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Chapter 27

Heterosis in a New Population

Data recently presented by Mangelsdorf and Smith (1949) indicate that corn was being grown in what is now southwestern United States and Mexico at least four thousand years ago. The corn grown in these prehistoric times was both a pod corn and a pop corn of relatively low yield capacity. Today in this same area an enormous variation exists. Direct derivatives of the ancient low yielding pod-pop type still can be found on a very limited scale in certain areas of Mexico, but these low yielding ancient corns now have been replaced largely by more vigorous and productive types.

Tremendous changes have been brought about in both type and yield capacity since ancient times. The modern varieties of Mexico have a yield capacity many times more than the ancient types. On the high plateau of Mexico a variety known as Chalqueño, whose pedigree in part can be traced back to an ancient pop corn, has yielded up to 125 bushels per acre. If the various evolutionary processes and the kinds of gene actions involved in the development of such high yielding varieties from the low yielding prehistoric types were known, we would certainly have a better understanding of the phenomenon of heterosis.

It is the purpose of this chapter to present, first, what seems to have been involved in the development of the modern, relatively high yielding varieties over a period of about four thousand years; and second, a discussion of the methods used and results obtained in the further improvement of some of the modern varieties in a short period of six years.

Perhaps the title might best have been "Heterosis in an Old Population" in the sense that the Mexican corns as a whole are much older than those in the United States. However, from the standpoint of modern corn breeding, it is a new population in that it involves new material on which to try the modern techniques of corn breeding developed in the United States. The successes and failures of standard techniques in this new population, together with certain modifications that are being tried, will be discussed.

HETEROSIS IN NATIVE OPEN-POLLINATED VARIETIES

The first obvious step in any breeding program in a new area is adequate testing of the varieties at hand. In the early years of the program, therefore, considerable time was devoted to a study and classification of the present-day varieties in Mexico (Wellhausen *et al.*, in collaboration with Mangelsdorf, 1951). Evidence presented in this report strongly indicates that many factors have been involved in the evolution of corn in Mexico, the most important of which are repeated here as follows:

1. Varieties in the ancient pod-pop corn type were probably at first chiefly brought about through mutation and by a partial release from the pressure of natural selection by man. There are four ancient races in Mexico which definitely trace back to a common parent. Where this common parent originated is still unknown. All have a sufficient number of different characters to warrant their classification as separate races, yet they all have a number of characters in common; namely, all are pop corns, two of the four are pod corns, all are early maturing, all have a low chromosome knob number, and all are relatively low in yield capacity compared to modern varietal standards. Since no record of the common ancestor is available, no direct comparisons can be made of the yield capacities of the ancient indigenous races as they exist today in Mexico and of their common ancestor. Judging from the Bat Cave material (Mangelsdorf and Smith, 1949) it is not at all unlikely that considerable increase in yield capacity was brought about through gene mutation alone.

2. It is distinctly evident from a study of the various collections that sometime during the history of the Mexican corns there was an influx of exotic types from countries to the south. As a result of the introgression of the ancient indigenous types into the exotic types, and vice versa, many new varieties and races came into existence.

3. Superimposed upon the above two evolutionary mechanisms was the introgression of teosinte germplasm. If Mangelsdorf and Reeves (1939) are right in their theory that teosinte originated as a cross between corn and Tripsacum, then this teosinte germplasm is largely Tripsacum germplasm. Practically all the modern more-productive types of corn contain some teosinte germplasm.

4. The fourth important factor in the evolution of corn in Mexico has been the geography of Mexico itself. Mexico is a mountainous country with many different climates and geographically isolated valleys. Corn is grown from sea-level up to 10,000 feet elevation under a wide range of rainfall conditions. In some areas rainfall is limited to five to ten inches for a period of four months. Other areas receive up to 100 or more inches in a period of six to ten

months. Different temperatures due to changes in elevation and different amounts of rainfall may occur in areas separated only by a few miles. Such conditions are conducive to the development of many different varieties of corn.

As a result of the above evolutionary factors operating over a period of at least four thousand years, there is a greater variation in the corns of Mexico today than in any country in the world. Without doubt the greatest single factor in the development of the modern high yielding agricultural types in Mexico has been the introduction of exotic types from the south. These exotic types were largely big-grained flour corns, which no doubt brought in a series of genes for higher yield that had not existed in Mexico before.

The various processes and types of gene action involved in the development of higher yielding varieties from the reciprocal introgression between the indigenous and exotic types, plus introgression of teosinte, are not easily explained.

Gene Combinations

These processes probably involved a gradual sifting of the gene combinations brought together by hybridization, and continuous backcrossing or re-hybridization of resulting hybrids or segregants. The complex pedigree of some of the modern high yielding varieties in Mexico, taken from Wellhausen *et al.* in collaboration with Mangelsdorf (1951), are shown in Figures 27.1–27.4. In these pedigrees each product of the indicated hybridization between two different races, or species in the case of teosinte, was higher yielding or better adapted to its native habitat than either one of the putative parents. For example, in Figure 27.1 Cónico is a better corn than either Palomero Toluqueño or Cacahuacintle, and Tuxpeño is a more productive corn than either Olotillo or Tepecintle. Chalqueño, which is somewhat more recent in the evolutionary scale, is more productive than either Cónico or Tuxpeño.

This does not necessarily mean that the same races crossed today would all show considerable heterosis in F_1. As a matter of fact many of the crosses indicated in the diagrams have been made and studied. In certain cases the F_1 hybrid, when tested in the environment best suited to one or both parents, showed considerable heterosis. In other cases it was no better than the better parent or was intermediate between the two parents. In some crosses the F_1 was definitely unadapted to the environment of either parent.

In the natural development of higher yielding corns from the intercrossing of different races, there were no doubt many instances in which the F_1 hybrids that first occurred between a native and an introduced variety were very poorly adapted to native conditions and showed no heterosis. A 50 per cent random dosage of an introduced variety is often more than sufficient to completely upset the physiology of a native variety that has adapted itself to a fixed environment over a long period of natural selection. Under natural conditions, however, any crossing that might take place between two varieties is purely at random and not complete. Hybrid plants that appear in a field of native corn in the succeeding generation, therefore, might be widely scattered. But no matter how little seed these F_1 plants may produce, if their flowering periods coincide, then germplasm would be passed on to the native variety through backcrosses.

Thus by repeated backcrossing and the sifting action that always takes place through natural and artificial selection, certain genes from an introduced population may be readily transferred to a native population. These might be additional favorable yield genes that express themselves in the native gene complex, or they might be other genes which permit the fuller expression of the yield genes which the native variety already contains, or both.

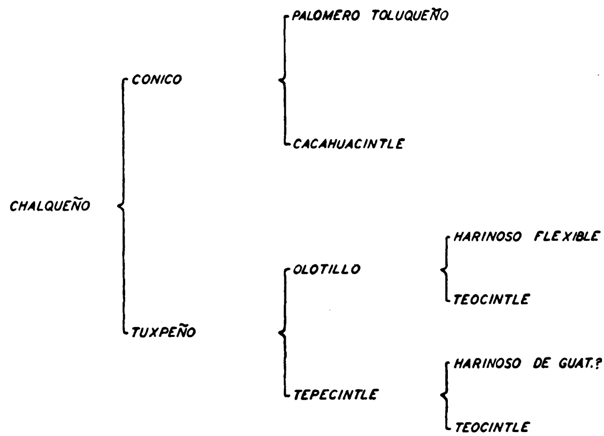

FIG. 27.1—Probable origin of Chalqueño.

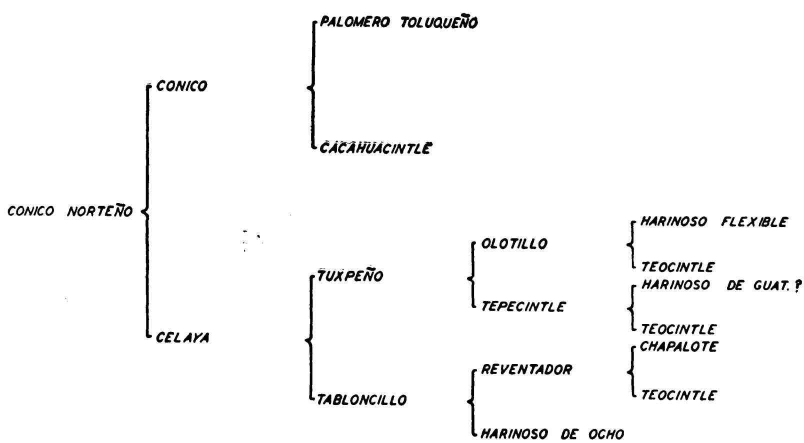

FIG. 27.2—Probable origin of Cónico Norteño.

A classical example of such introgression is the introgression of genes from teosinte into corn, a process which is still taking place in many areas of Mexico. Teosinte grows as a weed in the corn fields of certain areas. Also the Mexican farmers in some areas have been known to plant teosinte in their corn fields based on a belief that such a practice would make their native corns more drought resistant. The F_1 hybrids between corn and teosinte are very small-eared, and ears are difficult to collect because of their very brittle rachis. As such, the F_1's have no value in artificial selection. However, the F_1's shed pollen about the same time as the native corn variety, and a large number of backcrosses result with the corn parent as the female. Some of these are unconsciously selected as seed for the following year since they cannot be

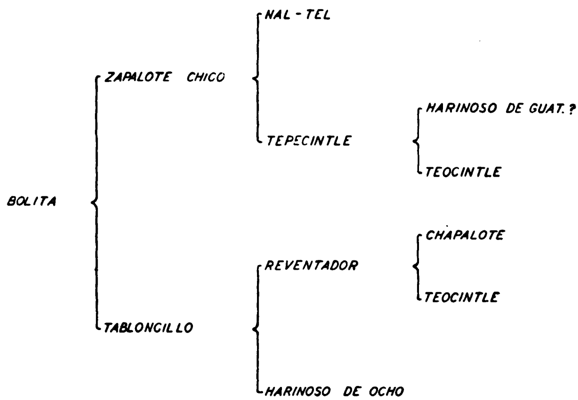

FIG. 27.3—Probable origin of Bolita.

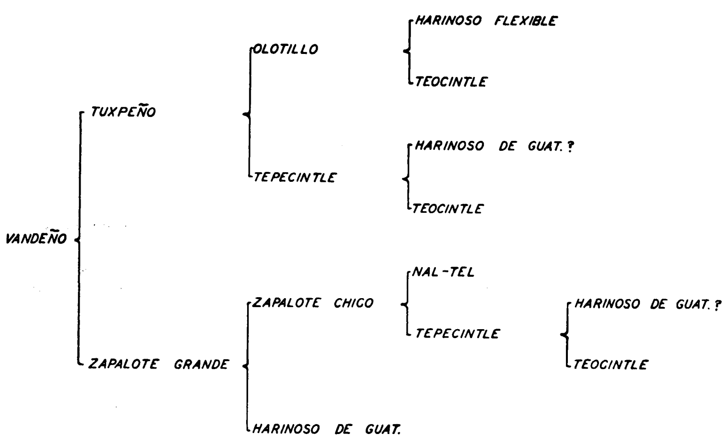

FIG. 27.4—Probable origin of Vandeño.

separated at time of harvest from the non-hybrid grains. These backcrosses then, bring about a second generation of backcrosses.

Through this sifting action certain genes from teosinte, such as those that condition greater drought resistance when in combination with the native corn gene-complex, become fairly well established. In a dry area any genes bringing about greater drought resistance would immediately affect the yield, and gene frequency for such characters would increase in the population through subsequent natural and artificial selection. Thus a new, improved higher yielding population under dry conditions may be brought about which will replace all other populations in its range of best adaptation. It must have been in this way that the old superstition of a greater protection from drought by interplanting corn with teosinte arose. How many other factors of survival value were obtained from teosinte is difficult to ascertain.

This is probably the most common manner in which higher yielding varieties for specific areas, especially the old corn areas, were built up. However, as old land wore out, new methods of corn cultivation and new areas in which corn could be produced were constantly sought. New environments for corn production thus came into existence throughout the years. These new environments often consisted of the artificial or natural drainage of old lake beds which brought into cultivation highly fertile areas with high water-holding capacity. In such areas, due to reserve moisture in the soil from the previous rainy season, corn could be planted as much as two months ahead of the beginning of the normal rainy season. This provided a six or eight month growing season instead of the usual four to six months. It was in such new environments, where plants could develop and fully express their yield capacity, that certain F_1 hybrids presented a much higher degree of heterosis and adaptation than in the native habitat of either one of their immediate parents.

Hybridization

Perhaps the outstanding example of a highly productive hybrid race that has developed in a relatively new environment in the central high plateau of Mexico is a late maturing race called Chalqueño. This race (Fig. 27.1) probably came into existence through the hybridization of the two distinct races, Cónico and Tuxpeño. Cónico is an early maturing corn that originated on the high plateaus of Central Mexico from the hybridization of an ancient indigenous high altitude pop corn called Palomero Toluqueño and an exotic race called Cacahuacintle. Tuxpeño, the other parent of Chalqueño, is a cylindrical dent adapted to the lowland coastal areas of Mexico. It probably came into existence through the intercrossing of two prehistoric races, Olotillo and Tepecintle, which in turn probably were derived from two different exotic flour corns through the introgression of teosinte.

Chalqueño, in the areas where it is grown today, is much more productive than either of its putative parents Cónico and Tuxpeño. In the highland regions to which Cónico is best adapted, neither Chalqueño nor Tuxpeño will mature, and in addition Tuxpeño is very heavily attacked by rust. On the other hand, in the lowland areas where Tuxpeño is best adapted, Chalqueño produces very little and Cónico produces practically nothing. A similar relationship has held with an artificial cross between Cónico and Tuxpeño in which half the germplasm was from one parent and half from the other. The artificial hybrid, as one might expect, was not as well adapted to the Chalqueño area as Chalqueño itself. Chalqueño over a period of many years of gene sifting no doubt concentrated those favorable growth genes best suited to its present environment and practically eliminated the frequency of other genes which were unnecessary or deleterious to its maximum development. The hybrid, nevertheless, was much superior to the two parents in the environment best suited to Chalqueño.

Here then is an example of the process which often happens in nature or in planned breeding programs. A hybrid between two parents adapted to widely different environments shows no hybrid vigor, as measured in yield, over either one of the two parents when grown in the native habitat of either parent. But in a new environment different from the one under which either parent developed, the hybrid may show extreme vigor. It is highly probable that many new varieties came into existence when new areas of land were brought under cultivation or when the native inhabitants migrated to new areas. Very often several different corns were brought together in these new environments which were not as well adapted as the hybrids that resulted between them. It is also highly probable that the first varietal hybrids were not as good on the whole as the varieties that developed from them through successive generations of backcrossing and gene sifting.

From a study of the origin and development of the various types of corn in Mexico, it seems that the most important factor in the evolution of the different productive races has been the gradual accumulation of favorable growth or yield genes in combination or balance with the proper "governing or regulating" genes in each specific environment. Maximum yield in a specific environment is not only dependent on favorable genes for such quantitative characters as ear and kernel size, number of ears, leaf area or photosynthetic efficiency, but also on genes which govern such functions as maturity, disease and drought resistance, or general adaptation.

The latter group might well be genes which some investigators have termed *bottleneck* genes. Such genes may inhibit the full expression of certain quantitative yield genes and thus prohibit the organism from reaching its maximum production allowed by a specific environment. An increase in yield capacity, therefore, often may not involve the accumulation of more favorable yield genes, but rather the removal of certain bottleneck genes. In new environments these bottleneck genes might be *relic* genes carried over from their old native habitat where they existed because they had survival value.

It would seem, therefore, that heterosis is the result of the combined effect of individual gene action (for growth) plus the interaction of all genes within the genotype (its genetic environment) in relation to the sum-total of all external influences acting upon the organism and governing expression of its gene complex. If heterosis in a cross between $A \times B$ is measured as the excess vigor or yield over the average of A and B, there may be no heterosis in the environment to which A or B is best adapted as shown with Chalqueño. Yet in some new environment different from that in which A and B developed, the excess vigor may be great, even exceeding that of A and B in their native environment, if such comparison could be made. Certainly the genotype is no different in any of the areas. The difference must be due to different interactions between over-all gene action and environment. It is no wonder that so many different ideas exist when it comes to the explanation of heterosis. It has no simple explanation.

IMPROVEMENT THROUGH BREEDING

In the evolution of corn in Mexico, the different varieties and races were brought together in a haphazard manner. Relatively few of the total combinations of races and varieties possible have been made, and when two varieties or races come together in a specific region by chance, there is no reason to believe that the particular combination was the best that could have been made for the area. Although some fairly productive varieties did develop, especially in the more fertile areas with higher rainfall, the possibilities of further over-all improvement are astonishing and offer a challenge to modern corn breeders.

The cooperative corn improvement program of the Mexican Government and the Rockefeller Foundation was begun about six years ago. Its objective was to provide higher yielding varieties or hybrids for the many different environments in the main corn producing areas. In most of Mexico, selection has been going on for many centuries for adaptation to low soil fertility and extreme climatic conditions. A variety or strain capable of producing something in the years of extreme drought or early frost was highly prized by the native Indians, even though it produced only a little more in good years. Low yields meant hunger, but a crop failure meant starvation. With modern means of transportation, crop failures in a region no longer mean starvation for the people of that region, and low fertility can and must be remedied before corn production can be greatly increased. The breeding program, therefore, was geared to the development of productive varieties or hybrids adapted to the average climatic conditions of a particular region, and a level of fertility that could permit maximum production under these average conditions. More productive varieties would pay the cost of soil improvement and pave the way for a generally higher level of corn production.

The program also is based on a gradual improvement year by year. As soon as a variety or hybrid was found to be superior to native varieties in a particular area, it was increased and distributed, although it still may have had many minor defects. When better varieties or hybrids become available, they are substituted for those previously released in the increase and distribution program.

The different steps involved in this gradual improvement program for any particular area have been as follows:

1. Variety testing. In this way good open-pollinated varieties were sometimes isolated for immediate distribution and as basic material for the breeding program to follow.

2. The improvement of the best native open-pollinated varieties through the formation of synthetics which could be propagated through open-pollination.

3. The formation and distribution of double cross hybrids which were good not only as double crosses but also as synthetics in advanced generations. For this purpose one generation selfed lines were used.

4. Finally, after many of the farmers have learned how to use hybrid corn, greater emphasis may be devoted to the formation of more specific, higher yielding uniform hybrids with highly selected and proven inbred lines.

Areas in Which Improvement Work Has Been Concentrated

The methods used and results obtained may be understood more clearly if the areas in which improvement programs were initiated are identified. Although corn is grown everywhere in Mexico, the most important commercial corn growing areas are found on the central plateau between 18 and 22 degrees latitude. It is within this area that the breeding work has been concentrated. To facilitate the work still further, the area was divided into five zones on the basis of elevation as follows:

Zone 1—2200–2600 meters elevation
- *a*) Late varieties with six months' growing season planted under irrigation
- *b*) Early varieties with four months' growing season under natural rainfall conditions

Zone 2—1800–2200 meters
Zone 3—1400–1800 meters
Zone 4—1000–1400 meters
Zone 5—0–1000 meters

The main breeding stations for these five zones are located in Zone 1 at 2200 meters, Zone 3 at 1600 meters, and Zone 4 at 1200 meters. With these three main stations and with the cooperation of farmers in making yield tests in outlying regions, it has been possible to cover the central plateau and certain tropical areas fairly completely.

Utilization of Good Native Open-pollinated Varieties

Since it is entirely possible that the original gene populations in the many different isolated valleys of a particular zone were not the same, one might expect to find a different variety in each valley as a result of natural and artificial selection. Often this was precisely the case. Out of 240 samples of corn collected in Zones 2 and 3 from areas with elevations ranging from 1400 to 2000 meters, and tested under conditions representative of these two zones, 15 varieties were outstanding. These consisted of three early, five medium, and seven late maturing varieties in relation to the normal growing or rainy season of the area in which tests were made. The best early varieties (Wellhausen, 1947) yielded from 15 to 49 per cent more than the average of 26 varieties of the same maturity. The best medium maturing varieties yielded from 30 to 54 per cent higher than the average of 57 varieties of medium maturity. The best late varieties yielded from 25 to 60 per cent more than the average of the 62 late varieties of similar maturity included in the tests.

A similar situation was found to exist in the valleys at higher elevations in the high plateau (Zone 1) among both the late and early varieties. A late variety commonly grown under irrigation in the fertile valleys of the State of Hidalgo was found to yield about 20 per cent more than a variety called Chalco widely used for irrigation plantings in the States of Mexico and Puebla (Wellhausen and Roberts, 1948). The best early varieties for Zone 1 were found in the State of Mexico, north of Mexico City, and these yielded from 15 to 20 per cent more than the average early varieties grown in Zone 1. On the whole, from 15 to 20 per cent increase in yield often could be obtained in some parts of all zones through the wider distribution of the best open-pollinated variety found within each zone.

Fundamental Methods in the Formation of Good Inbred Lines

Steps 2 to 4, as outlined above, imply the formation and use of inbred lines, and the degree of improvement one might expect depends upon the isolation of good, vigorous, disease-resistant lines that combine well with each other when used in synthetics or hybrids. In the formation of lines we have, in general, adhered to the following principles:

1. The use of diverse varieties adapted within a particular zone.
2. Rigid selection based on vigor and desirable agronomic characters.
3. Tests for combining ability after one generation of selfing.

Approximately 35 different varieties of corn belonging to eight different races have been inbred in the improvement program for central Mexico. These eight races are listed as follows in order of adaptation to elevation:

Race	Zone to Which Adapted
Cónico	1
Chalqueño	1
Cónico Norteño	2
Celaya	3 and 4
Bolita	3 and 4
Tabloncillo	3 and 4
Vandeño	4 and 5
Tuxpeño	5

All are races which have come into existence in more recent times and all have rather complex pedigrees as shown in Figures 27.1–27.4. So far only the outstanding varieties of each race have been inbred. It was concluded early in the breeding program that inbred lines for immediate use in a particular zone might best be obtained from the high yielding varieties adapted to that zone. It is entirely possible that in the future better hybrids may be obtained through the utilization of a wider base of germplasm. The latter procedure would require more time and more adequate testing. It would involve the extraction of the favorable yield factors from several races and their convergence into a synthetic variety or hybrid along with the proper *governing genes* for a given environment.

In the inbreeding program it has become apparent that vigor in the original plant or first generation selfed progeny (S_1) can be used to a considerable extent as a measure of the number of favorable yield genes with which the particular plant or line has been endowed. But vigor becomes less and less useful as an indicator of the number of yield genes in a particular line in the second, third, or fourth generations of inbreeding because of a greater number of bottleneck genes that are fixed with successive generations of inbreeding. In advanced inbred generations, two lines might be greatly different in vigor, yet equal in combining ability with a specific tester, because of similarities in their yield gene complex. As lines, they may be different in relative vigor because of certain different specific bottleneck genes or loci that mask the expression of genes or loci for growth and development.

The Mexican corn program not only involves the actual improvement of corn, but also the development and training of young corn breeders. In order to demonstrate more vividly that considerable effort may be saved by selecting only the best and most vigorous plants or lines for further work, several students visually classified the inbred lines available after one generation of selfing from five different varieties into four classes on basis of vigor. The most vigorous lines were classified as *A* lines. Those somewhat less vigorous or desirable were classified as *B*, and so on, with the least vigorous lines classified as *D*.

Although classifications were originally made into four categories, the *D* lines were discarded without further consideration. Of the remaining lines saved from each of the five different varieties, 3–6 per cent in each were classified as *A*, 12 to 15 per cent as *B*, and the remaining 79 to 85 per cent as *C*. All were topcrossed to a common tester, but only the topcrosses involving *A* and *B* lines were finally included in yield tests because of lack of space. Comparative yields of the *A* and *B* topcrosses are summarized in Tables 27.1–27.3.

Table 27.1 shows the results obtained with *A* and *B* lines from a variety known as Leon Criollo topcrossed on the variety Urquiza and tested at three locations. At each place the average yield of the topcrosses involving the *A* lines was slightly higher than those involving *B* lines. But what is more important, the percentage of lines increasing the yield over the tester parent was much higher among the *A* lines than among the *B* lines.

Table 27.2 shows the performance of *A* and *B* lines from Urquiza topcrossed on Leon Criollo when tested at two different locations. Again the average yield of the *A* topcrosses was higher than that of the *B* topcrosses, and the percentage of topcrossed lines yielding more than the tester was higher among the *A* lines than among the *B* lines.

The same thing was true in *A* and *B* lines obtained from three other varieties when topcrossed on Urquiza, as summarized in Table 27.3. These data definitely indicate that the probability of obtaining good general combiners

TABLE 27.1

COMPARATIVE YIELDS OF *A* AND *B* S_1 LINES OF LEON CRIOLLO IN TOPCROSSES WITH URQUIZA AT 3 LOCATIONS*

Location	Class	No. of Lines	Average Yield of Topcrosses in % of Check	Per Cent of Lines Increasing Yield 25% or More of Check
I........	*A*	31	116	32
	B	60	113	23
II........	*A*	33	122	39
	B	64	108	20
III.......	*A*	33	92	18
	B	45	90	14

* Variety Urquiza was used as check.

TABLE 27.2

COMPARATIVE YIELDS OF *A* AND *B* S_1 LINES OF URQUIZA IN TOPCROSSES WITH LEON CRIOLLO AT TWO LOCATIONS*

Location	Class	No. of Lines	Average Yield of Topcrosses in % of Check	Per Cent of Lines Increasing Yield of Check
I........	*A*	13	111	69
	B	33	97	40
II........	*A*	19	102	63
	B	56	90	28

* Leon Criollo was used as check.

as measured by the testers used, is higher among the more vigorous and agronomically better lines.

The experiment has been carried somewhat further. Inbreeding was continued in the various S_1 families originally classified as *A*, *B*, and *C*. After three generations of selfing, the advanced lines on hand were topcrossed on two different testers and the resulting topcrosses were tested for yield. On the basis of average topcross performance, certain of the advanced inbred lines were selected as worthy of keeping for further work. The number selected from each of several varieties together with their classification is given in Table 27.4.

TABLE 27.3

COMPARATIVE YIELDS OF *A* AND *B* S_1 LINES OF MICH. 21, PUE. 16, AND MEX. 39 IN TOPCROSSES WITH URQUIZA*

Variety	Class	No. of Lines	Average Yield of Topcrosses in % of Check	Per Cent of Lines Increasing Yield of Check
Mich. 21	*A*	21	110	76
	B	21	105	67
Pue. 16	*A*	22	85	9
	B	10	74	0
Mex. 39	*A*	11	101	55
	B	14	92	29

* Urquiza was used as check.

TABLE 27.4

NUMBER OF LINES SELECTED FROM FOUR VARIETIES ON BASIS OF TOPCROSS TESTS AFTER THREE GENERATIONS OF INBREEDING AND THEIR CLASSIFICATIONS IN S_1

Variety	No. of Original S_1 Lines Inbred	No. of S_3 Lines Selected	No. Originally Classified as *A* and *B* in S_1	
			A	*B*
Mich. 21	219	9	8	1
Mex. 39	131	2	1	1
Leon Criollo	218	5	4	1
Chalqueño	67	22	15	7

As pointed out before, in the first three varieties listed above, 3–6 per cent of the lines were classified as *A*, 12–15 per cent as *B*, and the rest were classified as *C*. In Chalqueño, the S_1 families were discarded more heavily and the 67 S_1 families selected for further inbreeding were classified as follows: 16*A*, 35*B*, and 13*C*. It is clearly evident that by far the majority of S_3 lines saved for further study after testing in topcrosses came from the S_1 families originally classified as *A*.

In the early stages of the program, about five hundred plants were inbred in each variety. At harvest, about two hundred, or 40 per cent, were selected for further work. The above data indicate that, as far as the varieties listed were concerned, the same results might have been obtained with a more drastic elimination of lines at the beginning of inbreeding.

Selection of testers for use in the isolation of good inbred lines is always a problem. In Mexico, chief concern in the early stages of the breeding program was the isolation of lines with good general combining ability. For this purpose the inbred lines in each zone were topcrossed on at least two different testers, usually unrelated adapted open-pollinated varieties. The good combiners, when selected on average topcross performance, often were disappointing when crossed inter se. In those zones where two varieties were available which, when crossed, produced a desirable hybrid agronomically, a reciprocal method of testing was used. With this method, inbreds from variety *A* were topcrossed on variety *B*, and inbreds of variety *B* were topcrossed on variety *A*. Good combiners thus isolated from variety *A* were crossed with good combiners from variety *B* to form single crosses and subsequently double crosses. This method of double cross formation was more efficient than the recombination of lines with so-called general combining ability from the above method. Where a good single cross of first generation inbred lines was available that could be used as a tester to isolate inbred lines which combine well with it, this cross proved more efficient than either of the above two methods in the formation of good double crosses.

Utilization of Semi-inbred Lines in Synthetics and Hybrids

Almost from the beginning of hybrid corn production, breeders have sought to discover methods of utilizing superior inbred strains in more or less permanent combinations. In a country such as Mexico, where the majority of the farmers will not readily adopt a practice of securing new hybrid seed for each planting, superior synthetic varieties would have real advantage.

As Sprague and Jenkins (1943) pointed out, four factors operate to determine the yield of advanced generations of hybrids: (1) the number of lines involved, (2) the mean yield of these lines, (3) the mean yield of all of their possible single crosses, and (4) the percentage of self pollination. Since maize is almost wholly cross-pollinated, the last factor may be largely ignored.

Which of the remaining three factors is the most important has not been determined to date.

Wright (1922) has shown that with random mating the vigor and productiveness of an F_2 is less than that of the F_1 by an amount equal to $1/n$th of the difference between the F_1 and the average of the parental lines where n is the number of parental lines involved. These theoretical conclusions of Wright are adequately supported by experimental data from maize (Neal, 1935; Kiesselbach, 1933; Wellhausen and Roberts, 1949).

In the past, in estimating the number of lines to use in a synthetic, apparently it was assumed that the F_1 mean in Wright's formula could be taken as a constant value regardless of the number of lines involved. If this assumption were correct, then the more lines involved the higher would be the yield of the resulting synthetic. In actual practice, however, synthetics with a large number of lines have yielded little more than the open-pollinated varieties adapted to the same area. As indicated by Kinman and Sprague (1945), the assumption of a constant mean yield for all F_1 combinations seems unwarranted. In any series in inbred lines, there are some that combine better than others, and it is much easier to obtain four inbred lines that yield well in all possible combinations than ten or sixteen. Therefore, to bring about the highest mean yield of all possible single crosses, the use of relatively few lines is indicated.

It can be shown by holding the F_1 yields as a constant that a better synthetic might be made with four more productive lines than with eight less productive. For example, assuming the mean yield of all single crosses involved to be 120 per cent, an F_2 of a synthetic involving four lines with a mean yield of 80 per cent will be 110 per cent, while a synthetic involving eight lines yielding only 30 per cent will yield 109 per cent in F_2. Kinman and Sprague (1945) concluded that in general the most efficient number of lines to be included in a synthetic will vary with the range in combining ability among the inbreds available as parents. However, on the basis of their study, four to six lines appeared to be the most efficient number, the smaller number being most efficient when more productive lines, yielding at least 75 per cent of open-pollinated variety, were involved.

Theoretically, therefore, the best synthetics would result from the use of four to six lines which are as productive as possible and which are good combiners inter se. Certain practical aspects also must be taken into consideration. If the inbred lines that are combined into a synthetic are greatly different in type and maturity, the resulting F_2 may be extremely variable for these two characters and may require considerable selection before distribution as a new variety. Variation is often a serious objection for many farmers who have become used to their more-uniform highly selected old varieties. The resistance of farmers to synthetic varieties which are variable and which are not strikingly higher yielding is often so great that it is difficult to obtain wide scale distribution and use.

Considerable success was achieved in the formation of synthetic varieties from double topcrosses in the early stages of the Mexican program, as described by Wellhausen and Roberts (1949). Nevertheless, in consideration of all factors, it seemed that the most logical procedure would be the formation of good double cross hybrids which would also make good synthetics in advanced generations. In this way, the more progressive farmers could take advantage of the higher yield capacity of hybrids, while less progressive farmers would still benefit by planting the advanced generation progeny. Also much wider use of improved seed could be obtained more easily and rapidly since hybrids always make a better showing than synthetics. With time, through education, demonstration, and the formation of better hybrids, the demand for hybrid seed could be increased gradually, and use of advanced generation seed gradually would decrease. Some of the hybrids obtained for Zones 1 and 3 and their relative value as synthetics will be discussed below:

Results in Zone 1

In Zone 1, for March and April plantings under irrigation or under conditions where subsoil moisture is sufficient for germination, the race Chalqueño has become widely distributed. Some of the results obtained in the attempt to improve this long season race are given in Table 27.5.

The variety listed as Chalco in Table 27.5 represents an average variety of the race Chalqueño, and its yield for the sake of comparison has been taken as 100. Variety V-7 is one of the best varieties found in the race, and has been widely distributed as an improvement of the common variety Chalco. Its two-year average yield in comparison to Chalco was 118 per cent.

Hybrid H-2 is a cross between two composites, one of which (Hgo. Comp. 1) was made up of a composite of five first generation selfed lines (S_1) from the variety V-7, that were good in topcrosses with the variety Urquiza, of the race Cónico Norteño. The other (Urq. Comp. 1) was made up of a composite of five S_1 lines from the variety Urquiza, selected on the bases of their combining ability in topcrosses with a variety similar to Chalco. Urquiza was the only variety of the different races tried in Chalqueño territory that was fairly well adapted. Hybrids between two such composites are of interest because the parents may be propagated as open-pollinated synthetic varieties, thus eliminating the necessity of forming single crosses and the maintenance of four inbred lines, as is the case in a double cross.

The yield of hybrid H-2 was only slightly higher than the open-pollinated variety V-7. Work is under way to find out how much this hybrid might be improved through reciprocal recurrent selection.

The three-way hybrid H-1 was made by using a single cross involving an

S_1 line of Urquiza (Urq. 54) and an S_1 line of Chalqueño (Hgo. 3-5) as the female parent, with a very vigorous first generation selfed line Mex. 37-5 also from Chalqueño as the pollinator. This hybrid involving one Urquiza line and two Chalqueño inbreds has been one of the best combinations to date of Urquiza and Chalqueño lines. In general, hybrids of inbred lines from Chalqueño and inbred lines of Urquiza have been disappointing in comparison with the yield of the variety V-7, although the Chalqueño lines in the crosses were selected on the basis of combining ability with the variety Urquiza, and Urquiza lines on the basis of their combining ability with a variety of Chalqueño. None of the hybrids, including H-1, approached very closely the

TABLE 27.5

RELATIVE YIELDS IN PER CENT OF CHALCO FOR THREE LONG SEASON VARIETIES AND HYBRIDS IN 1948 AND 1949

Variety or Hybrid	Pedigree	Relative Yields in Per Cent		
		1948	1949	Average
Chalco	Open-pollinated	100	100	100
Variety V-7	Selected O.P.	117	120	118
Hybrid H-2	Hgo. Comp. 1× Urq. Comp. 1	120	125	122
Hybrid H-1	(Urq. 54×Hgo. 3-5)× Mex. 37-5	134	130	132

yield, ear size, and depth of grain of the best 10 per cent of the plants in the variety V-7.

If a hybrid could be made in which 80–90 per cent of the plants approached the yield of the best 10 per cent of the plants in the variety V-7, it would be an excellent hybrid. If such a hybrid is to be obtained, another line of approach seems warranted. The best approach to this immediate ideal is probably through the recombination of lines from V-7 or other varieties within the race Chalqueño rather than bringing in outside germplasm, since no race or variety has as yet been found which in F_1 crosses with V-7 has been as good as V-7. The question of selecting the proper tester for use in isolating the high-combining genotypes, inter se, needs further study. Perhaps a tester made up as a double cross or as a synthetic of the most vigorous, most agronomically desirable, highest yielding, and best combining Chalqueño lines would be the one to use. Against this nucleus of concentrated adapted germplasm, other lines from V-7 or lines from other varieties of Chalqueño, regardless of vigor, could be tested for their combining ability. Those that increased the yield of the tester could then be pooled, and this pool could be concentrated further by another round of selfs and outcrosses to the tester. The objective would be to concentrate the factors which complement those of the tester to bring about the ideal hybrid. If successful, the final hybrid could consist of a cross between two pools of germplasm, rather than individual inbred lines, with the tester used as the female parent if so desired.

The race Cónico (Figs. 27.1 and 27.2) is almost universally distributed in Zone 1 where it is used for June plantings at the beginning of the rainy season. With respect to general plant characters it is probably the poorest corn in Mexico. The plants are sparsely leafed, have a poor tassel, and have an extremely weak root system. As a normal practice, dirt is hilled around each individual stalk to keep the plants upright until harvest. Its one outstanding feature is its ability to grow and develop grain of high test weight under relatively low temperature conditions.

To improve this race, incorporation of germplasm from another race with a strong root system seemed highly desirable. The materials most likely to be of use were the earliest varieties of the race Cónico Norteño. For the purpose of improving the corn varieties for the rainy season of Zone 1, therefore, two varieties were selected. One, designated as Mex. 39, was one of the best yielding varieties of the race Cónico at 2200 meters elevation. The other, designated as Leon I, was a good yielding early variety of the race Cónico Norteño commonly grown in Zone 2 at 1800 to 2000 meters elevation. This second variety was a little late in maturity in Zone 1 and was not as well adapted to the cool growing season as was Cónico. Selected first generation selfed lines from Mex. 39 were topcrossed on Leon I and selected S_1 lines from Leon I were tested with Mex. 39. The best combiners with the respective testers under conditions best suited to Cónico were then crossed in all possible combinations, and tested for yield. From these results a double cross that might also make a good synthetic was predicted, made, and tested. The pedigree of this double cross, its yield relative to Mex. 39, and its probable yield in F_2 are given in Table 27.6.

The female parent of this double cross consisted of a single cross between two S_1 lines from Leon I (Race Cónico Norteño). The male parent consisted of a cross between an S_1 line and a composite of four S_1 lines all from Mex. 39 (Cónico). This pollinator also is being propagated and used as a synthetic variety with good results.

Although based on only one year's results, the data in Table 27.6 indicate substantial differences in yield capacity between the hybrid and the open-pollinated variety Mex. 39. Perhaps what is more important at the moment is that the advanced generation progeny of this hybrid shows promise of being substantially superior in yield capacity to Mex. 39 which is one of the better varieties of the race Cónico. The actual yields of the double cross and the six possible single crosses between the four parental lines, together with the open-pollinated variety Mex. 39 as check in Table 27.6, were all determined in the same experiment under the same conditions. In calculating the yield of the F_2 generation, however, the average yield of the four parental lines was estimated as 70 per cent of Mex. 39. In view of the fact that the S_1 lines involved were the most vigorous within their respective varieties, this estimation is conservative. Actual yields of the F_2 generation in comparison with Mex. 39 and the double cross hybrid are not yet available.

Results in Zone 3

Zone 3 comprises the corn belt of Mexico and produces more commercial corn than any other area. In the eastern part of Zone 3, an area commonly referred to as the Bajío, the race Celaya (Fig. 27.2) is widely distributed

TABLE 27.6

YIELD AND PER CENT DRY MATTER OF A DOUBLE CROSS HYBRID COMPARED TO THE OPEN-POLLINATED VARIETY MEX. 39 AND TO ITS F_2 YIELD*

Hybrid	Av. Yield Kg./Ha.	% D.M.	Yield in % of Check
(LI 27 × LI 193) × Mex. 39-26 × Mex. 39 Comp. 1	3795	71	148
Mex. 39 O.P. (check)	2568	69	100
Av. of all possible singles	3506	70	136
Av. of parental lines (est. 70% of check)	1798	......	70
F_2 (calculated by Wright's formula)	3079	......	120

* Calculated from average yield of the three inbreds and one composite and their six possible single crosses.

and is apparently a recent introduction into the area. The predominating corn in the Bajío area at one time must have been the race Cónico Norteño. But as the root rot organism populations built up, the varieties of Cónico Norteño rapidly dropped in yield because of their almost complete root rot susceptibility. Celaya probably originated in the State of San Luis Potosí which is adjacent to the Bajío, but at a lower elevation than is common in Zone 3. When introduced into the Bajío, it was a late variety and was first grown only by farmers who had irrigation and could plant corn considerably ahead of the rainy season. As irrigation farming increased, the race Celaya became very popular and widespread. Selection pressure operated in the direction of earliness, and certain varieties were developed which were more productive than Cónico Norteño on the better soils and under conditions of a normal rainy season. The rainy season begins about July 1 and ends in October.

In the western part of Zone 3, the predominating types are varieties of the race Tabloncillo and inter-mixtures of Tabloncillo, Celaya, and a third complex from the mountains in southern Jalisco. The breeding work for Zone 3 was concentrated in the Bajío and had the following objectives:

1. The development of hybrids and synthetics higher yielding than Celaya, with a high degree of root and ear-rot resistance, which have general adaptation to Zone 3 under irrigation.

2. The development of early drought resistant hybrids and synthetics for Zone 3, which are adapted to the normal rainy season of the area, and which have a high degree of root and ear-rot resistance.

Since the variety Celaya already had considerable root and ear-rot resistance, it was used as basic breeding material in the attempt to attain the above objectives.

One of the first attempts at the improvement of Celaya involved the production of double topcrosses. In this method, two different high yielding varieties adapted to Zone 3 were used as testers. One of these, designated as Gto. 59A, was one of the better late varieties found within the race Celaya. The other, designated as Jal. 35, was a high yielding variety obtained from southern Jalisco. This latter variety apparently was derived from a highly heterogeneous mixture of several races that came together in southern Jalisco: Tabloncillo, Celaya, and the Jaliscan mountain complex (Wellhausen *et al.*). Inbred lines (S_1) from Gto. 59A and other varieties of the race Celaya were topcrossed with Jal. 35, and S_1 inbred lines from Jal. 35 and similar varieties were topcrossed on Gto. 59A. These topcrosses were then tested in three locations in Zone 3 with Celaya as a check. As a result of these tests, the ten best topcrosses with Gto. 59A were selected and each crossed with each of the ten best topcrosses with Jal. 35. Subsequently, the resulting double topcrosses were tested at two different locations in Zone 3. Finally, two double topcrosses were selected and released for commercial production. The yields of the two double topcrosses for commercial production together with the yields of Celaya are given in Table 27.7. These comparative

TABLE 27.7

YIELDS OF TWO DOUBLE TOPCROSSES IN COMPARISON TO THE OPEN-POLLINATED VARIETY CELAYA

Hybrid	Pedigree	Yield Kg./Ha.	Yield in % of Celaya
H-305	(M30-60×Gto. 59A)× (L II 123×Jal. 35)	4845	120
H-301	(L II 123×Gto. 59A)× (M30-33×Jal. 35)	4411	108
Celaya*	Open-pollinated variety	4092	100

* The variety of Celaya used as a check in this and in the following tables is the one being maintained by the Agricultural Experiment Station in Leon, Gto.

yields are based on an average of four replications in each of 20 experiments in two different localities and are highly significant statistically.

The double topcross hybrid H-305 yielded 20 per cent more than Celaya and was equal to Celaya in maturity. Hybrid H-301 yielded only 8 per cent more than Celaya but was about ten days earlier. In normal years this is a decided advantage in adaptation to the variable rainy season of the Bajío. The major portion of the 2000 hectares planted in 1948 for hybrid seed production in the Bajío was used for the production of these two double topcross hybrids. According to a formula presented by Mangelsdorf (1939), the gain in yield of these two double topcrosses in F_2 would be about half of what they showed in F_1 over Celaya. The results of an experiment set up to measure the difference in yield between the F_1 and F_2 generations of eight different double topcrosses made up as described above are given in Table 27.8. The data are based on an average of four replications in each of two locations.

TABLE 27.8

COMPARISON OF F_1 AND F_2 GENERATION YIELDS OF EIGHT DOUBLE TOPCROSSES IN PER CENT OF CELAYA

Generation	Double Topcrosses								Average
	1	2	3	4	5	6	7	8	
F_1.......	132	115	111	99	94	101	98	89	105
F_2.......	123	104	70	92	93	117	114	114	103
Celaya...	100	100	100	100	100	100	100	100	100

According to the data presented in Table 27.8, the differences in yield between the F_1 and F_2 generations were statistically significant only in the double topcrosses 3 and 8. In topcross 8 the difference was in favor of the F_2 generation. Some of the double topcrosses undoubtedly held a certain advantage in yield over Celaya in the F_2, but further data are needed before accurate conclusions can be drawn with respect to the comparative yield capacities of the F_1 and F_2 generations of double topcrosses.

Although some improvement was achieved over Celaya by means of the multiple topcross method, the direct recombination of lines from Celaya has given better results. Celaya definitely offers the best breeding material for Zone 3. Crosses between Celaya and other races in Zone 3 such as Cónico Norteño and Tabloncillo have been disappointing. The race Cónico Norteño introduces some earliness, but it also contributes susceptibility to root rot and ear-rots. The race Tabloncillo of western Mexico behaves in a similar manner. In addition, it introduces certain undesirable ear characters.

As shown in Table 27.9 some outstanding hybrids have been attained through a recombination of lines from Celaya. The Celaya lines used in the hybrids of Table 27.9 were isolated by topcrossing with a variety of the race Cónico Norteño and with the variety Jal. 35. The two hybrids, H-309 and H-307 were made with S_1 lines, while H-310 was made with S_2 lines. Both H-309 and H-307 gave slightly better all around performance in yield and in disease resistance than did H-310, but H-309 was the best of the three in yield, disease resistance, and general agronomic characters. Its yield, as

TABLE 27.9

YIELDS OF DOUBLE CROSSES MADE FROM S_1 AND S_2 LINES COMPARED WITH THE AVERAGE YIELD OF CELAYA, H-301, AND H-306*

Hybrid	Pedigree	Yield Kg./Ha.	% of Av. of Checks
H-309...	(C 123×C 243) ×(C 90×Ag. 172)	4549	123
	Av. of checks	3703	....
H-307...	(Ag. 172×C 79)×(C 67×C 90)	4032	119
	Av. of checks	3375	....
H-310...	(M30-60-3×C 243-2-2) ×(Ag. 172-2×G 61-5-4)	4437	118
	Av. of checks	3760	....

* An average of two years' data from two locations.

shown in Table 27.9, was 23 per cent higher than an average of the three varieties used as checks. The checks, in addition to Celaya, included two double topcross hybrids (H-301 and H-306) which brought the level of yield of the checks up to 107 per cent of Celaya. The actual difference between H-309 and Celaya, therefore, would be somewhat greater than 23 per cent.

Hybrid H-309 should also make a good synthetic because: (1) the average yield of the six single crosses possible between the four inbred lines is very nearly the same as the yield of the double cross H-309, and (2) because the four S_1 lines were among the most vigorous obtained from Celaya. The actual yield relationship between F_1, F_2, and F_3 progenies, where available for a series of double crosses in a randomized block experiment with eight replications, is given in Table 27.10.

All yields in Table 27.10 are expressed in per cent of Celaya. All double cross hybrids with the exception of No. 1, involve S_1 lines from varieties of the race Celaya. Hybrid No. 1 was made with S_2 lines from varieties of the race Celaya. Hybrid No. 2 contains the same lines as H-309 in Table 27.9, but in a slightly different combination. This combination has resulted in slightly higher double cross yield, but should have no effect on yields of the F_2.

As shown in Table 27.10, the F_2 generation progeny of the better double cross hybrids with S_1 lines retained a substantial advantage in yield (12 to 20 per cent) over the open-pollinated variety Celaya. Hybrid No. 1 with S_2 lines was included to see if it would actually show a greater drop in yield between F_1 and F_2 than the others.

From Table 27.11 it is evident that the F_2 or F_3 yields of the double

TABLE 27.10

YIELDS OF F_1, F_2, AND F_3 GENERATION PROGENY OF SEVEN DOUBLE CROSS HYBRIDS IN PER CENT OF THE VARIETY CELAYA

No.	Pedigree	F_1	F_2	F_3
1....	(Gto 61-5-4×Ag. 172-2)×(M30-60-3×C 243-2-2)	118	103	101
2....	(C 123×C 90)×(C 243×Ag. 172)	140	112	......
3....	(C 123×M30-60)×(C 90×C 243)	139	107	111
4....	(C 123×C 90)×(C 243×M30-60)	150	118	......
5....	(C 123×C 90)×(C 243×Ag. 32)	149	119	......
6....	(C 123×C 90)×(Ag. 32×Ag. 172)	146	120	......
7....	(C 123×C 243)×(L II 67×L II 90)	127	......	101
8....	Celaya	100	100	100

L. S. D. = 12.5%

TABLE 27.11

YIELD OF F_1, F_2, AND F_3 PROGENIES IN PER CENT OF F_1

No.	Pedigree	F_1	F_2	F_3
1....	(Gto 61-5-4×Ag. 172-2)×(M30-60-3×C 243-2-2)	100	87	86
2....	(C 123×C 90)×(C 243×Ag. 172)	100	80	.....
3....	(C 123×M30-60)×C 90×C 243	100	77	80
4....	(C 123×C 90)×(C 243×M30-60)	100	79	.....
5....	(C 123×C 90)×(Ag. 32×C 243)	100	79	.....
6....	(C 123×C 90)×(Ag. 32×Ag. 172)	100	82	.....
7....	(C 123×C 243)×(L II 67×L II 90)	100	.....	80

crosses with S_1 lines was consistently about 80 per cent of the yield in F_1, whereas the F_2 of the double cross with S_2 lines was 87 per cent of the F_1. This is not significantly higher, but also not significantly lower as one might expect on the basis of the lower yields of the S_2 lines.

The few F_3 yields available were not greatly different from those of the F_2. The assumption that in general, barring selection, there is no further reduction in yield beyond F_2 has been adequately supported by experimental data. Sprague and Jenkins (1943) tested the F_1, F_2, F_3, and F_4 of one 24 line and four 16 line synthetics in various districts in Iowa. There was little difference between the various advanced generations, the F_2, F_3, and F_4 yielding 94.3, 95.4, and 95.1 per cent as much as the F_1 respectively. Kiesselbach (1933) compared the yield of the F_2 and F_3 generations of 21 single crosses. The yield of F_2 and F_3 was approximately the same, being 38.4 and 37.8 bushels per acre respectively. Wellhausen and Roberts (unpublished) compared the average yields of the F_1, F_2, F_3, and F_4 generations in 18 topcrosses. The average yield was 10.8, 9.9, 9.6, 9.8 kilos per plot for the F_1, F_2, F_3, and F_4 generations respectively.

In the attempt to obtain still greater yield over Celaya, approximately 1000 S_2 and S_3 lines were crossed with the single cross C 67 × C 90. Both lines in this single cross were first generation selfs from Celaya, and the majority of the lines crossed with it were from varieties of this race. It is of interest to note the kind of lines that gave the highest yields in combination with C 67 × C 90. Among the ten that were finally selected as the best combiners with C 67 × C 90, three were from the variety Jal. 35, one from a variety from the State of Coahuila in northern Mexico, and the rest were from Celaya. The total number of lines included from Jal. 35 and from other varieties not classified as belonging to the race Celaya were relatively small compared to the total number of Celaya lines involved in the test. However, four of the ten best combiners with respect to yield came from varieties outside the race Celaya. This is in line with the belief that the possibility of obtaining high yielding hybrids is greater in the combination of lines from different varieties than in the combination of lines from the same or closely related varieties. Nevertheless, hybrids obtained from a recombination of Celaya lines were satisfactory in yield and generally more disease resistant and more acceptable from an agronomic standpoint than hybrids between Celaya and non-Celaya lines.

In the yield test results of all possible single crosses between the ten selected good combiners with the tester C 67 × C 90, the two lines C 110-3 and C 126-5 from Celaya (the same variety from which the tester lines were obtained) were of considerable interest. These two lines were not only good combiners with the single cross tester C 67 × C 90, but also combined well with each other. The single cross C 110-3 × C 126-5 was among the highest of all the 45 possible single crosses among the ten selected lines.

The tester single cross which was made up of two average S_1 Celaya lines would tend to isolate genotypes which contribute the greatest number of additional yield factors to its own genotype. These genotypes could be very much alike or greatly different. Apparently the two genotypes represented by the lines C 110-3 and C 126-5 were greatly different both genotypically and phenotypically. In ear type they seemed to be opposite extremes in the range of segregation among Celaya lines. As shown in Figure 27.5, C 110-3 is a line with a fairly long 8-rowed ear, and phenotypically appears to be a segregant in the direction of Tabloncillo which is one of the probable progenitors of the race Celaya. The other, C 126-5, has a fairly short ear and a high row number and apparently is a segregant in the direction of Tuxpeño which is the other probable progenitor of the race Celaya.

If selection for ear type, using Celaya as the ideal, had been a factor in the development of inbred lines, then both C 110-3 and C 126-5 probably would have been discarded. Selection for type may be a mistake in those varieties

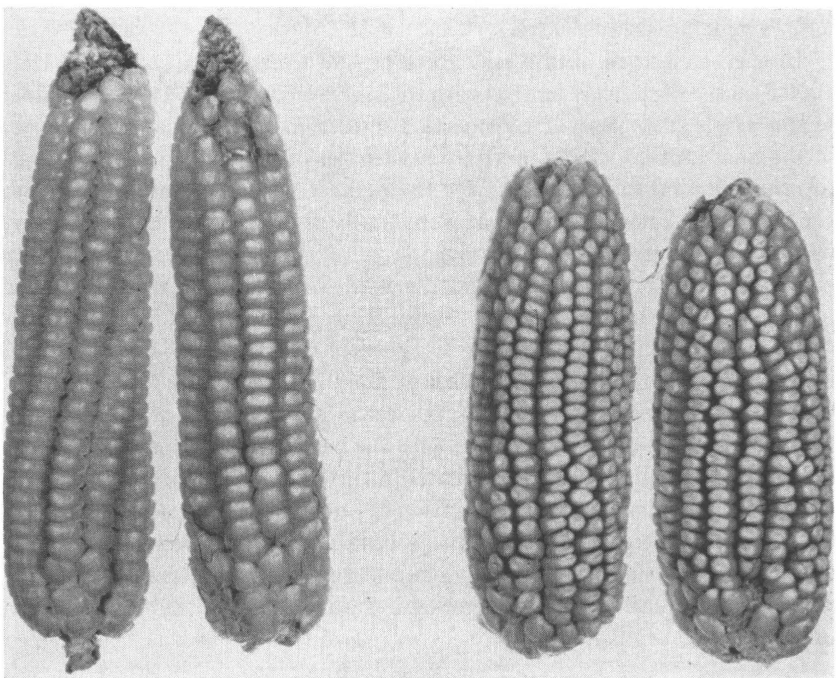

FIG. 27.5—Typical ears of the two inbreds C 110-3 (*left*) and C 126-5 (*right*). Both are from the race Celaya, which probably originated from the hybridization of Tabloncillo and Tuxpeño. C 110-3 phenotypically appears to be a segregant in the direction of Tabloncillo and C 126-5 appears to be a segregant in the direction of the tropical many-rowed cylindrical dent Tuxpeño.

which apparently have not reached equilibrium, or in which segregants closely resembling one putative parent or other appear. It may be an especially bad practice if the lines from the same variety are to be recombined into hybrids. In the recombination of lines from the same variety, it remains to be seen whether good hybrids can be more readily made by a recombination of lines which phenotypically are opposite extremes, or from those lines which resemble more closely the type of the variety from which they came. Probably both types are needed.

Hybrids and synthetics developed from Celaya lines were well adapted to regions with supplemental irrigation, and to certain of the regions in Zone

3 where rains are generally well distributed throughout the rainy season. However, in many areas of Zone 3, the corn is often subjected to long periods of drought. Since drought generally reduces the total length of time for growth, varieties are needed which are not only drought resistant, but also earlier in maturity than Celaya.

So far, no good hybrids earlier than Celaya have been obtained from a recombination of early Celaya lines. It became necessary to look elsewhere for material which would give the desired earliness and drought resistance when combined with Celaya. The two races Cónico Norteño and Tabloncillo, which overlap Celaya in its distribution in Zone 3, were found to be undesirable because of their high susceptibility to both root and ear-rots, although they were early in maturity. In the search for suitable material, a race called Bolita, found in a small valley in Oaxaca about 500 miles from the Bajío, has shown considerable promise. It probably originated in the Valley of Oaxaca through the hybridization of Tabloncillo and an early maturing tropical race called Zapalote Chico (Fig. 27.3). The Valley in Oaxaca where Bolita probably originated has the same elevation and has a climate similar to parts of the Bajío. Bolita, when grown in the Bajío, was found to be early maturing, very resistant to ear-rots, and generally resistant to root rots. Its yield capacity, however, was considerably below that of Celaya in years with good rainfall distribution.

Through a method of reciprocal testing of lines of Bolita with Celaya and lines of Celaya with Bolita, S_1 lines of Bolita were isolated, which when combined with certain S_1 lines of Celaya, produced hybrids superior to both Bolita and Celaya in the drier areas of Zone 3. One of these hybrids, made with a single cross of two S_1 Celaya lines (C 90 $\times$ C 67) as a female parent and a synthetic of four S_1 Bolita lines as a pollinator, is now being produced for large scale testing. Preliminary data obtained on this hybrid, called Celita, are given in Table 27.12.

In the first three localities where Celita was tested, the rainfall was either well distributed or supplemented by one irrigation in a period of extreme drought. Under these conditions as evident in Table 27.12, Celita was about equal in yield with the standard variety Celaya. But at Irapuato under extreme drought conditions, Celaya yielded only 741 kilos per hectare (about 12 bushels per acre) while Celita yielded 1441 kilos per hectare, or about 23 bushels per acre. Also as indicated in Table 27.12 by the differences in per cent dry matter at harvest, Celita was considerably earlier in maturity than Celaya. Celita is also fairly resistant to root rots and much more resistant to ear-rots than the best hybrids made with Celaya lines.

It appears, therefore, that the hybrid Celita, under conditions normal for Celaya, is equal to it in yield, but under severe drought conditions it is greatly superior. This hybrid also is superior to Bolita under both normal and dry conditions although the data are not presented in the table. Here then is another case where a hybrid between S_1 lines of two different races under one set of conditions is no better than the better of the two parents, but, under a different set of conditions, is superior to both.

Double cross hybrids made from S_1 lines of Celaya in combination with S_1 lines of the race Cónico Norteño have in general given good results in Zone 2, with yields ranging from 20 to 25 per cent higher on the average than the native varieties commonly grown in the area.

TABLE 27.12

YIELD OF CELITA AND PERCENTAGE DRY MATTER AT HARVEST COMPARED TO CELAYA AT FOUR DIFFERENT LOCATIONS, 4 REPLICATIONS EACH

Locality	Yield Kg./Ha.		% Dry Matter	
	Celita	Celaya	Celita	Celaya
Vista Hermosa...	3793	3806	68	60
Guadalajara.....	4069	3760	80	69
León...........	4273	4223	75	66
Irapuato.........	1441	741	81	77

In the tropical areas (Zones 4 and 5) hybrids were under test for the first time in 1950. These involved principally combinations of S_1 and S_3 inbred lines from the races Tuxpeño and Vandeño (Fig. 27.4).

Lines Selfed Once versus Lines Selfed More Than Once in Hybrid Formation

The use of S_1 lines in the early stages of a breeding program has many advantages. It means that testing for combining ability can begin in the first generation of selfing. It can, in fact, begin with selected open-pollinated plants which may be simultaneously selfed and crossed. Lines thus isolated in a breeding program where uniformity is not of prime importance can be utilized immediately in the formation of hybrids and synthetics. Since S_1 lines are more vigorous than advanced generation selfed lines, they also have a definite advantage in the formation of synthetics. It has never been definitely determined whether high yielding hybrids can be obtained more readily with homozygous lines than with heterozygous lines. Jenkins (1935) has shown that crosses of lines selfed only once are on the average as productive as crosses involving the same lines selfed six to eight generations. This may indicate, as Jenkins suggests, that the effects of selection are almost exactly balanced by the loss of good genes through the rapid attainment of homozygosity.

Some data have been accumulated to date in the Mexican program which may have some bearing on the relative value of S_1 lines versus more homozygous lines in the formation of hybrids.

Preliminary data on the relative combining ability between S_1 and the S_3 lines selected from each S_1 are available from topcrosses to the same tester. Each topcross with an S_1 line was tested for yield in the same experiment with the corresponding topcrosses involving the lines obtained from that S_1 after three generations of selfing and selection for desirable agronomic characters. The number of S_3 lines in each S_1 family varied from one to sixteen, some families having a larger number of desirable S_3 lines with respect to agronomic characters than others.

A frequency distribution of the differences in topcross yields in per cent between S_1 line topcrosses and the average of the S_3 line topcrosses within each family is given in Table 27.13. The differences are expressed as S_1 minus

TABLE 27.13

DISTRIBUTION OF DIFFERENCES IN TOPCROSS YIELDS BETWEEN S_1 LINES AND THE AVERAGE OF THE S_3 LINES WITHIN EACH FAMILY (S_1 − AVERAGE OF S_3's)

	MINUS														
Class center	75	70	65	60	55	50	45	40	35	30	25	20	15	10	5
Frequency	1	..	..	..	..	1	..	2	2	4	6	3	9	12	12
	PLUS														
Class center	0	5	10	15	20	25	30	35	40	45	50	55	60	65	
Frequency	25	18	18	3	3	3	4	4	2	..	4	1	..	1	

Number of observations = 138 Mean = +0.90

the average of the S_3 within the respective S_1 family. The class mid-points, therefore, range from 0 to 65 per cent positive and from 0 to 75 per cent negative, with class intervals of 5 per cent. A positive difference means that the S_1 topcross yield exceeded the average of the S_3 topcrosses. A negative difference indicates that the average of the S_3 topcrosses was higher than the S_1 topcross within the same family. It is evident from Table 27.13 that the distribution of the differences approaches very closely that of a normal curve. That is, there were as many cases in which the S_1 exceeded the average of the S_3 as there were cases in which the average of the S_3 exceeded the S_1. The mean difference between the 138 pairs was +0.90 per cent. These data indicate that visual selection in advanced selfed generation progeny based on agronomic characters is largely at random with respect to combining ability. If visual selection in successive generations of inbreeding had been effective in increasing combining ability, then the above curve would have been skewed in the direction of the negative differences.

Upon further inbreeding of S_1 lines at random without selection for combining ability, one would expect to end up with about as many advanced generation inbred lines which exceed the S_1 in combining ability with a specific tester as lines which were below that of the S_1. In other words, the distribution in relation to the S_1 yield would follow that of a normal curve.

In Table 27.14 are given the distributions of the yields of S_1 and S_3 topcrosses of 12 families from the same race of corn (Chalqueño). All of the S_1 and S_3 lines within each family were topcrossed on an S_1 line from the race Celaya, and all topcrosses were tested under the same conditions. The class in which the S_1 topcross of each family fell is indicated by the number in bold face type. It is evident from the table that the number of S_3 lines from each family tested are insufficient to show a normal distribution. However, in nearly every case where more than three S_3 lines were available for comparison, some were no better, some were significantly better, and still others were significantly worse than the respective S_1 line in combining ability. It appears, therefore, that in certain cases considerable increase in the yield of specific combinations involving S_1 lines can be obtained through further inbreeding and selection for specific combining ability.

TABLE 27.14

FREQUENCY DISTRIBUTIONS OF S_1 AND S_3 LINE-TOPCROSS YIELDS OF 12 FAMILIES. CLASS IN WHICH S_1 LINE-TOPCROSS OF EACH FAMILY FALLS IS INDICATED BY NUMBER IN BOLD FACE TYPE

Class Mid-points (Yield of Topcrosses in % of Checks)	65	75	85	95	105	115	125	135	145	155	165	175	185	195	205
Family and Frequency															
Hgo. 9-4								**1**	2						7
Ch. II 148							1		**2**	1					3
M. 37-5					1	2		**1**	1	3	1				
Hgo. 4-5				1	1		**4**	2	3	3		1			
Hgo. 1-5			1				**1**		1	1					
Hgo. 3-4						1		**2**							
Hgo. 2-3					1			**2**							
Ch. II 187					1	**2**									
Hgo. 1-8				1	**1**	1									
Hgo. 6-11		1	1	1	**3**		1								
Hgo. 3-5		1	**2**		2	1	1								
Ch. IV 146			**2**		1										

Further evidence that better yields can be obtained through the substitution of S_2 or S_3 lines in a specific S_1 combination is presented in Table 27.15.

This table is divided into two parts. In column A is given the yield of each specific single cross made with S_1 lines. In column B is given the yield of each corresponding single cross of two advanced lines selected from the S_1 lines given in column A in the second or third generation of inbreeding. Selection of the S_2 or S_3 lines in each case, however, was not based on test crosses for specific combining ability with the other line involved. The advanced lines used were picked from among their sister lines largely on the basis of desirable agronomic characters. It may be seen in Table 27.15 that, although in many instances the differences were small, the yield of the crosses of S_2 or S_3 lines exceeded that of the corresponding cross with S_1 lines in every

TABLE 27.15

YIELDS OF SINGLE CROSSES BETWEEN S_1 LINES COMPARED TO YIELDS OF SINGLE CROSSES BETWEEN TWO LINES*

Crosses	Yields of Crosses between S_1 Lines (A)	Yields of Crosses between S_2 and/or S_3 Lines (B)	Differences A−B
1.......	5935	6873	−938
2.......	6074	6630	−556
3.......	6340	6560	−220
4.......	5172	6514	−1342
5.......	5056	6479	−1423
6.......	5669	6306	−637
7.......	5588	6259	−671
8.......	5970	6202	−232
9.......	5970	6190	−220
10.......	6005	5935	+70
11.......	5334	5843	−509
12.......	4535	5577	−1042
13.......	5368	5473	−105
14.......	5542	4964	+578

N = 14.
Mean difference = 517.6 ± 147 kilos (or 9.2 per cent).

* Derived from the respective S_1's after two or three generations of inbreeding and selection for agronomic characters only. (Kilos per hectare.)

case except two. The average difference between the fourteen paired crosses was 9.2 per cent. It is highly probable that a greater increase would have been obtained had the various S_2 or S_3 lines also been picked on the basis of tests for specific combining ability. However, since selection can make a choice only between the alleles present in a particular S_1, a point of diminishing returns may be rapidly reached upon straight selfing. Experiments are under way to determine in what generation of selfing maximum gains may be reached.

The data in Table 27.14 are of further interest from the standpoint of relationship between the combining ability of S_1 lines and the advanced generation selfed lines obtained from them. In this table it is evident that in those families where the S_1 lines were poor combiners with a given tester, the S_3 lines obtained from them on the average also tended to be poor. In those families where the S_1 lines were good combiners, the S_3 lines obtained from them were also good. A correlation coefficient of 0.69 was obtained between the topcross yields of S_1 lines and the average topcross yields of the S_3 lines derived from each. This highly significant correlation coefficient, based on the same 138 pairs whose differences were distributed as shown in Table 27.13, indicates a high degree of relationship between the performance of S_1 and the average performance of lines obtained from each through subsequent generations of inbreeding. It seems, therefore, that tests for combining ability in the S_0 or S_1 generation would serve to separate the families that are good combiners from families that are poor combiners with respect to a given tester in the early stages of the inbreeding program.

CONCLUSIONS AND SUMMARY

Although the yield results are based on relatively few years' data, it is evident that the methods used in the improvement of corn in Mexico during the six years that the Mexican program has been under way have given excellent results. In some areas considerable improvement in corn yields was obtained by the wider distribution of certain good native, open-pollinated varieties that had developed in isolated areas through chance hybridization and subsequent natural selection. In areas where two different adapted varieties were available which expressed a certain degree of heterosis when crossed, the formation of double topcrosses offered a means of rapid improvement over the native varieties.

It has also been shown that excellent three-way or double cross hybrids can be made from first generation selfed lines. Some of these same double crosses in advanced generations have made good synthetics. This means that those farmers who cannot or are unwilling to plant newly crossed seed every year may still have a 12–20 per cent advantage in yield over their native varieties. Hybrids made from crosses of two synthetics, each consisting of a pooled set of closely related S_1 lines that combined well with a different pooled set of related S_1 lines, have shown some promise in the greater simplification of hybrid seed production. In this way the maintenance of lines for hybrid seed production can be greatly simplified.

The use of first generation selfed lines in the early stages of a new breeding program obviously has many advantages. Whether such lines can be maintained for a reasonable period of time without much change in combining ability remains to be determined. So far through a composite sib method of propagation they have been maintained reasonably "pure."

Data have been presented which indicate that hybrids made from more homozygous lines might be superior to those made with lines selfed only once.

It remains to be shown whether more uniform hybrids actually would be superior to hybrids made with S_1 lines in a country such as Mexico. Variations in climate from year to year in any one valley in Mexico are usually extreme. Under such conditions, a high degree of uniformity in a hybrid may actually be a detriment over a period of years.

The problem of what tester or testers to use in isolating lines of high combining ability continues to be a difficult one. Usually the tester chosen depends upon the use to be made of the lines. Judging from the segregants obtained upon inbreeding in some of the races of maize, a point may have been overlooked in the selection of lines and testers. This appeared to be especially true in those races where it was necessary to recombine lines from the same race to obtain immediate improvement. In some of the races upon inbreeding, especially Bolita, Chalqueño, and Vandeño, inbred line segregants often appeared which were very similar to the putative parents of the particular race (Wellhausen *et al.* in collaboration with Mangelsdorf, Fig. 98). If these races had reached equilibrium on an individual gene loci basis, one would not expect to get the parental types in subsequent inbred generations from 500 ears selfed at random in the original population. It appears, therefore, that many of the modern races in Mexico are not in equilibrium on an individual gene loci basis, but consist of blocks of genes in equilibrium with each other. Although it is difficult to estimate the age of some of the modern varieties, these gene blocks obtained from the various ancestors seem to have persisted more or less intact through many generations.

If blocks of germplasm as received from various ancestors are still intact in some of the modern high yielding races, then it may not be as difficult as it once seemed to reconstruct a hybrid that would approach the yield of the ideal plant in a particular variety by the recombination of inbred lines from that variety. Isolation of good lines for such recombination may involve different procedures. A method based on selection for origin and type, with subsequent crossing to an unrelated variety or varieties for the determination of combining ability, may not be the best procedure.

Selection for vigor and type in an environment best suited to a race such as Chalqueño, which probably originated from the hybridization of two different races neither of which is adapted to the environment best suited for Chalqueño, would eliminate those segregants in the direction of either one of the putative parents. It is probable that with the elimination of such segregants, many genes are discarded that are needed to reconstruct the ideal chance hybrids which often appear in a particular variety or race through open pollination. Selection for vigor and type also would tend to select those genotypes which are similar, and more nearly like those of the variety from which they came, than the extreme segregants.

Tests for combining ability of a group of lines from the same variety, based on crosses with an unrelated variety or varieties, tend to select those genotypes which combine well with the particular tester, but do not differentiate lines that combine well among themselves. Thus it seems that new methods of isolating the good combiners must be sought in those races of hybrid origin in which improvement is desired through inbreeding and recombination of lines within the race.