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Chapter 11

Hybridization in
the Evolution of Maize

All varieties and races of maize so far studied prove upon inbreeding to contain numerous heterozygous loci, and all respond to inbreeding with a marked decline in vigor and productiveness. Since contemporary maize is both heterozygous and heterotic, it is probable that the factors which have been responsible for bringing about the present conditions are also factors which have played an important, if not the principal role, in the evolution of maize.

All of the steps involved in the evolution of maize are not yet known. Archaeological remains have told us something of the early stages of maize under domestication, and we can draw additional inferences about its original nature from its present-day characteristics. Our knowledge of the nature and extent of its present variation, although far from complete, is already substantial and is growing rapidly. By extrapolating forward from ancient maize, and backward from present-day maize, we can make reasonably valid guesses about some of the intermediate stages and about some of the evolutionary steps which have occurred in its history.

The earliest known archaeological remains of maize, as well as the best evidence of an evolutionary sequence in this species, occur in the archaeological vegetal remains found in Bat Cave in New Mexico in 1948. This material which covers a period of approximately three thousand years (from about 2000 B.C. to A.D. 1000) has been described by Mangelsdorf and Smith (1949). It reveals three important things: (1) that primitive maize was both a small-eared pop corn and a form of pod corn; (2) that there was an introgression of teosinte into maize about midway in the sequence; (3) that there was an enormous increase in the range of variation during the period of approximately three thousand years resulting from teosinte introgression and interracial hybridization.

INTERRACIAL HYBRIDIZATION IN MAIZE

For additional evidence on interracial hybridization in maize we may turn to existing races of maize. Among these the Mexican races are of particular interest and significance, not because maize necessarily originated in Mexico, since there is considerable evidence that it did not, but because Mexico is a country where primitive races, which in other places are to be found primarily as archaeological remains, still exist as living entities. It is possible in Mexico to find all stages between ancient primitive races and modern highly-developed agricultural races. One has only to place these racial entities in their proper sequence in order to have at least the outline of an evolutionary history.

Wellhausen et al. (1951) have recently made a comprehensive study of the races of maize of Mexico. They recognize twenty-five distinct races as well as several additional entities which are still somewhat poorly defined, but some of which may later be described as races. They divide the known races into four major groups as follows:

Group	No. Races
1. Ancient Indigenous	4
2. Pre-Columbian Exotic	4
3. Prehistoric Mestizos	13
4. Modern Incipient	4

Origin of Mexican Races of Maize

Ancient Indigenous races are those which are believed to have arisen in Mexico from the primitive pod-pop corn similar to that whose remains were found in Bat Cave in New Mexico. The races in this group are called indigenous not because they necessarily had their primary origin in Mexico, but because they are thought to be the product of indigenous differentiation from a remote common ancestor. The differentiation is assumed to have resulted from independent development in different localities and environments with hybridization playing little if any part.

Four races of the Ancient Indigenous group—Palomero Toluqueño, Arrocillo Amarillo, Chapalote, and Nal-tel—are recognized. All of these, like their primitive ancestor, are pop corn. Two of the four—Chapalote and Nal-tel—are forms of pod corn. All have small ears, and all are relatively early in maturity.

Pre-Columbian Exotic races are those which are believed to have been introduced into Mexico from Central or South America before 1492. Four of these races—Cacahuazintle, Harinoso de Ocho, Oloton, and Maíz Dulce—are recognized. The evidence for their antiquity and exoticism derives principally from two sources: all have South American counterparts; all except Maíz Dulce have been parents of hybrid races, some of which are themselves relatively ancient.

Prehistoric Mestizos,[1] thirteen in number, are races which are believed to have arisen through hybridization between Ancient Indigenous races and Pre-Columbian races and hybridization of both with a new entity, teosinte. The term prehistoric rather than pre-Columbian is used for this group because, although all are prehistoric in the sense that there is no historical evidence of their origin, it is not certain that all are pre-Columbian.

Modern Incipient races are those which have come into existence in the post-Columbian period. These races, of which four are recognized, have not yet reached a state of genetic equilibrium. They are recognizable entities but are still changing.

The seventeen races comprising the two last groups all appear to be products of hybridization, either between races in the first two groups, or between these races and teosinte. In several cases, secondary and even tertiary hybridization seems to have occurred.

That a race is the product of previous hybridization seems highly probable when the following four kinds of evidence are available.

1. The race is intermediate between the two putative parents in a large number of characteristics.

2. The putative parents still exist and have geographical distributions which make such hybridization possible and plausible.

3. Inbreeding of the suspected hybrid race yields segregates which approach in their characteristics one or the other of the two putative parents—in some cases both.

4. A population quite similar to the race in question can be synthesized by hybridizing the two putative parents.

Wellhausen *et al.* (1951) have presented all four kinds of evidence for the hybrid origin of a number of the present-day Mexican races. They have presented similar but less complete evidence for the remainder.

The variety Conico, for example, which is the most common race in the Valley of Mexico, is clearly the product of hybridizing the ancient Palomero Toluqueño with the exotic Cacahuazintle. Conico is intermediate between these two races in many characteristics. The two putative ancestral races still are found in isolated localities in the Valley of Mexico. The race is intermediate in its characteristics between the two suspected parents. Inbreeding yields segregates which almost duplicate in their characteristics one of the parents—Palomero Toluqueño. Segregates approaching the other suspected parent, Cacahuazintle, also result from inbreeding but this parent is never exactly duplicated. Obviously the race has become something more complex than a mixture of equal parts of two earlier races. Nevertheless the crossing of Palomero Toluqueño and Cacahuazintle still produces a hybrid which in many respects is scarcely distinguishable from the suspected hybrid race. The data in Table 11.1 show that Conico is intermediate between Palo-

1. Mestizo is the Latin-American term for a racial hybrid.

mero Toluqueño and Cacahuazintle in a large number of characteristics. They also show how closely a recently-made hybrid of these two ancient races resembles the suspected hybrid race, Conico. Ears of the three races and the hybrid are illustrated in Figure 11.1.

The hybrid race, Conico, has in turn been the ancestor of still more complex hybrid races. A Modern Incipient race, Chalqueño, which has originated in historical times in the vicinity of the village of Chalco in the Valley of Mexico,

TABLE 11.1

COMPARISON OF CONICO WITH ITS PUTATIVE PARENTS*

CHARACTERS	RACES			
	Palomero Toluqueño	F₁ Hybrid	Conico	Cacahua- zintle
Ears and plants:				
Ear diameter, mm................	37.1	45.2	45.1	53.2
No. rows grain...................	21.8	18.6	15.7	16.2
Width kernels, mm...............	4.6	6.8	7.4	9.8
Thickness kernels, mm...........	2.8	3.6	3.9	5.3
Diameter peduncle, mm..........	8.0	9.2	9.8	10.6
Length ear, cm..................	9.8	11.8	12.6	14.7
Height plant, cm.................	175	200	193	210
Tillering index..................	.26	.35	.22	.39
Pilosity score..................	3	4	3–4	4
Internal ear characters:				
Ear diameter, mm................	34.0	....	42.4	47.0
Cob diameter, mm...............	19.5	....	19.0	27.7
Rachis diameter, mm.............	10.4	....	9.6	11.7
Length kernels, mm..............	11.4	....	14.8	14.0
Estimated rachilla length, mm......	.4	....	1.6	3.6
Cob/rachis index................	1.88	....	1.98	2.37
Glume/kernel index..............	.40	....	.32	.57
Rachilla/kernel index.............	.04	....	.11	.26
Pedicel hairs score..............	0	....	2–4	4
Rachis flap score...............	0	....	2–3	3

* After Wellhausen *et al.*

is undoubtedly the product of hybridizing Conico with Tuxpeño, a productive lowland race of the Prehistoric Mestizo group. Since Tuxpeño is itself a hybrid, the postulated pedigree for Chalqueño, which is shown in Figure 11.2, becomes quite complex.

In the pedigree of Tuxpeño a distinction has been made (by employing different styles of type) between the facts which are well-established and those which are largely based upon inference. There is little doubt that Conico is a hybrid of Palomero Toluqueño and Cacahuazintle, or that Chalqueño is a hybrid of Conico and Tuxpeño. There is little doubt that Tuxpeño is a hybrid derivative of Tepecintle, but it is not certain that the other parent is Olotillo, although this is the best guess which can be made with the
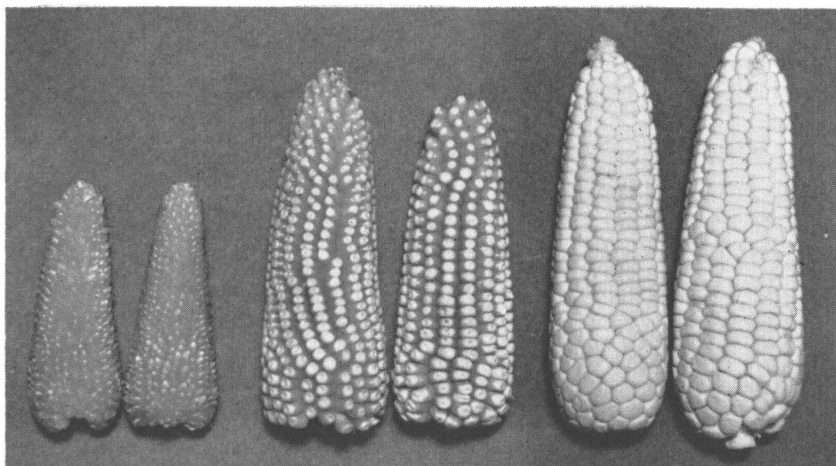
FIG. 11.1—Ears of the Mexican maize races Palomero Toluqueño, Conico, and Cacahuacintle. Conico is intermediate between the two other races and is thought to be the product of their hybridization.
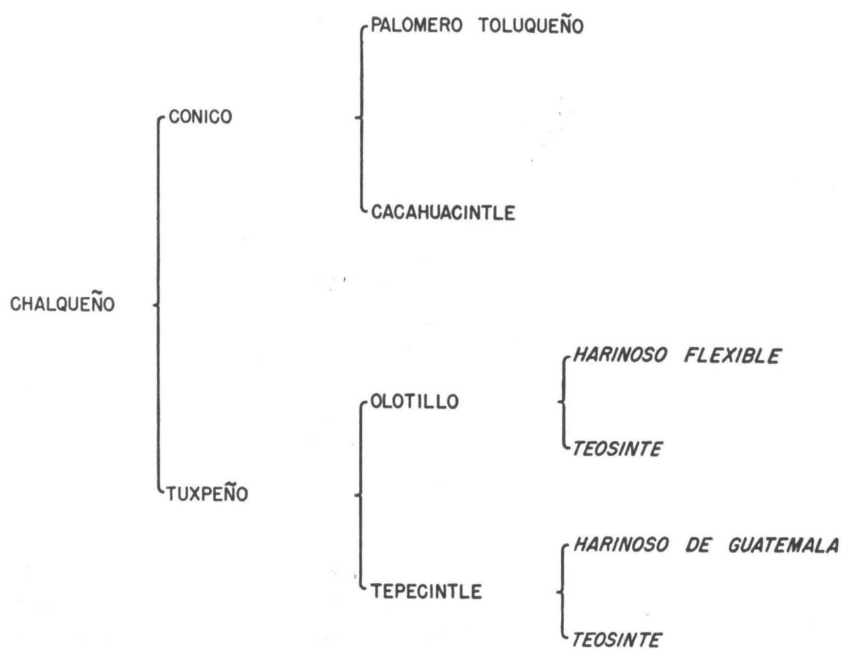

FIG. 11.2—The postulated geneology of the Mexican race Chalqueño. Parts of the genealogy not well established by experimental evidence are shown in italics.

evidence now at hand. That Olotillo and Tepecintle are both hybrid races involving teosinte is even more difficult to prove, although data on chromosome knobs presented by Wellhausen *et al.* tend to substantiate such a conclusion.

There is at least no doubt that interracial hybridization has been an important factor in the evolution of maize in Mexico. Has this hybridization produced heterosis, or has it merely resulted in Mendelian recombination? The extent to which the suspected hybrid races remain intermediate between the two putative parents suggests that natural selection (operating in a man-made environment) has tended to preserve the heterozygote and to eliminate the segregates which approach homozygosity. It is at least certain that the hybrid races are intermediate between their putative parents in their characteristics to a remarkable degree and that they are highly heterozygous. Even in the absence of natural selection favoring the more heterozygous individuals, there would seem to be a tendency for repeated interracial hybridization to create an ever-increasing degree of heterosis. This is the consequence of the fact that maize is a highly cross-pollinated plant, and that heterozygosity does not diminish after the F_2 in cross-fertilized populations in which mating is random.

Wright (1922) has suggested that the vigor and productiveness of an F_2 population falls below that of the F_1 by an amount equal to $1/n$ of the difference between the production of the F_1 and the average production of the parental stock, where n is the number of inbred strains which enter into the ancestry of a hybrid. The formula is also applicable to hybrids in which the parental stocks are not inbred lines, but are stable open-pollinated varieties in which random mating does not diminish vigor. It is, of course, not applicable to hybrids of single crosses which are themselves subject to diminished vigor as the result of random mating.

Hybrid Vigor in Advanced Generations

The rate at which hybrid vigor diminishes in a population after the F_2 generation is related to the proportion of outcrossing. This is true whether hybrid vigor depends upon heterozygosity or upon the cumulative action of dominant genes, and irrespective of the number of genes involved and the degree of linkage. With complete selfing the amount of hybrid vigor retained is halved in each succeeding generation. With complete outcrossing the amount of hybrid vigor falls to one-half in the F_2 and thereafter remains constant. With a mixture of selfing and outcrossing an intermediate result is to be expected. This can be calculated from the following formula presented by Stephens (1950):

$$h = \tfrac{1}{2} [(1 - k) h' + k] .$$

In this formula h is the proportion of F_1 vigor retained in the current generation, h' is the proportion retained in the preceding generation, and k is

the proportion of outcrossing. The formula is based upon the assumption that gene action is, on the average, additive.

It is obvious (according to this formula) that the percentage of hybrid vigor retained in later generations of a cross will approach but never fall below $k/2$. Since the value of k in the case of maize lies usually between .9 and 1.0, it is apparent that the amount of hybrid vigor retained in later generations of maize crosses will (with random mating) seldom fall below the one-half, which is characteristic of the F_2.

There are experimental data which tend to show that advanced generations of maize crosses behave approximately as would be expected from the formulae of Wright and Stephens.

Kiesselbach (1930) compared the $F_1, F_2,$ and F_3 of 21 single crosses with the parental inbred lines. The average yield of the inbreds was 24.0 bushels. The average yield of the F_1 was 57.0 bushels. The theoretical yield of the F_2 is 40.5 bushels. The actual yield was 38.4 bushels which does not differ significantly from the theoretical. The yield of the F_3 was 37.8 bushels which is almost identical to the F_2 yield.

Neal (1935) compared the yield in F_1 and F_2 of 10 single crosses, 4 three-way crosses, and 2 double crosses. The theoretical reduction in yield between the F_1 and F_2 in these three groups (based upon Wright's formula) should have been 31.1 per cent, 21.0 per cent, and 15.2 per cent respectively. The actual reduction was 29.5 per cent, 23.4 per cent, and 15.8 per cent. The agreement could scarcely have been closer.

There is abundant evidence from maize crosses to show that equilibrium is reached in F_2, and that in the absence of selection there is no further reduction in yield in the F_3. Data from the experiments of Kiesselbach (1930), Neal (1935), and Sprague and Jenkins (1943) are summarized in Table 11.2.

The data so far presented are concerned with crosses of inbred strains. Do hybrids of open-pollinated varieties behave in the same way? Since open-pollinated varieties, although not homogeneous, are stable in productiveness they should behave in crosses in the same way as inbred strains. Data from advanced generations of topcrosses presented by Wellhausen and Roberts (1949) indicate that they do. The theoretical yields of the F_2 of a topcross can be computed from a formula suggested by Mangelsdorf (1939).

Wellhausen and Roberts compared the F_1 and F_2 generations of 31 different topcrosses each including the open-pollinated variety Urquiza and two inbred lines of unrelated varieties. The latter were in all cases first-generation selfs. The mean yield of the 31 F_1 hybrids (in terms of percentage of Urquiza) was 132 per cent. The mean yield of the corresponding 31 F_2 hybrids was 126 per cent. Since the yields of the first-generation selfed lines entering into the cross is not known, it is impossible to calculate with precision the theoretical yield of the F_2. However, it is known that good homozygous inbreds yield approximately half as much as open-pollinated varieties

(Jones and Mangelsdorf, 1925; Neal, 1935) which means that inbreds, selfed once and having lost half of their heterozygosity, should yield 75 per cent as much as the open-pollinated varieties from which they were derived. Assuming that the single-cross combinations involved are at least equal to the top-cross combinations—132 per cent—we compute the theoretical F_2 yield of the topcrosses at 117 per cent, which is considerably less than the 126 per cent actually obtained in the experiments. From the results it can be concluded that hybrid combinations including open-pollinated varieties of maize retain a considerable proportion of their vigor in advanced generations.

There is also some evidence to indicate that the amount of heterosis which occurs when open-pollinated varieties are used in hybrid combinations may be

TABLE 11.2

SUMMARY OF EXPERIMENTS DEMONSTRATING EQUILIBRIUM
REACHED IN F_2 AND NO ADDITIONAL YIELD REDUC-
TION IN F_3 OF MAIZE CROSSES

INVESTIGATORS	CLASS OF HYBRIDS	No. HYBRIDS TESTED	YIELD IN PER CENT OF F_1		
			F_1	F_2	F_3
Kiesselbach, 1930	Single crosses	21	100	68.0	66.0
Neal, 1935	Single crosses	10	100	70.5	75.7
Neal, 1935	3-way crosses	4	100	76.6	75.8
Sprague and Jenkins, 1943	Synthetics	5	100	94.3	95.4
Total and averages		40	100	76.9	78.2

considerably higher with Latin-American varieties than with varieties commonly grown in the United States. Wellhausen and Roberts report single topcrosses yielding up to 173 per cent of the open-pollinated variety and double topcrosses up to 150 per cent. A recent report from the Ministry of Agriculture of El Salvador (1949) shows four different hybrids between open-pollinated varieties yielding about 50 per cent more than the average of the parents. Such increases are not surprising, since the varieties used in the experiments are quite diverse, much more so than Corn Belt varieties.

All of the data which are available on the yields of advanced generations of maize crosses, whether the parents be inbred strains or open-pollinated varieties, tend to show that a substantial part of the hybrid vigor characteristic of the F_1 is retained in subsequent generations. Thus maize under domestication is potentially and no doubt actually a self-improving plant. Distinct more-or-less stable varieties or races evolve in the isolation of separated regions. Man brings these varieties or races together under conditions where cross-fertilization is inevitable, and a new hybrid race is born. Repeated cycles of this series of events inevitably lead to the development,

without any direct intervention of man, of more productive races. If, in addition, natural selection favors the heterozygous combinations as it does in Drosophila (Dobzhansky, 1949), then the retention of hybrid vigor in advanced generations of maize crosses will be even greater than that indicated by the experimental results.

INTER-SPECIFIC HYBRIDIZATION OF MAIZE AND TEOSINTE

Superimposed upon these evolutionary mechanisms, at least in Mexico and Central America, is a second kind of hybridization which involves the introgression of teosinte into maize. The importance of this evolutionary factor would be difficult to overemphasize, for as Wellhausen *et al.* have shown all of the more productive races of maize of Mexico show evidence of past teosinte introgression.

The genetic nature of teosinte need not enter into the present discussion. Dr. R. G. Reeves and I concluded some years ago that teosinte is not, as many botanists have supposed, the ancestor of maize, but is instead the progeny of a cross of maize and Tripsacum. This conclusion has not yet been experimentally proven, and although there is much evidence to support it, it is by no means universally accepted by other students of corn's ancestry. For the purpose of this discussion we need not debate this particular point, since we need only to recognize that there is a well-defined entity known as teosinte which occurs as a weed in the corn fields of central Mexico and as a wild plant in Southwestern Mexico, Guatemala, and Honduras.

Teosinte is far more common than formerly supposed. Twenty-five years ago its occurrence was known in only three or four localities in Mexico. Since then, numerous additional sites have been described in Mexico and Guatemala, and recently a locality in Honduras has been added (Standley, 1950).

Teosinte is the closest relative of maize. It has the same chromosome number (ten) as maize, and hybridizes easily with it to produce hybrids which are completely fertile, or almost so. The chromosomes of corn and teosinte are homologous to the extent that they pair almost completely. Crossing over between teosinte and corn chromosomes is of the same order as crossing over in pure corn (Emerson and Beadle, 1932).

Present-Day Hybridization

Since both teosinte and maize are wind-pollinated plants and since they hybridize easily, it is almost inevitable that hybridization between the two species should occur in any region where both are growing. There is no doubt that such hybridization is constantly occurring, and that it has been going on for many centuries. F_1 hybrids of corn and teosinte have been collected in both Mexico and Guatemala. They are especially common in Central Mexico where teosinte grows as a weed. In 1943, I obtained some data on the extent to which hybridization occurs near the village of Chalco where teosinte is a common weed in and around the corn fields. In a field where teosinte oc-

curred abundantly as a weed permission was obtained from the owner to tag and harvest 500 consecutive plants. Of the 500 plants tagged, 288 proved to be maize, 219 were teosinte plants, and 3 were F_1 hybrids. Of the 288 ears classified as maize, 4 showed definite evidence of contamination with teosinte in earlier generations. In addition, one ear was found in an adjacent row (not part of the sample of 500 plants) which was identical in its characteristics with a first backcross to teosinte.

The plants in this field therefore furnished unmistakable evidence of hybridization, both present and during the recent past, between maize and teosinte. One plant out of every 167 plants in the field was a vigorous F_1 hybrid shedding abundant pollen which became part of the general pollen mixture in the field. The F_1 hybrids themselves, in spite of their vigor, have a low survival value. The Mexican farmer makes no distinction between teosinte and the F_1 hybrids. Both are left standing in the field when the corn is harvested. The pure teosinte disperses its seeds which are enclosed in hard bony shells, and a new crop of teosinte plants appears the following spring. But the F_1 hybrids have no effective means of seed dispersal, and their seeds, only partially covered, are quite vulnerable to the ravages of insects and rodents.

Both maize and teosinte are quite successful in occupying distinct niches in Mexican corn fields. The one, a cultivated plant, depends for its survival upon its usefulness to man. The other, a weed, depends for survival upon its well-protected kernels and its efficient method of dispersal. There is no such niche for the F_1 hybrid. It is discarded by man as a cultivated plant, and it cannot compete with teosinte as a weed. "Finding no friend in either nature or man" (to use Weatherwax's apt description) the F_1 hybrids would be of no evolutionary significance were it not for the fact that they hybridize with both parents. Thus there is a constant introgression of teosinte into maize and of maize into teosinte. In the vicinity of Chalco, in Mexico, this process has gone on so long and the teosinte has become so maize-like in all of its characters, that maize and teosinte plants can no longer be distinguished until after the pistillate inflorescences have developed. The teosinte of Chalco has "absorbed" the genes for hairy leaf sheaths and red color characteristic of the maize of the region. Individual plants of teosinte have been found which have the yellow endosperm color of corn, although teosinte is normally white-seeded.

The introgression of teosinte into maize in Mexico today is an established fact. The question is how long this process has been going on and whether it is strictly a local phenomenon or whether it has affected the maize varieties of America.

Practically all students of maize and its relatives recognize that teosinte varieties differ in the degree to which they have become maize-like. Longley (1941), for example, considers the teosinte of Southern Guatemala to be the least maize-like and that of Mexico the most maize-like.

Rogers (1950) has shown that teosinte varieties differ quite markedly in their genes governing the characteristics in which maize and teosinte differ, especially characters of the pistillate inflorescence, tillering habit, and response to length of day. He attributes these differences to varieties in the type and amount of maize germplasm which has become incorporated into teosinte.

If teosinte varieties differ in the amount and kind of maize contamination which they now contain, it is difficult to escape the conclusion that maize varieties must likewise differ in the amount of teosinte contamination. There is little doubt that maize varieties do differ in this respect.

Ancient Hybridization

The prehistoric maize from Bat Cave has already been briefly mentioned. The earliest Bat Cave corn, dated at approximately 2000 B.C., shows no evidence whatever of teosinte introgression. Beginning about midway in the series (which would be about 500 B.C. if the sequence were strictly linear but which, according to unpublished radio-carbon determinations made by Libby, is probably somewhat later) cobs make their appearance which are scarcely distinguishable from the cobs which we have produced experimentally by crossing corn and teosinte. Weatherwax (1950) regards this evidence of teosinte introgression as far from conclusive, and it is, of course, quite impossible to prove that a cob a thousand years or more old is the product of hybridization of maize and teosinte. Nevertheless, it is true that teosinte introgression produces certain definite effects upon the cob, as some of us who have studied the derivatives of teosinte-maize crosses on an extensive scale are well aware.

When it is possible to duplicate almost exactly in experimental cultures specimens found in nature, the odds are at least somewhat better than even that the resemblance between the two specimens is more than coincidence. There is little doubt in my mind that the later Bat Cave corn is the product of contamination with teosinte. Certainly it differs from the earlier Bat Cave corn quite strikingly, and it is exactly the way in which it would be expected to differ if it is the product of teosinte introgression.

Significance of Chromosome Knobs

Mangelsdorf and Reeves (1939) suggested some years ago that the deeply staining heterochromatic knobs, characteristic of the chromosomes of many varieties of maize, are the result of the previous hybridization of maize and teosinte, or more remotely of maize and Tripsacum. There has been much indirect evidence in support of this hypothesis (especially Mangelsdorf and Cameron, 1942; Reeves, 1944), and the recent studies of Wellhausen *et al.* on Mexican races of maize provide additional evidence of this nature. Chromosome knob number in Mexican races is closely correlated with the characteristics of the races. The four Ancient Indigenous races, assumed to be relatively pure corn, have an average chromosome knob number of 4.2.

The four Pre-Columbian Exotic races, also believed to be relatively free from contamination, have an average chromosome knob number of 4.3. The thirteen Prehistoric Mestizos and the four Modern Incipient races (all except one of which are assumed to involve teosinte introgression) have chromosome knob numbers of 7.1 and 8.0, respectively.

It is interesting to note that in races for which hybridization is postulated the hybrid race, although usually intermediate in chromosome knob number between its two putative parents, resembles most closely the parent with a high knob number. For the eleven hybrid races for which chromosome knob numbers are available, not only for the hybrid races but for the two suspected parent races, the data (Table 11.3) are as follows: the average of the lower-

TABLE 11.3
CHROMOSOME KNOB NUMBERS OF MEXICAN HY-
BRID RACES OF MAIZE AND OF THEIR
PUTATIVE PARENTS*

HYBRID RACE	RACE	PARENTS	
		Lower	Higher
Tabloncillo..............	7.6	low	8.0
Comiteco................	5.6	5.0	7.0
Jala....................	7.5	5.6	7.6
Zapalote Chico..........	11.7	5.5	9.0
Zapalote Grande.........	7.4	7.0	11.7
Tuxpeño................	6.1	6.3	9.0
Vandeño................	8.1	6.1	7.4
Chalqueño..............	6.8	1.0	6.1
Celaya....·..........	8.5	6.1	7.6
Conico Norteño..........	8.0	1.0	8.5
Bolita.................	8.6	7.6	11.7
Averages...........	7.8	5.1	8.5

* Data from Wellhausen *et al.*

numbered parent was 5.1 knobs, of the higher-numbered parent, 8.5 knobs, of the hybrid, 7.8 knobs. The fact that the average knob number in the hybrid races approaches the average knob number of the higher parents suggests, perhaps, that natural selection has tended to retain the maximum amount of teosinte introgression and hence the maximum number of knobs.

The Effects of Hybridizing Maize and Teosinte

There is no doubt that maize and teosinte are hybridizing in Mexico and Central America today, and there is at least a strong indication that they have done so in the past. What have been the effects of that hybridization?

One valid way of determining what happens when teosinte introgresses into maize is to produce such introgression experimentally. This has been done on an extensive scale by crossing an inbred strain of maize, Texas 4R-3,

with four varieties of teosinte, and by repeatedly backcrossing (three times in most instances) the hybrids to the inbred strain, retaining various amounts of teosinte germplasm through selection. The end result is a series of modified inbred strains approximately like the original 4R-3—all relatively isogenic except that parts of one or more chromosome segments from teosinte have been substituted for homologous parts from maize.

That the substitution involves chromosome segments or blocks of genes and not single genes is strongly indicated by the fact that the units have multiple effects and that there is breakage within the units in some cases, although in general they are transmitted intact. Their mode of inheritance and their linkage relations can be determined as though they were single genes. Yet each of the units affects many if not all of the characters in which maize and teosinte differ. The block of genes on chromosome 3, for example, although inherited intact as a single hereditary unit, affects number of ears, size of ear, number of seeds, size of seeds, number of rows of grain, staminate spikelets on the ear, and induration of the rachis. In addition it has a concealed effect, discussed later, upon such characters as response to length of day and the development of single spikelets. The block of genes on chromosome 4 has practically the same effects in somewhat greater degree, but this block shows definite evidence of breakage or crossing over which is of the order of 30 per cent.

These blocks of genes are not random samples of teosinte germplasm, but represent definite genic entities which are transmitted from teosinte to maize in the process of repeated backcrossing. Different varieties of teosinte yield comparable if not identical blocks of genes, and the same variety of teosinte in different crosses does likewise. Regardless of the amount of introgression of maize which teosinte has undergone in its past history, and regardless of the differentiation which has occurred between varieties of teosinte, there are still regions in all varieties of teosinte, perhaps near the centromeres, which have remained "pure" for the original genes.

Effects in Heterozygous Condition

When these blocks of genes are introduced into maize they have profound effects which differ greatly in the heterozygous and homozygous condition. Since maize and teosinte represent completely different morphological and physiological systems (especially from the standpoint of their pistillate inflorescences and their response to length of day), this substitution, of segments of chromatin from one species for homologous segments from the other, represents a drastic interchange of parts comparable, perhaps, to installing a carburetor or other essential part from one make of car into another. In the F_1 hybrid of corn and teosinte where the blocks of genes are heterozygous, there is no particular functional difficulty. Here the two complete systems are operating simultaneously and the result is a vigorous hy-

brid, vegetatively luxuriant, potentially capable of producing great numbers of seed. Measured solely by total grain yield, the F_1 hybrid does not exhibit heterosis since its grain yield is considerably less than that of corn, but measured in terms of number of seeds, or number of stalks, or total fodder, the hybrid certainly exhibits heterosis.

In the modified inbred in which a block of genes from teosinte has been substituted for a block of genes from maize, the situation is quite different. There are no functional aberrations so long as the block of genes from teosinte is heterozygous. Under these circumstances it has very little discernible

FIG. 11.3—Ears of a teosinte-modified inbred strain 4R-3 which are isogenic except for an introduced block of genes from chromosome 3 of Florida teosinte. The ear at the left lacks the block of teosinte genes, the center ear is heterozygous for it, the ear at the right is homozygous for it. Note the high degree of dominance or potence of the maize genes.

effect. Figures 11.3, 11.4, and 11.5 show ears of corn heterozygous for blocks of genes from chromosomes 3 and 4 respectively, compared to "pure" corn in the same progeny. The blocks of genes from corn are much more "potent" (a term proposed by Wigan, 1944, to describe the integrated dominance effects of all genes) than the block of genes from teosinte, at least in the striking characteristics which differentiate the two species. This is in itself a noteworthy phenomenon since corn is not strongly "dominant" or more potent than teosinte in the F_1 hybrid, where both species contribute more or less equally.

FIG. 11.4—These ears are the exact counterparts of those in Figure 11.3 except that the block of teosinte genes was derived from chromosome 4 of Florida teosinte.
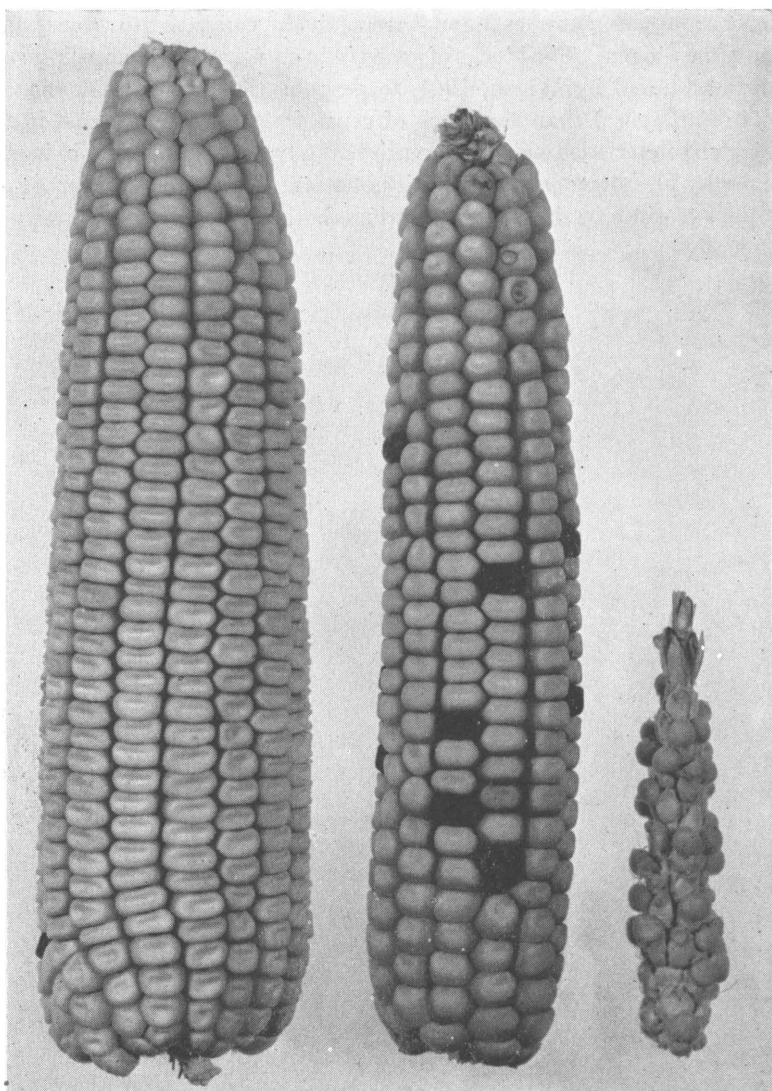
Fig. 11.5—When the inbred 4R-3 is crossed with No. 701 the hybrid ear illustrated above (*left*) is produced. When a modified strain of 4R-3 (*right*) which has had three blocks of genes from Durango teosinte substituted for corresponding maize genes is crossed with No. 701, the hybrid (*center*) is much more maize-like than teosinte-like. The hybrid, being multiple-eared, bears a substantially greater number of seeds than either parent and in one experiment was appreciably more productive.

The reason for the strong potence of maize over teosinte in blocks of genes introduced from teosinte into maize, is to be found in a phenomenon termed "antithetical dominance" which has been postulated by Anderson and Erickson (1941) on theoretical grounds. These writers assumed that in species hybrids such as that between maize and Tripsacum, the F_1 would be intermediate but that backcrosses to either parent would strongly resemble the recurrent parent. The basis for this assumption is that the possibilities for successful recombination of two such different systems is remote.

The conception of antithetical dominance has some relationship to Richey's opinion (1946) that dominance in some cases is no more than a condition where one allele is capable of doing the entire job, or most of it, while the other allele merely stands by. According to this interpretation, genes are not favorable because they are dominant, but are dominant because they are favorable. They reveal their presence by doing something.

There is, in any case, little doubt that something of the general nature of antithetical dominance or the kind of dominance postulated by Richey is involved in the teosinte-maize derivatives. Both teosinte and maize are about equally potent in the F_1 hybrid, but a small amount of teosinte germplasm incorporated into maize in the heterozygous condition is definitely lacking in potence.

Effects in Homozygous Condition

Since a block of teosinte genes introduced into maize is largely recessive in its effects when heterozygous, its effects should become much more apparent in the homozygous condition. This is indeed the case. The ear on the right in Figures 11.3, 11.4, and 11.5 illustrates the effects of one or more blocks of teosinte genes incorporated in a homozygous condition in the inbred strain 4R-3.

The combination of traits from corn and teosinte which occurs in these homozygous teosinte derivatives is characterized by a distinct lack of harmony in the development of the pistillate inflorescence. The husks are too short for the ears, the glumes are too small for the kernels and tend to constrict the growing caryopses producing misshapen kernels. The vascular system is inadequate for the number of kernels borne on the ear, and there are many shrunken kernels as well as numerous gaps where no kernels have developed. Germination of the seeds is often poor, and viability of short duration. Homozygous combinations of this kind obviously have a low survival value. Indeed it has been difficult to maintain some of them in artificial cultures.

These unfavorable effects of teosinte introgression in the homozygous condition may be nothing more than the result of substituting parts of one well-integrated system for corresponding parts of another. They may, however, also involve "cryptic structural differentiation" of the kind suggested by

Stephens (1950) for species of Gossypium, although the extent of this cannot be great, otherwise some combinations would be lethal. But whatever the cause, there is little doubt about the reality of the unfavorable effects. Therefore, if the repeated hybridization of corn and teosinte which has occurred in the past has had any permanent effect, one of two things or both must have happened: (1) The undesirable effects of teosinte have become recessive as the result of natural selection for modifying factors. (2) The regions of the chromatin involving teosinte genes have been kept heterozygous. There is some evidence that both may have occurred.

There is some evidence, by no means conclusive, that maize varieties of today have *absorbed* teosinte germplasm in the past and are now *buffered* against the effects of teosinte genes. There is at least no doubt that when the same variety of teosinte is crossed on a series of maize varieties, considerable variation is displayed by the F_1 hybrids in the potence of the maize parents.

In general, varieties which show some evidence of previous contamination with teosinte are more likely to produce maize-like F_1 hybrids than those which do not show evidence of such contamination. Corn Belt inbreds as a class produce the most maize-like F_1 of any of stocks tested. Figure 11.6 illustrates a case where a South American stock (an inbred strain derived from the Guarany corn of Paraguay) is less potent in crosses with two varieties of teosinte than is a North American stock (a genetic tester). I also have observed that blocks of teosinte genes introduced into an inbred strain of Guarany by repeated backcrossing have a greater effect than these same blocks introduced into Texas 4R-3 or Minn. A158, both of which seem already to contain appreciable amounts of teosinte.

If the increased potency of teosinte-contaminated maize proves to be generally true, then the reason for it is that there has been a selection of modifying factors which have tended to suppress the most unfavorable conspicuous effects of the teosinte introgression. Otherwise, varieties of maize containing teosinte germplasm should produce hybrids which are more teosinte-like, rather than more maize-like, than the average. This is convincingly demonstrated experimentally by crossing the original inbred 4R-3 and one of its modified derivatives with the same variety of teosinte (Florida type). The results are illustrated in Figure 11.7.

The F_1 of 4R-3 × teosinte is a typical F_1 hybrid, intermediate between its parents. It has both single and double spikelets and, although the fact is not revealed by the illustration, it has approximately the same type of response to length of day as does maize. In marked contrast, when a derived strain of 4R-3 (in which a block of teosinte genes on chromosome 3 has been substituted for a corresponding block of maize genes) is crossed with the same teosinte, the F_1 hybrid is scarcely distinguishable in its pistillate spike from pure teosinte. Furthermore, it has teosinte's response to length of day. Plants of this hybrid started in the greenhouse in February did not flower

until the following October and November. This derivative of a maize-teosinte hybrid, therefore, carries at least two concealed characteristics of teosinte: single spikelets and response to length of day. Genes for these two characters do not express themselves in the derivative itself, but their presence becomes immediately apparent when the derivative is crossed with teosinte. The situation is comparable to the concealed genes for hair color and texture
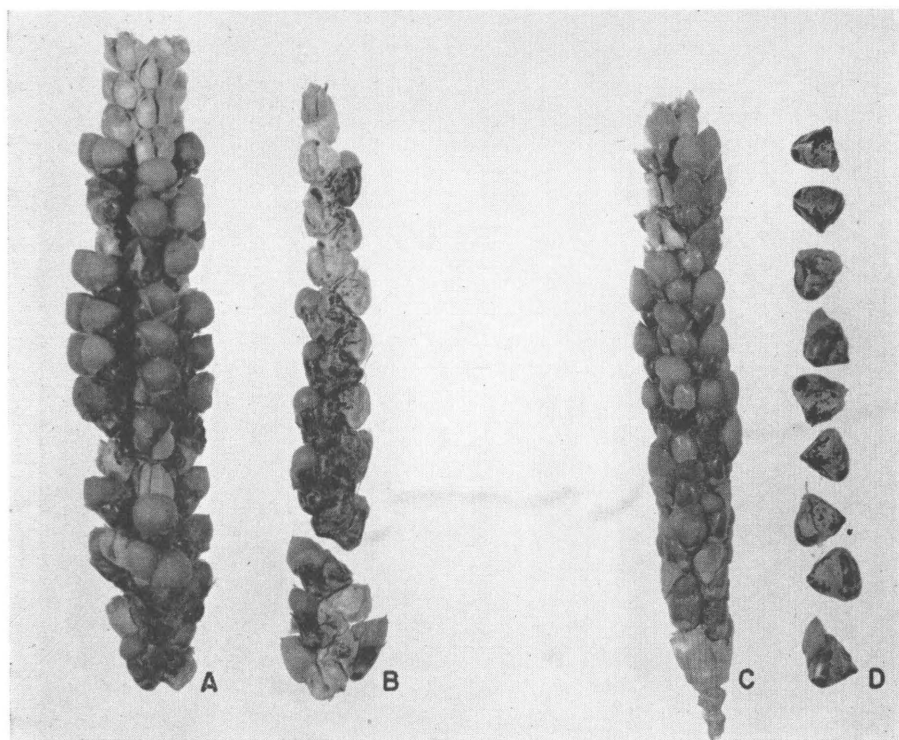

FIG. 11.6—A North American stock is more potent in crosses with Nobogame teosinte (*A*) and Durango teosinte (*C*) than the Guarany corn from Paraguay (*B* and *D*). This is attributed to previous introgression of teosinte accompanied by the evolution of modifier complexes in North American varieties.

in persons who are completely bald. The genes are there but have no opportunity to express themselves.

Since varieties of maize which appear to be the product of previous teosinte contamination, such as those of the Corn Belt, behave quite differently in crosses from stocks known to be contaminated, there is at least an indication that such contamination has become modified through selection acting upon the modifier complex. More data are obviously needed on this problem.

A second question which arises in considering the effects of the natural hybridization of corn and teosinte is whether there is any mechanism which

tends to maintain the maize-teosinte loci in a perpetual state of heterozygosity. It already has been shown that homozygous teosinte genes in the maize complex are decidedly deleterious. Therefore, if the teosinte genes are
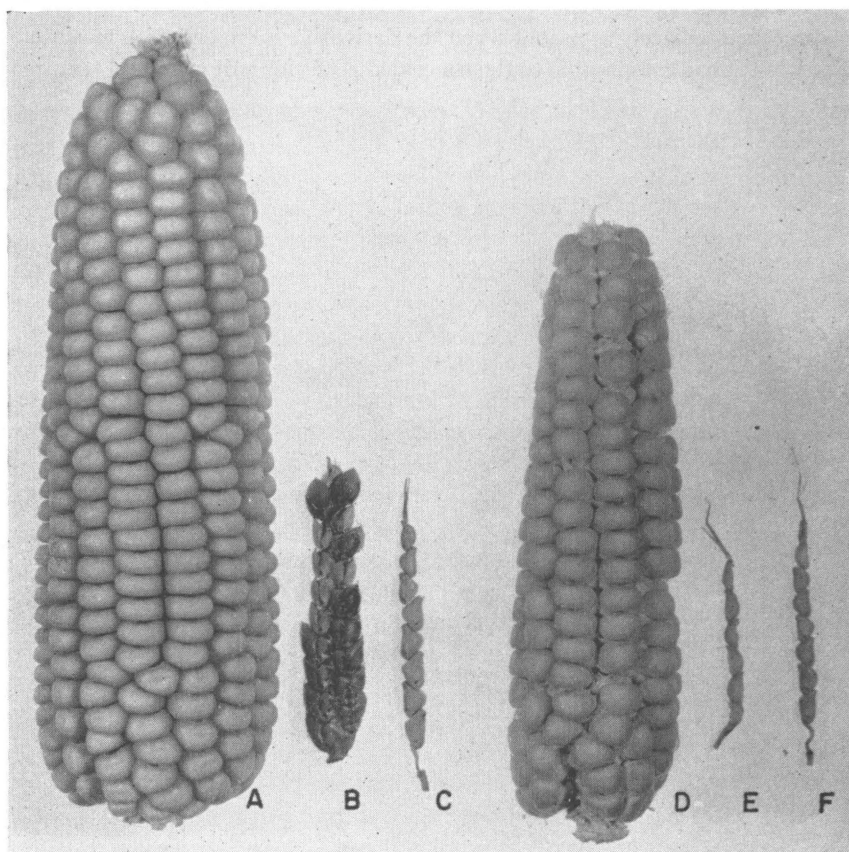

FIG. 11.7—When the inbred 4R-3 (A) is crossed with Florida teosinte (C), the F_1 hybrid ears (B) are maize-like in having four-ranked ears, some double spikelets, and partially naked seeds. When a teosinte-modified strain of 4R-3 (D) is crossed with Florida teosinte (F), the F_1 hybrid (E) is much more teosinte-like. The spikes are two-ranked, single, and the seeds are completely enclosed. The teosinte derivative obviously carries "concealed" genes for these teosinte characteristics.

to survive their deleterious effects, they must be modified through selection or the genes must be maintained in a more or less heterozygous state. It may be assumed that the latter mechanism would operate only if heterozygosity for a group of maize-teosinte genes confers a distinct selective advantage making the heterozygous combination superior, not only to the homozygous teosinte genes (as it obviously is) but also to the corresponding homozygous maize genes.

Data are available both from my experiments and those of R. G. Reeves (1950), conducted independently, to indicate that heterozygosity for a block of teosinte genes does sometimes confer a selective advantage. In 1944, in my experiments, five Corn Belt inbred strains were crossed with the Texas inbred 4R-3, as well as with four modified strains of 4R-3 in which teosinte genes had been substituted for maize genes. The four modified strains may be briefly described as follows:

Strain	No. Blocks Genes	Teosinte Variety
Modified 4R-3 Strain A.........	2	Florida
Modified 4R-3 Strain B........	2	Florida
Modified 4R-3 Strain C.........	3	Durango
Modified 4R-3 Strain D.........	3	Durango

The F_1 hybrids were grown in 1945 in two replications in a modified Latin-Square yield test. Several hybrids were omitted for lack of sufficient seed. The results are shown in Table 11.4.

TABLE 11.4

AVERAGE YIELDS IN BUSHELS PER ACRE OF HYBRIDS OF CORN BELT INBREDS WITH TEXAS 4R-3 AND ITS TEOSINTE-MODIFIED DERIVATIVES

4R-3 OR DERIVATIVE	CORN BELT INBREDS				
	K155	38–11	L317	701	CC24
4R-3 (check)...........	108.6	85.2	99.0	100.2	100.2
Modified Strain A......	102.6	....	....	87.0	88.8
Modified Strain B......	126.6*	82.8	109.8	....	78.6
Modified Strain C......	94.2	75.6	66.0	97.8	92.4
Modified Strain D......	93.0	57.0	71.4	146.4*	79.8

* Difference probably significant.

Of the 17 hybrids tested, only 3 proved to be better than the corresponding checks in total yield, and in only 2 of these is the difference significant. Although the data are not extensive, there is some indication that the Corn Belt inbred strains used in these experiments differ in their ability to "combine" with the teosinte derivatives.

Perhaps more important than total yield, from the standpoint of selective reproductive advantage, is total number of seeds per plant (Table 11.5). Here 6 of the 15 hybrids for which data are available were superior to the checks, 4 of these significantly so.

These results, so far as they go, are in agreement with the recently published results of Reeves (1950). Reeves tested 49 modified 4R-3 lines in hybrids with a common tester. He found none significantly better than the check in yield, although several were superior in heat-tolerance. Reeves

found, however, that when teosinte germplasm was introduced into another inbred strain, 127C, the results obtained in the hybrids were somewhat different. In 1946, 6 hybrids out of 25 were better than the check, 3 of them significantly so. In 1947, 15 hybrids out of 49 were better than the check, 6 of them significantly so. Reeves suggested that the difference between 4R-3 and 127C in their response to teosinte introgression lies in the fact that 4R-3 already contained considerable amounts of teosinte germplasm while 127C does not. The suggestion is supported by differences in the morphological characteristics of the two lines.

There was also an indication in Reeves' experiments that the entries with

TABLE 11.5

AVERAGE NUMBERS OF SEEDS PER PLANT IN HYBRIDS OF
CORN BELT INBREDS WITH TEXAS 4R-3 AND ITS
TEOSINTE-MODIFIED DERIVATIVES

4R-3 OR DERIVATIVE	CORN BELT INBREDS				
	K155	38–11	L317	701	CC24
4R-3 (check).............	849	636	925	1132	1179
Modified Strain A.........	756	....	....	1095	807
Modified Strain B.........	937	....	1107*	....	....
Modified Strain C.........	1419*	809	746	1696*	885
Modified Strain D.........	770	573	843	1811*	864

* Difference probably significant.

teosinte genes made their best showing in 1947, a season of severe drought.

Considering all of the results together it may be concluded that: (a) blocks of teosinte genes in the heterozygous condition do in some instances improve the total yield of the plants which contain them; (b) even more frequently do such blocks of genes increase the total number of seeds produced; (c) there is some evidence that the teosinte derivatives impart resistance to heat and drought to their hybrids.

In those crosses in which the heterozygous combination is superior to either of the homozygous combinations, a block of maize genes or a block of teosinte genes, natural selection would undoubtedly favor, at least initially, the heterozygous combination. If the block of genes were one involving the region of the centromere where crossing-over is reduced, it is quite possible that the block of genes would be retained more or less intact for a considerable number of generations. The maintenance of heterozygosity through natural selection also would be promoted if, as in the case of Drosophila studied by Dobzhansky, one set of genes is superior in adapting the organism to one kind of environment while the other set contributes to adaptation

to a wholly different environment which the organism also encounters periodically.

It cannot be proved that such a situation exists in the case of maize which has become contaminated with teosinte, but it is quite possible that it does. For example, human selection when practiced would tend to favor the larger-seeded, larger-eared individuals with a minimum of teosinte contamination. Natural selection would favor the individuals with the larger number of seeds, hence those with an appreciable amount of teosinte contamination. These two forces operating simultaneously or alternately would tend to perpetuate the heterozygote. Similarly, if maize germplasm were superior in seasons of excessive moisture and teosinte germplasm in seasons of drought (for which there is some evidence), there would be a tendency for natural selection to perpetuate heterozygous combinations. It cannot be demonstrated that any of these hypothetical situations actually exist. There is no doubt, however, that present-day maize is highly heterozygous, and there is more than a suspicion that repeated hybridization with teosinte has been responsible for part of the heterozygosity.

DISCUSSION

The present-day heterozygosity of maize may involve a variety of different factors and forces which have operated during its past history. Two of these are now reasonably clear: interracial hybridization, and introgression of teosinte into maize.

When interracial hybridization occurs, hybrid vigor not only manifests itself in the first generation, but also persists in part through an indefinite number of subsequent generations. Maize under domestication is, therefore, potentially a self-improving plant. The evidence from Mexican races of maize indicates that repeated interracial hybridization has been an extremely important factor in the evolution of maize in Mexico. There is every reason to believe that the situation in Mexico, so far as interracial hybridization is concerned, is typical of other parts of America.

The second factor, introgression of teosinte, which is believed to have played an important role in the evolution of maize, is not so easily demonstrated. There is no doubt, however, that teosinte is hybridizing with maize in Guatemala and Mexico today, or that this hybridization has occurred in the past. It would be surprising indeed if such hybridization had no effect upon the evolution of maize. There is every indication that it has had a profound effect. All of the most productive modern agricultural races of maize in Mexico show evidence of contamination with teosinte, not only in their external characters, but also in their internal cytological characteristics.

It can be shown experimentally that teosinte germplasm, when introduced into maize, may sometimes have a beneficial effect when heterozygous, but is always deleterious when homozygous. Therefore it follows that after maize

and teosinte have hybridized, and after there has been an introgression of teosinte into maize: (1) the teosinte genes must be eliminated or, (2) their effects must be changed through the accumulation of a new modifier complex, or (3) they must be kept in a heterozygous state. There is evidence, but not final proof, that both of the two last-named factors have operated during the evolution of maize. Interracial and interspecific hybridization accompanied by sustained heterosis are therefore regarded as two important factors in the evolution of maize.

SUMMARY

1. Evidence is presented to show that both interracial and interspecific hybridization, accompanied by heterosis, have been factors in the evolution of maize.

2. The races of maize of Mexico are cited as an example of interracial hybridization. Of the 25 Mexican races described by Wellhausen *et al.*, 14 are considered to be the products of interracial hybridization.

3. The hybrid vigor, which occurs when races of maize are crossed, is capable of persisting in part in subsequent generations. Maize under domestication is therefore potentially a self-improving plant.

4. Interspecific hybridization of maize and teosinte is occurring in Guatemala and Mexico today, and there is evidence—archaeological, morphological, and cytological—that it has occurred in the past.

5. Introgression of teosinte into maize in experimental cultures is sometimes beneficial when the teosinte genes are heterozygous, but is always deleterious when they are homozygous.

6. It, therefore, seems probable that the persistence of teosinte germplasm in races of maize has been accompanied either by development of modifier complexes which have made the teosinte genes recessive in their action, or by the maintenance of a continued state of heterozygosity.

7. The possibility that heterozygosity in maize has been preserved by natural selection as it has been in Drosophila is discussed.