.L. McGraw, and K.J. Boote. 1978. Physiological aspects of peanut yield improvement. Crop Sci. 18: 1015 - 1020.

Jennings, P.R. 1964. Plant type as a rice breeding objective. Crop Sci. 4: 13-15.

_____. 1974. Rice breeding and world food production. Science 186: 1085-1088.

_____, and R.C. Aquino. 1968. Studies on competition in rice. III. The mechanism of competition among phenotypes. Evolution 22: 529-542.

_____, and J.H. Cock. 1977. Centres of origin of crops and their productivity. Eco. Bot. 31: 51-54.

Kanneberg, L.W. and R.B. Hunter. 1972. Yielding ability and competitive influence in hybrid mixture of maize. Crop Sci. 12: 274-277.

Kawano, Kazuo, Alvaro Amaya, Pablo Daza, and Mario Rios. 1978a. Factors affecting efficiency of hybridization and selection in cassava. Crop Sci. 17: 373-376.

_____, Pablo Daza, Alvaro Amaya, Mario Rios, and Wania M.F. Goncalvez. 1978b. Evaluation of cassava germplasm for productivity. Crop Sci. 17: 377-380.

_____, H. Gonzalez, and M. Lucena. 1974. Intraspecific competition, competition with weeds, and spacing response in rice. Crop Sci. 14: 841-845.

_____, and Akira Tanaka. 1967. Studies on the competitive ability of rice plant in population. J. Fac. Agr., Hokkaido Univ., Sapporo, Japan.

McEwan, J.M. 1973. The performance of semi-dwarf wheats in New Zealand: Implications for New Zealand wheat breeding. p 557-559. In E.R. Sears and L.M.S. Sears (eds). Proc. Fourth Int. Wheat Genet. Symp., Agric. Exp. Stn. College of Agr. Univ. Missouri, Columbia, Mo.

Oka, Hikoichi and Went-tsai Chang. 1964. Evolution of response to

growing conditions in wild and cultivated rice forms. Bot. Bull. Acad. Sinica. 5: 120-138.

Purseglove, J.W. 1968. Tropical Crops. Dicotyledons 1, p 332. John Wiley and Sons, New York.

Robinson, Raoul A. 1976. Plant Pathosystems. p 184. Springs-Verlag. New York.

Sims, H.J. 1963. Changes in the hay production and the harvest index of Autralian oat varieties. Aust. J. Exp. Agric. Anim. Husb. 3: 198-202.

Singh. I.D. and N.C. Stoskopf. 1971. Harvest index in cereals. Agr. J. 63: 224-226.

Syme, J.R. 1970. A high-yielding Mexican semi-dwarf wheat and the relationship of yield to harvest index and other varietal characteristics. Aust. J. Expt. Agric. Anim. Husb. 10: 350-353.

Tanaka, A., K. Kawano, and J. Yamaguchi. 1967. Photosynthesis, respiration, and plant type of the tropical rice plant. Int. Rice. Res. Inst. Tech. Bull. No. 7.

Yamaguchi, Junichi. 1974. Varietal traits limiting the grain yield of tropical maize. IV. Plant traits and productivity of tropical varieties. Soil Sci. Plt. Nutr. 20: 287-304.

TABLE 1. RELATIONSHIP OF HARVEST INDEX (A) AND TOTAL PLANT WEIGHT (B) WITH RICE GRAIN YIELD (Y) UNDER DIVERSE ENVIRONMENTAL CONDITIONS. 1/

Average yield of experiment (ton/ha)	r_{YA}	V_A/V_Y	r_{YB}	V_B/V_Y
5.26	0.222	0.381	0.886**	0.997
7.44	0.177	0.414	0.886**	1.065
7.82	0.723**	0.693	0.682**	0.690
8.03	0.591**	0.684	0.536**	0.843
8.14	0.288	0.568	0.574**	0.969
8.14	0.534**	0.672	0.230	0.813
8.81	0.893**	0.911	0.074	0.457
9.13	0.820**	0.673	0.240*	0.386
9.18	0.764**	0.971	0.236	0.810
9.28	0.744**	0.651	0.096	0.567
9.59	0.657**	1.182	0.078	0.727

r : Correlation coefficient

$V/_V$: Relative size of variance of harvest index or total plant weight to that of yield (variables are converted into logarithmic scale).

1/ Data from 11 varietal yield trials conducted in northern coast of Peru. Variation in yield level was caused by differences in nitrogen application and plant spacing. The general yield level was high because of the extremely high productivity of Peruvian north coast but the relative yield comparison may be valid.

TABLE 2. RELATIONSHIP OF HARVEST INDEX (A) AND TOTAL PLANT WEIGHT (B) WITH CASSAVA ROOT YIELD (Y) UNDER DIVERSE ENVIRONMENTAL CONDITIONS*.

Location	Average yield of experiment (ton/ha)	r_{YA}	V_A/V_Y	r_{YB}	V_B/V_Y
Carimagua	4.9	0.813**	0.615	0.840**	0.530
Carimagua	15.3	0.691**	0.406	0.932**	0.748
Carimagua	19.1	0.773**	0.640	0.889**	0.712
Caribia	24.1	0.582**	0.710	0.789**	0.738
Caribia	27.3	0.852**	0.690	0.807**	0.436
Caribia	29.8	0.711**	0.499	0.821**	0.760
CIAT	26.3	0.840**	0.956	0.242	0.042
CIAT	27.8	0.817**	0.907	0.409	0.321
CIAT	28.6	0.918**	1.040	0.542	0.254
CIAT	30.4	0.763**	0.823	0.551**	0.476
CIAT	37.2	0.668**	0.708	0.767**	0.670
CIAT	42.1	0.776**	0.767	0.525*	0.404

r : Correlation coefficient

$V/_V$: Relative size of variance of harvest index or total plant weight to that of yield (variables are converted into logarithmic scale).

*Data from replicated yield trials in three years at three locations.

TABLE 3. YIELDS OF VARIOUS CROPS WITHIN AND OUTSIDE THEIR CENTERS OF ORIGIN.

(Data extracted from the FAO Production Yearbook, 1977).

Crop	Center of origin	Area planted in center of origin (1000 ha)	Yield in center of origin (ton/ha)	Area planted outside center of origin (1000 ha)	Yield outside center of origin (ton/ha)
Wheat	West Asia	26,966	1.41	209,605	1.82 (129) 1/
Rice	South Asia	84,199	1.85	58,909	3.31 (179)
Maize	Mexico through Andean region of Latin America	10,241	1.22	106,662	3.02 (248)
Barley	West Asia	6,592	1.33	87,383	2.05 (154)
Sorghum	North east Africa	5,841	0.70	45,894	1.33 (190)
Potato	Andean region of Latin America	615	8.20	17,869	14.41 (176)
Cassava	Northern South America	306	8.48	12,216	9.01 (106)
Groundnut	South east South America	124	0.94	17,872	0.96 (104)
Soybean	China	14,236	0.87	30,388	1.67 (192)
Field bean	Andean region of Latin America	6,079	0.50	21,821	0.60 (120)
Cow pea	Africa	5,035	0.20	135	0.70 (350)
Sugarcane	South Asia	4,923	47.62	7,784	58.74 (123)
Banana	South Asia	846	11.37	2,069	13.23 (116)
Coffee	North east Africa	656	0.27	7,266	0.48 (178)

1/ Yield outside the center of origin as a percentage of that within.

TABLE 4. CASSAVA ROOT YIELDS OF CIAT LINES AND TRADITIONAL CULTIVARS ON EXPERIMENT STATION AND FARMERS IN THE CAUCA VALLEY OF COLOMBIA (HIGH YIELD ENVIRONMENT).

	On experiment station (CIAT-Palmira, 8 season average)	On farms (Caicedonia, 5 year average)
Root yield of CIAT lines[1/] (ton/ha)	45.3	32.2
Root yield of traditional cultivars (ton/ha)	25.5	29.3
Agronomic description of cultural environment	Fertile soil Favorable rain fall Good land preparation Good preparation of planting stakes Good weeding No fertilizer application No irrigation No chemical application	The same on the experiment station

1/ CIAT line ..... Genotype selected or developed by the CIAT cassava program

Yield ..... Average of upper 50% of all the CIAT lines tested.

Data source ..... Agronomy and varietal improvement sections, CIAT cassava program (CIAT, 1975, 1976, 1977, 1978, 1979, Kawano *et al*, 1978).

TABLE 5. CASSAVA ROOT YIELDS OF CIAT LINES AND TRADITIONAL CULTIVARS ON EXPERIMENT STATION AND FARMS ON THE NORTHERN COAST OF COLOMBIA (LOW TO MEDIUM YIELD ENVIRONMENT).

	On experiment station (ICA-Caribia, 7 season average)	On farms fields with improved cultural practice (9 trial average)	On farms without improved cultural practice
Root yield of CIAT lines 1/ (ton/ha)	32.2	17.6	7.3
Root yield of traditional cultivars (ton/ha)	22.9	11.6	8.4
Agronomic description of cultural environment	Medium fertile soil Long dry season Good land preparation Good preparation of planting stakes. Good weeding No fertilizer application No irrigation No chemical application	Poor to medium soils Long dry season Good land preparation Good preparation of planting stakes. Good weeding No fertilizer application No irrigation No chemical application	Poor to medium soil Long dry season Poor or no land preparation Poor preparation of planting stakes. Poor or no weeding No fertilizer application No irrigation No chemical application

1/ CIAT line ..... Genotype selected or developed by the CIAT cassava program

Yield ..... Average of upper 50% of all the CIAT lines tested.

Data source ..... Agronomy, Economics, and Varietal improvement sections, CIAT Cassava program (CIAT, 1975, 1976, 1977, 1978, 1979, 1980, Kawano *et al* 1978).

TABLE 6. CASSAVA ROOT YIELDS OF CIAT LINES AND TRADITIONAL CULTIVARS UNDER HIGH AND MEDIUM INPUT TECHNOLOGIES ON AN EXPERIMENT STATION IN THE LLANOS OF COLOMBIA (LOW YIELD ENVIRONMENT).

	With high input technology (2 year average)	With medium input technology (11 trial average)
Root yield of CIAT lines[1/] (ton/ha)	35.2	20.2
Root yield of traditional cultivars (ton/ha)	15.6	14.7
Agronomic description of cultural environment	Infertile acid soil 4 months dry season Good land preparation Good preparation of planting stakes Good weeding 2 ton/ha of lime applied 1 ton/ha of 10-20-20 applied Frequent irrigation No fungicide and pesticide applied	Infertile acid soil 4 months dry season Good land preparation Good preparation of planting stakes Good weeding 0.5 ton/ha of lime applied 1 ton/ha of 10-20-20 applied No irrigation No fungicide and pesticide applied

1/ CIAT line ..... Genotype selected or developed by the CIAT cassava program.

Yield ..... Average of upper 50% of all the CIAT lines tested.

Data source ..... Agronomy, Soil Science, and Varietal Improvement sections, CIAT Cassava program (CIAT, 1975, 1976, 1977, 1978, 1979, Kawano *et al* 1978).

TABLE 7. SCHEMATIC DESCRIPTION OF DEGREE OF DIFFICULTY IN TROPICAL CROP BREEDING.

	Breeding is	
Factor related to breeding work	Less difficult	More difficult
Productivity level of environment	High	Low
Level of cultural practice	High	Low
Center of origin	Outside	Inside
History of production	Short	Long
Kind of crop (complexity of physiological yield factor)	Root/tuber crop	Legume grain crop
Kind of crop (mode of propagation)	Vegetative	Outcrossing
Kind of crop (possibility of further improvement)	Harvest index being yield limiting factor	Total biological yield being yield limiting factor.
Kind of crop (complexity of pest interactions).	Evergreen perennial with vegetative propagation	Annual with sexual propagation.
Kind of crop (Ease of cultivar replacement)	Seed propagation	Vegetative propagation.

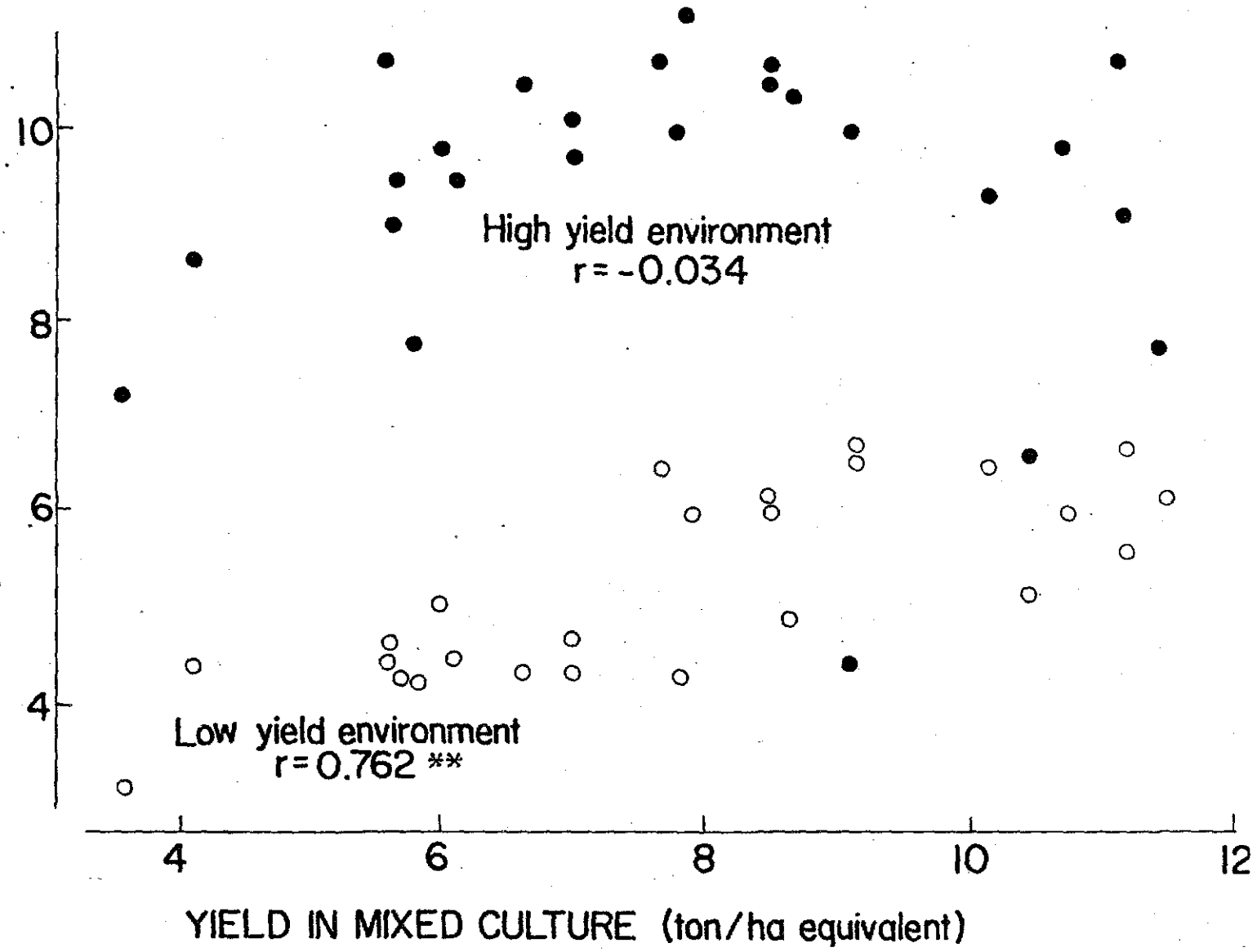

FIG. 1. Relationship between grain yield in mixed culture and that in monoculture (under high and low yield environments) of the same rice genotype.

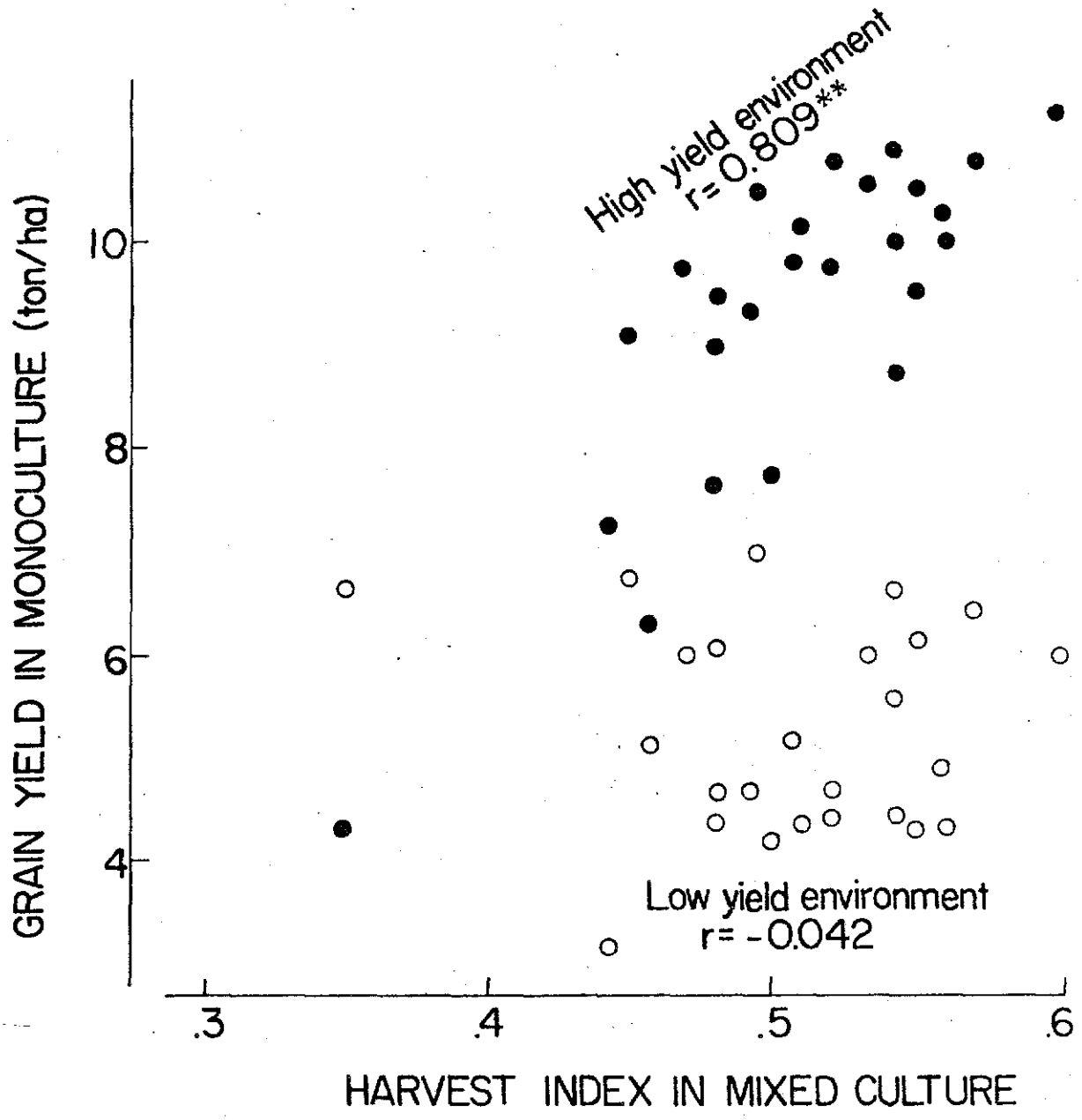

FIG. 2. Relationship between harvest index in mixed culture and grain yield in monoculture (under high and low yield environments) of the same rice genotype.

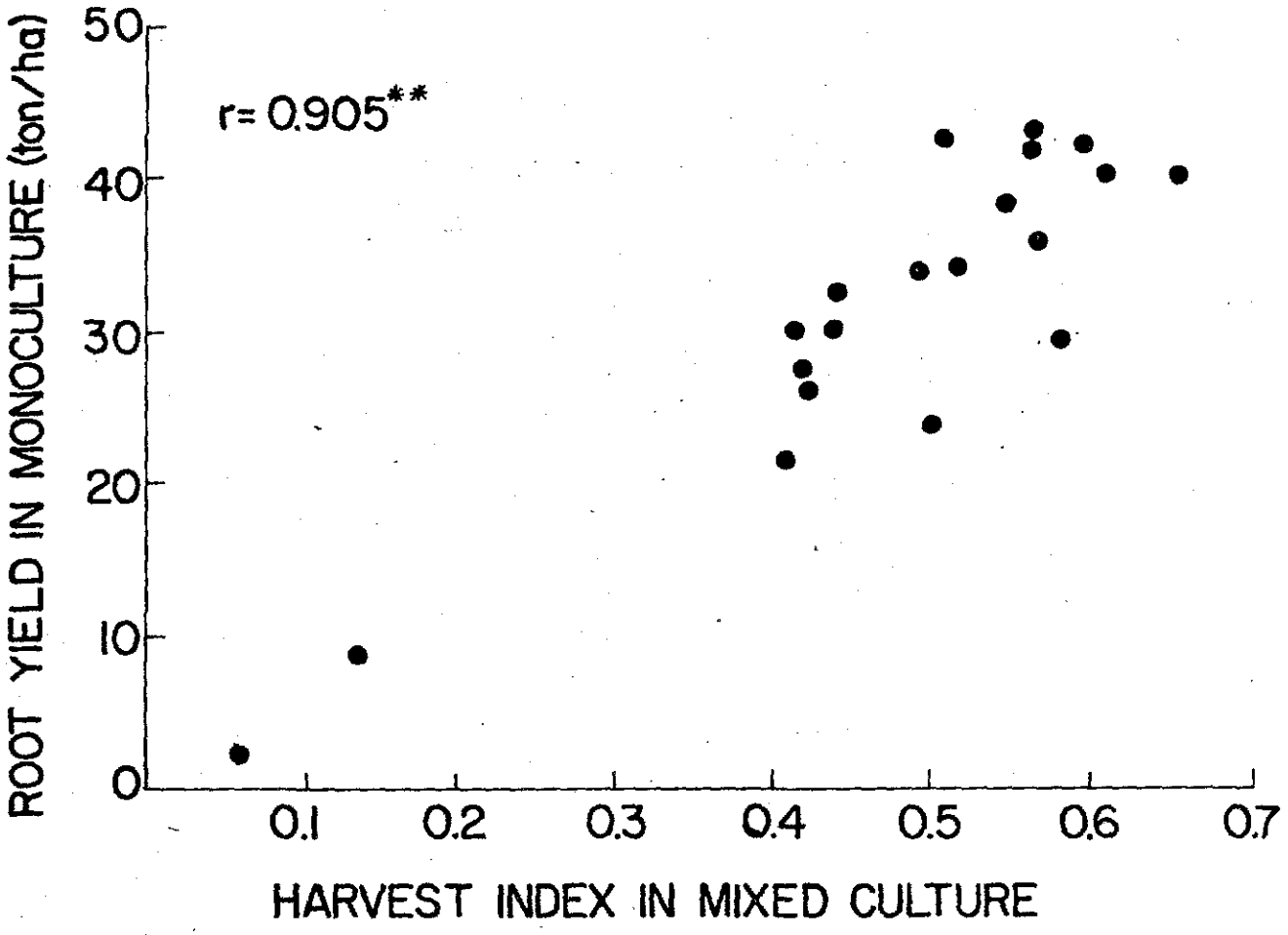

FIG. 3. Relationship between harvest index in mixed culture and root yield in monoculture of the same cassava genotype.

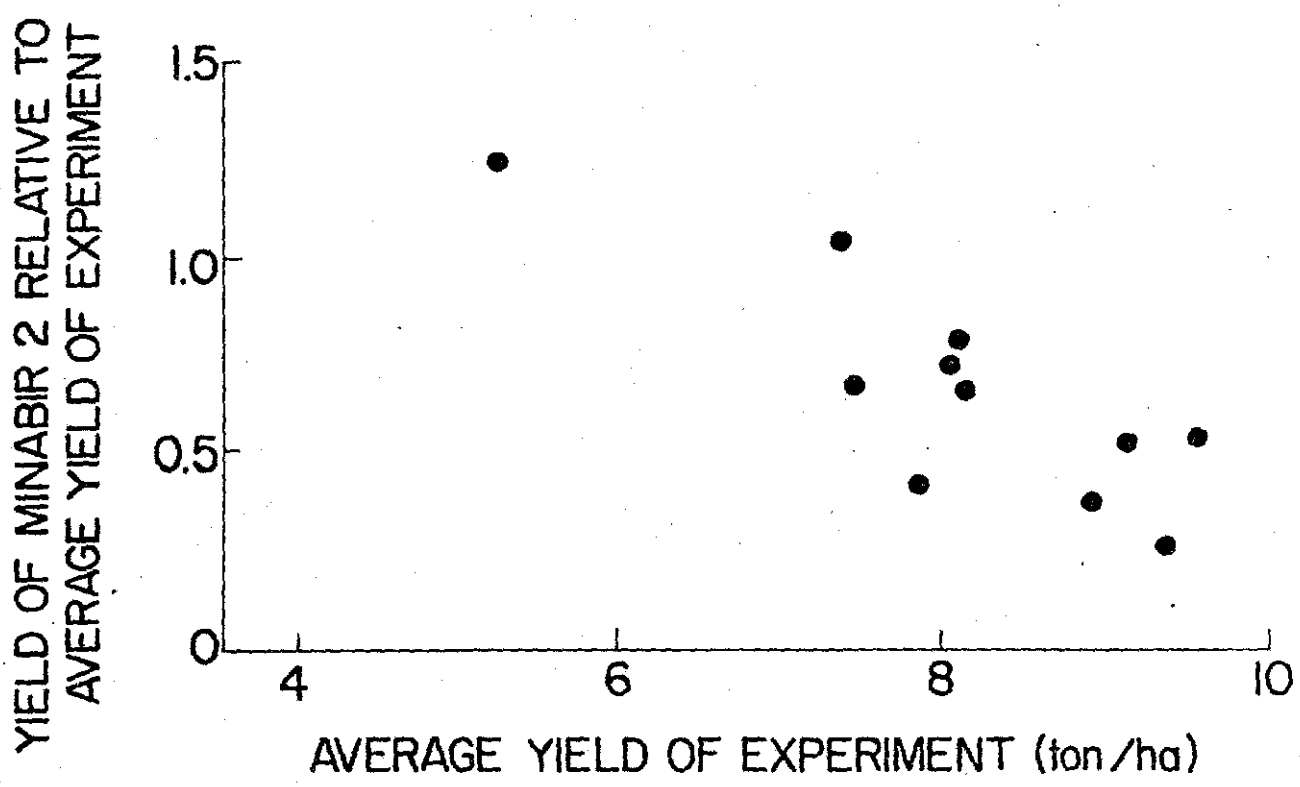

FIG. 4. Relationship between yield level of cultural environment and relative yield of traditional cultivar in rice.