THE BREEDING OF CACAO (*Theobroma cacao* L.)

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Introduction

Cacao is native to extensive areas of the humid lowlands of Tropical America. Wild populations have been reported in the headwaters of the tributaries of the Amazon and Orinoco rivers (Pound 1938, 1943; Baker *et al* 1953; Soria 1970). A high variability of fruit and seed characteristics has been reported among the populations. Each river and geographic region has a central type of fruit with a wide range of variability of shape and size. 'Amelonado' shape is the most common type all over the natural range; 'Calabacillos' are more restricted to the Orinoco, Guianas and northern part of Brazil, while cylindrical shapes with pointed and mammilar ends are more frequent in the southern tributaries of the Amazon. Along the tributaries of the foothills of the Andes there are several mixtures of types, with prevalence of globose 'Amelonados', like the 'Nacional' types and in some areas typical 'Cundeamor' and 'Angoleta' shapes, resembling 'Criollos'. The latest Ecuadorean expeditions to the Napo and San Miguel river systems reported a high frequency of near 'Criollo' types with large white seeds amongst many other fruit shapes (Soria 1970). This is the area considered (Cheesman 1944) as the center of diversity for cacao.

Cuatrecasas (1964), in his last review of the genus Theobroma, recognizes cacao as a single species with two subspecies: (a) *Theobroma cacao* L. subsp. *cacao,* which includes most of the cultivated varieties and forms, such as typical 'Criollo', 'Amelonado', 'Pentagona' and 'Trinitarios'; and (b) *Theobroma cacao* subsp. *sphaerocarpa,* which includes the 'Calabacillo' types. This classification is based mainly on the morphology of the fruit, but from the genetic point of view it is not fully justified. The more fertile and highest yielding hybrids obtained in the breeding programs come from crosses between genotypes of supposedly different subspecies. Apparently there are no barriers for exchange of genes between the subspecific groups and shapes only do not justify subspecific status, as they are controlled by independent pairs of genes. Chromosome number in cacao is 2n - 20 (Muñoz 1948).

Most of the main cacao research stations in the world have breeding programs aiming at the improvement of production, of disease and pest resistance and quality. Two main methods have been used for breeding: individual tree selection to obtain clones for vegetative propagation and selection of sexual families with or without controlled pollination.

Variability and genetics of the most important characteristics

A review of the information on the variability and genetics of the main characteristics of cacao (Soria 1975) indicated that most of the characteristics had a wide range of genetic variability. However, there was scarce information on their mechanisms of inheritance. The majority of the pigmentation characters, like of fruits, seeds and flushes seem to be controlled by single major genes and modifiers. Sizes, weights and production of fruits and beans are of quantitative inheritance.

Yield and yield components The main objective of cacao breeding is to increase yields. Yield is a very variable character, made up of several components of quantitative nature and highly influenced by environment.

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The variability of the main yield components was studied by Pound (1932-33, 1934) and several other workers (Glendinning 1963; Esquivel and Soria 1967; Bartley 1969).

The most important yield components are: number of fruits per tree, number of beans per fruit, wet or dry bean weight per fruit and per tree, and weight of individual beans.

Glendinning (1963) found a very high correlation between the number of fruits produced and the total wet weight of their seeds, indicating that in some populations the number of fruits is a good estimate of yield. However, others (Pound 1932-33; Bartley 1965; Esquivel and Soria 1967) suggest that production is better estimated by wet bean weight.

Bartley (1964) indicated that yield heritability of wet bean weight measured by the variation within crosses as compared with that within clones was very low. On the other hand, Atanda and Toxopeus (1971) in Nigeria, analyzing pod yield records of local x Trinitario hybrids for 19 years found that 89.8% of the total variance was due to the influence of progenies, which they consider as a relative measure of heritability. Later, Atanda (1972) using 10-year records of a progeny trial reported that 61.5% of the total variance was due to progeny effect.

Soria *et al* (1974), using individual tree bean wet weight records of 48 F_1 hybrids, representing top crosses of six Trinitario and two Criollo clones, crossed to six Amazon clones, studied the general combining ability and heritability of yield and its components. Heritability estimated by the ratio of additive genetic variance to the total phenotypic variance for wet bean production from 3-year records was 17.3%, but became 89% when based on one season's production. Heritability for number of beans per fruit calculated with one-season records was 43%.

Amazon clones P-7, P-12 and IMC-67 had a high general combining ability, while SCA-6 and several other Trinitario clones had medium to low general combining abilities for yield. The high combining ability of some clones seems to depend on their high contribution of additive genetic variance to their progenies. These clones can be recommended as more reliable sources of hybrid seed production.

Incompatibilities Among the important features to be considered in the breeding of cacao is its mechanism of self-incompatibility. Knight and Rogers (1955) were the first to describe five S alleles of incompatibility in cacao, proposing that its inheritance followed the sporophytic model, with dominance in the series. Afterwards, Cope (1962) showed that even though the sporophytic action model proposed by Knight and Rogers satisfactorily explained the inheritance in the majority of the incompatibility cases, it did not explain several exceptions. He accepted the existence of the proposed alleles and added one, and the presence on the dominant stage of two complementary pairs (A/-, B/-) independent of the incompatibility alleles was needed to produce the substrate over which the genes of the S incompatibility series can act. When one or or both complementary gene pairs are in the recessive stage, the substrate is not produced and all the S genotypes would act as self-compatible. The series of S alleles in its dominance order would be:

$$S_0 = S_1 > S_2 = S_3 > S_4, S_5 > S_6$$

Lockwood (1976) has pointed out the consequences and the dangers for the use in commercial plantings of hybrids with self-incompatility alleles that could promote a high frequency of cross-incompatible plants. For this reason, the genotypes of the parents should be known for released hybrids.

Heterosis Several authors (Russell 1952; Soria 1964; Atanda 1972) have reported data showing the outstanding hybrid vigor for yield and other characteristics of cacao in crosses between cultivars of different genetic origin. The frequent occurrence of this phenomenon in breeding programs has provided high yielding progenies in most of the Cacao Research Stations around the world.

Breeding

The main objectives of breeding have been: improvement of yield, disease and pest resistance or tolerance, and quality.

Two main methods have been used to breed cacao: a) individual tree selection, with vegetative propagation of the selected trees, and b) production of sexual families, by open- or hand -pollination.

Individual tree selection The basic methodology for selection of cacao clones for yield was developed in Trinidad (Pound 1933: Cheesman and Pound 1934). The so-called 'pod value', i.e. the number of pods needed to make one pound of dry cacao, and 'seed index', the average dry weight per seed, were considered the main pod constants for selection of individual trees. The limits of selection in Trinitario populations were: trees producing 50–100 pods per year, with up to 7.5 of 'pod value' and from 1.5 to 1.8g of 'seed index'. In the majority of 'Forastero' types, the limits were: production of 100 to 200 fruits per year, 'pod value' of 10 to 12 and 'seed index' from 1 to 1.2g (Pound 1932).

Between the 40s and 50s, following the Trinidad methodology and adjusting the 'pod value' and 'seed index' limits to the local variability of the cacao population, three selections were made in the main research centers of Tropical America. Many clones have been selected also for resistance to specific diseases and yields. There are large collections of high yielding clones in Trinidad, Ecuador, Brazil, Costa Rica, Venezuela, Mexico, Colombia and Guatemala.

In spite of the high yield performance in trials of many clones, farmers in Tropical America have not adopted them for new planting or replanting schemes because of the higher initial costs for propagation and more specialized handling required for vegetatively propagated cultivars than for seedling progenies.

In most of the Cocoa Research Centers of West Africa, clones have been selected for use mainly as parents of improved progenies. Many of the clones of Ghana, Nigeria, Sierra Leone and the Ivory Coast, were selected from progenies of the F_1 crosses of Amazon clones introduced from Trinidad, in 1944, to WACRI, Tafo, Ghana (Rogers 1955). Also selections have been made in local 'Amelonado' and 'Trinitario' populations to be used as parents of breeding programs.

In Cameroun and Madagascar (Braudeau 1969), clones have been selected in 'Trinitario' and 'Criollo' populations for use in plantings by vegetative propagation.

Sexual families

1. F_2, F_3 open-pollinated progenies of Amazon crosses

Because of the lack of acceptance by farmers, of clonal material for new plantings, cacao breeders started in the late 40s to shift the emphasis of research from clonal to sexual progeny selection. This was started in West Africa with the introduction to Ghana, in 1944, of ten F_1 families of Amazon clones crosses (T.60 = Pa-7 x Na-32; T.63 = Pa-35 x Na-32; T.65 = Pa-7 x IMC-47; T.72 = Na-32 x IMC-60; T.73 = Na-33 x IMC-60; T.76 = Pa-35 x Na-31; T.79= Na-32 x Pa-7; T.82 = Na-32 x Pa-35; T.85 = IMC-60 x Na-34; T.87 = IMC-60 x Na-34). The progenies of these selections showed very good yields and more precocity and tolerance to swollen shoot than West African 'Amelonado' cacao in Ghana and Nigeria, leading to the release of F_2 and F_3 progenies (Rogers 1955) to farmers.

In the Ivory Coast, breeding was started in 1965 with the introduction of several WACRI families coming from F_1 crosses of Amazon clones. The best F_2 families were selected for distribution to farmers (Braudeau 1969).

2. F_1 progenies of selected clonal crosses

In an effort to combine the witches' broom resistance of the small seeded clones SCA-6 and SCA-12 with other susceptible high yielding and large seeded clones, the first F_1 crosses of SCA x ICS clones were tested in Trinidad at the beginning of the 50s (Montserrin and DeVerteuil 1957; Bartley 1958). The first reports indicated remarkable precocity and high yielding characteristics of the hybrids. These results stimulated in other countries of Tropical America (Ecuador, Costa Rica, Brazil, Venezuela) research for the production of high yielding F_1 hybrids between clones resistant to some diseases with other clones having agronomically desirable characteristics. Many F_1 hybrids are now distributed for new planting or replanting programs in the Tropical American countries.

The main basis of selection of the crosses to be tested has been a different genetic origin of parental clones and desirable agronomic characteristics without previous evaluation of the combining 'abilities' of the parents and the heritabilities of yield and yield components. Luckily, hybrid vigor and high yields were a common phenomenon in crosses between parents of different genetic origin.

Breeding experiments carried out in Ghana with F_1 crosses between Amazon x Amazon, Amazon x Amelonado, and Amazon x Trinitario clones, reported better yields for Amazon x Amelonado than for Amazon x Trinitario hybrids (Glendinning 1967). However, doubts are expressed about the real advantages of the superiority of yield of the hybrids to Amelonado, due to patterns of yield and other factors (Lockwood 1974).

In the Ivory Coast (Besse 1975), 12 F_1 biclonal hybrids had been selected to be released to the farmers, primarily on the basis of their yield potential and commercial quality, including also some resistance to *P. palmivora.*

The potential of improving pod production above F_1 single crosses by double crosses has been reported in Nigeria (Atanda 1972). New data at Turrialba have shown that several three way crosses overyielded to single crosses. These reports suggest that three way and double crosses are potentially good methods to improve yields and for the incorporation of genetic resistances to pests and diseases.

Due to the narrow genetic basis in Ghana, Nigeria and Ivory Coast, efforts have been made in the last years to introduce a large amount of germplasm from different sources from Tropical America.

3. Genetic approach breeding

Top crosses and diallel crossing experiments have been planted in several stations (Bartley 1969; Soria *et al* 1974; Opeke and Jacob 1969) in recent years to select parents for high yielding hybrids. Few reports have been published of yield performances. Clones P-7, P-12 and IMC-67, showed high general combining ability in a topcross trial at La Lola, Costa Rica, testing several Amazon, Trinitario and Criollo clones. Clone SCA-6 showed less general good combining ability, while in Trinidad a higher combining ability was reported (Bartley 1968) for this clone over others, including P-12 and IMC-67. The high reproductive value of these clones is confirmed by the outstanding yields of their hybrids reported by many cacao stations. Thus, these clones can be used with more confidence in breeding programs and in the production of improved seeds for the farmers, as their additive genetic contributions for yield are high, resulting in a good performance, even in open-pollinated progenies. Some clones seem to have good specific combining abilities, which will be useful also for the production of certain hybrids.

As larger sizes of fruits and beans are among the most desirable components of yield, these attributes should be selected for, and should be more easily obtained in cacao breeding if their heritability is high. Economically it is more important to handle less fruits to achieve the same production, and with larger seeds the husk percentage is also reduced.

More efforts are needed to study the genetics of yield, yield components, disease and pest resistance, and quality, in order to achieve a sound and effective progress in cacao breeding.

Pure line breeding:

Reports from Trinidad (Bartley 1969) indicate that some S_1 inbred lines of several ICS clones, top-crossed to SCA-6, have shown very good yield performances, particularly S_1 of ICS-1, ICS-6, ICS-44, and ICS-70. Similar results have been reported from Brazil (Carletto *et al*-1975) with F_1 of S_1 inbred lines of local clones. These results indicate that good progress could be achieved by the use of inbreeding as a method of developing homozygous superior parents. This method is applicable only with self-compatible clones and in order to look for more uniform F_1 crosses.

Haploid breeding:

Several cacao haploid plants had been obtained in Ivory Coast (Dubin 1974) from polyembryonic seeds leading to the possibility of the obtention of homozygous lines after duplication of chromosones by colchicine. This method, applied to clones of high general combining abilities, will lead to the production of high yielding uniform hybrids or homozygous hybrids for resistance to pests and diseases.

4. Disease Resistance

Worldwide, the most important disease is 'black pod' caused by *Phytophthora palmivora.* Many clones resistant to local strains of the pathogen have been reported in several countries (Soria 1975). Studies in Ghana (Amponsah 1969) and in Costa Rica (Soria and Esquivel 1968) have suggested quantitative inheritance, with some dominance of resistance of the possible mechanism of inheritance. F_1 hybrids of crosses between resistant (R) x resistant (R) have higher levels of resistance than crosses between resistant x susceptible (intermediate) and than susceptible x susceptible.

Ceratocystis fimbriata:

Wilt is a serious disease in several areas of Tropical America. Several resistant clones to this disease have been found (Delgado and Echandi, 1965; Espinosa 1970) and on the basis of the reaction of all combination progenies of resistant and susceptible clones it has been suggested that the resistance is controlled by recessive genes (Soria and Salazar 1965). For *Ceratocystis* areas, hybrids with at least one resistant parent are recommended.

Initial resistance was reported on the clone SCA-6 for *Crinipellis perniciosus* (witches broom), but recently reports from Trinidad and Ecuador have indicated that the SCA clones lost their resistance (Chalmers 1972). No new sources of resistance have been reported again. Studies carried out with swollen shoot virus in West Africa have not detected immune clones to the disease. They have indicated that several high Amazon clones, particularly the Iquitos group, transmit some resistance to their progenies (Lockwood 1974, 1975).

Very little breeding has been reported for other diseases, mainly because of the lack of sources of resistances.

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Discussion

M. Iizuka, Japan: I would like to have your opinion about the following two points. 1. According to Dr. Cope, F. W. (1962) in Trinidad, self-incompatibility of cacao is higher in materials from the center of diversity than in those grown in peripheric areas. Do you observe the same phenomenon in your materials? 2. You mentioned in your presentation that resistance to *Ceratocystis* was associated with recessive genes. How many genes are concerned? In the case of the Japanese pear, recessive homozygotes showed resistance to *Alternaria Kikuchiana*.

Answer:

1. All the varieties cultivated in Africa and in tropical America have mainly self-incompatible genotypes. These varieties apparently represent populations extracted from the borders of natural distribution of cacao where many recessives occur, as self-incompatibility. Self-incompatible types are common among the clones and seedlings obtained from Dr. Pound's

first and second expeditions to the Amazon basin to collect resistant types to witches' broom. The incompatibility alleles of cacao were identified in the material collected in the Amazon basin and the greatest frequency of different incompatibility genotypes has been reported to originate from areas near the centre of diversity as indicated by Dr. Cope. This fact could reinforce Dr. Chessman's proposal that the center of diversity is located in the area surrounded by the Nayo Caqueta and Orte guara rivers.

2. We do not know yet the number of recessive genes which control resistance to *Ceratocystis fimbriata.* In a paper which I published in 1965, I suggested that at least two pairs of genes were controlling the character, but I have not been able to produce decisive data to confirm this hypothesis.

J. T. Rao, India: What is the reason for the low percentage in fruit formation as compared with the number of flowers? Do the flowers drop off or do the fruit fall off when small, like in the case of mango?

Answer: Indeed, the percentage of fruit set is very low (2-5%). This seems to be related to a low population of pollinating insects as compared with the number of flowers. We have been able however to increase by ten times the fruit set by the use of hand pollination. However, the trees which have been heavily pollinated will escape flowering in the next cropping season and in many cases they do not survive. This seems to be due to the low carbohydrate storage capacity of the cacao tree.

J. T. Carlos, Jr., The Philippines: Have you identified any genetic marker(s) to enable cacao breeders and seed producers to distinguish between hybrid and non-hybrid seedlings in the nursery?

Answer: Yes, when markers like white seeds and albino leaves are available, it is possible to make such a distinction. Criollo origin clones and Catongo from Brazil are white-seeded parents. Crosses with red or purple seeded parents should give purple or red-seeded seeds in the white seeded parent owing to pseudo-xenia effect. Any white-seed or albino leaf seedling is a self.

H. Fujimaki, Japan. Are there any differences in productivity among different morphological phenotypes of fruit size or fruit color?

Answer: It has been demonstrated that color of fruit has no effect on cacao productivity. High positive correlations have been reported for seed yield and number of fruit produced by tree. This is advantageous as regards yield of seed weight for trees with large sized fruit. Among the most important criteria for tree selection, one should mention the so-called "fruit index". Plants with a lower index (less fruit to make 1 kg. of dry seeds) are preferred mainly because of the larger size of the fruit.