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Fertility Relationships in Maize-Teosinte Hybrids

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Digest

This bulletin reports the degree of fertility found in crosses of maize with several different varieties of teosinte. The teosintes used were the Mexican varieties Durango, Chalco, Nobogame and New, and the Guatemalan varieties Huixta and Florida.

Hybrids of the Mexican teosinte varieties with maize exhibit approximately normal fertility, although the percentage fertility increases slightly with the use of the Chalco, Nobogame and Durango varieties, respectively. Hybrids of maize with the Huixta variety of northern Guatemala exhibit relatively normal fertility, although the percentage is somewhat below that found in the Mexican teosinte-maize hybrids. In contrast, the F_1 hybrid of maize with the Florida variety of southern Guatemala shows an average pollen fertility of 49 percent.

A study of several backcross populations involving the Florida teosinte variety reveals that the maize parent has a pronounced effect on the degree of sterility, and that a definite linkage exists between sterility and marker genes on chromosome 4. These results indicate that some factor or factors on the fourth chromosome, located very close to Tu, and between Tu and su_1, account for most of the sterility in this hybrid involving the Florida variety.

Results from this experiment, as well as the findings of other workers, indicate that the Mexican teosintes, northern Guatemalan teosintes and maize are similar in chromosome structure. In addition, the existing evidence indicates that differences on the fourth chromosome are of primary importance in distinguishing the southern Guatemalan teosintes from maize, and to some extent from the other teosinte varieties.

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Fertility Relationships in Maize-Teosinte Hybrids

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MAIZE IS A MEMBER of the grass family Gramineae, and all types are classified within a single species, *Zea mays* L. Annual teosinte, which is the closest known relative of maize, has the same chromosome number, 10, and produces fertile hybrids when crossed with maize. Teosinte was originally assigned the generic rank of *Euchlaena* Schrad., as separate from *Zea* L., but Reeves and Mangelsdorf (11) have proposed a revision making *Euchlaena* and *Zea* congeneric, and suggested that annual teosinte be designated as *Zea mexicana* (Schrad.) R. & M.

Fertile hybrids between maize and teosinte were first produced by Harshberger (3), who called attention to this as proof that they were close relatives. Studies of maize-teosinte hybrids have been conducted by numerous investigators since that time, and all have shown that the two species may be crossed easily and fertile hybrids obtained. Although the maize-teosinte hybrids so far investigated have proved fertile, the degree of fertility has been found to depend somewhat on the variety of teosinte used in the cross. Likewise, cytological observations of hybrids involving certain varieties of teosinte have shown that the chromosomes do not always pair normally.

Kuwada (4) reported that the F_1 hybrids of maize and Florida teosinte, a commercial variety which was originally obtained from southern Guatemala, had regularly 10 pairs of chromosomes, but in two of the pairs the chromosomes were of different lengths. Longley (5), in a study of the F_1 hybrids of maize and the Chalco variety from Mexico, found 10 bivalents of regular behavior at meiosis. Beadle (2) studied F_1 hybrids of several varieties of teosinte with maize, and found no irregularities during meiosis in crosses involving the Mexican varieties Durango and Chalco. However, in Florida teosinte-maize hybrids two unpaired bivalents were frequently present, and sometimes as many as four were found. Pollen sterility in this hybrid was approximately 32 percent. In a cross between Durango and Florida teosinte the pollen sterility averaged as high as 66.8 percent, and examinations at meiosis showed more irregular behavior than was found in the Florida teosinte-maize hybrid. Mangelsdorf and Reeves (9) studied the fertility in hybrids of Florida and Durango teosinte with maize, and reported that the Florida teosinte-maize hybrids produced approximately 50 percent sterile pollen, while the Durango teosinte-maize hybrids exhibited normal fertility.

Detailed cytological investigations have produced evidence as to the exact chromosomes involved in the irregular behavior of certain maize-teosinte hybrids. In a study of pairing relations between corn and teosinte chromosomes, through the use of translocations which served as chromosome markers, Arnason (1) found that chromosomes 1, 2 and 6 behaved regularly in both Durango and Florida teosinte hybrids with maize, as did also chromosome 7 in a Florida teosinte-maize hybrid. Two heteromorphic pairs were observed in the cross with Florida teosinte, but they were not identified, although chromosome 5 was suspected of being one of the unequal pairs, and chromosome 8, 9 or 10 the other.

Longley (6) studied the chromosome morphology of several varieties of teosinte from Mexico and Guatemala. He reported that chromosomes of the Mexican teosintes most nearly resembled those of maize, while chromosomes of the teosintes from northern Guatemala were somewhat more maize-like than those from southern Guatemala. A cytological examination of chromosomes in Florida teosinte-maize hybrids revealed that chromosomes 5 and 9 of teosinte were consistently longer than their maize homologs, and that the long arm of these two chromosomes did not always pair completely. Longley (7) also reported that from one to four chromosome bridges are not uncommon in Florida teosinte-maize hybrids, indicating that there may be several differences in the linear arrangement of the genes between the two parents.

O'Mara (10) studied hybrids of maize with the Guatemalan varieties Nojoya, Moyuta and Florida, and found that the Nojoya hybrid was quite normal at meiosis, but that the latter two were somewhat irregular. Two and four univalents were found in both the Florida and Moyuta hybrids with maize, and bridges or fragments were often present at metaphase. Cytological observation of a Florida-Nojoya teosinte hybrid revealed the same type of behavior as found in the Florida teosinte-maize hybrid. In addition, a detailed analysis of each chromosome in this hybrid indicated, that with respect to maize, Florida teosinte had an undetermined rearrangement in the long arm of chromosome 4, as well as rearrangements on chromosomes 8 and 9. The Nojoya teosinte-maize hybrid produced normal pollen, while approximately one-third of the pollen was deficient in starch in the hybrid of Florida teosinte with maize.

These previous studies of maize-teosinte hybrids reveal that the teosinte varieties of Mexico and northern Guatemala produce hybrids with maize of normal fertility and regular meiotic behavior. The varieties from southern Guatemala, however, when crossed with maize, have in all instances shown a marked degree of sterility in addition to irregular meiotic behavior.

The experiment reported in this bulletin was conducted to determine the degree of sterility in F_1 hybrids between maize and several teosinte varieties, and if possible to determine the mechanism and chromosomes leading to this partial sterility in certain maize-teosinte hybrids.

Materials and Methods

The teosintes used in this study were the Mexican varieties Durango, Chalco, Nobogame and New, and Huixta from northern Guatemala, and Florida, an importation to this country from southern Guatemala. In addition to the F_1 hybrids of these teosintes and maize, several maize backcross populations, as well as several inter-varietal teosinte hybrids, were studied.

Since it has been shown that Florida teosinte-maize hybrids exhibit a considerable degree of sterility, a more extensive study was made with this particular variety of teosinte. Maize stocks with marker genes were crossed with Florida teosinte, and the F_1 hybrids were backcrossed to recessive maize stocks. In this manner, by classification of the backcross progenies, any linkage of pollen sterility with marker genes on particular chromosomes might be determined. All chromosomes, with the exception of the second and seventh, were tested by the use of such genes.

Samples from all plants studied were obtained by shaking pollen into small glassine bags so that it might be stored and examined at a later date. Examination of the pollen was made by mounting the samples in lactic acid to which a few drops of iodine had been added. This procedure restored the grains to their normal size, and made the normal type distinguishable from those which had aborted. Slides were made of the pollen collected from each plant in all populations, and approximately 300 grains were counted on each slide. All grains staining dark and appearing to be of normal size were counted as fertile, and all other types were designated as sterile. In this latter class three main types could be distinguished: those completely devoid of starch and often collapsed, grains of approximately normal size but with only a small amount of starch, and grains below normal in size and usually somewhat deficient in starch content. After counts were made from samples of all plants, the percentage fertility was determined for each individual plant.

Mexican Teosinte-Maize Hybrids

Pollen examined from the F_1 hybrid of Durango teosinte x maize was normal in appearance. An average of 99.0 percent fertile pollen was obtained in a count of 25 plants. Pollen was also examined from a large number of plants in two (Durango teosinte x maize) x maize backcross populations, and none of the plants exhibited an abnormal degree of sterility. About three-fourths of the plants examined in both progenies were above 95 percent in fertility, while the others were only slightly below this figure.

The F_1 hybrids of Chalco teosinte x maize also exhibited relatively normal fertility, although the average percent of fertile pollen was slightly less than that for the Durango teosinte-maize hybrids. Samples from 30 plants gave an average of 95.8 percent fertile pollen.

These results indicate that the chromosomes of the Chalco variety, although still quite similar to those of maize, differ to a slightly greater degree than do those of the Durango variety. Certain gene combinations may occasionally be obtained through segregation which do not permit normal pollen development. It is also possible that irregularities in meiosis may sometimes occur due to small differences in homology between the parental chromosomes. At least it seems reasonable to conclude that the chromosomes of the two parental types do not always complement each other, and that such differences lead to the slightly below-normal fertility found in the Chalco teosinte-maize hybrids.

A somewhat different situation from that found in either the Durango or Chalco teosinte-maize crosses was encountered on examination of the Nobogame teosinte-maize hybrid. Of the 30 F_1 plants examined, 24 were essentially normal with an

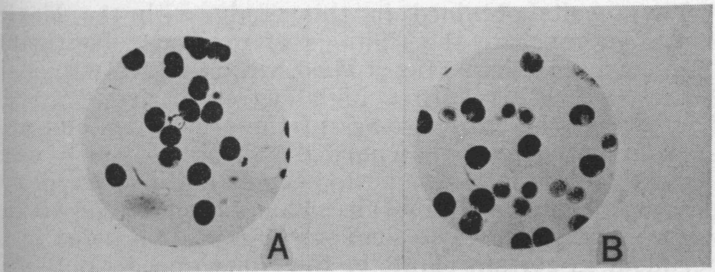

Figure 1. Pollen from plants of the F_1 hybrid Nobogame teosinte x maize. A. Normal pollen. B. Semi-sterile pollen.

average fertility of 96.7 percent, while the other 6 were semi-sterile with an average fertility of 50.2 percent. The abortive pollen of the semi-sterile plants was usually small with very little starch, although a few of the grains were completely empty. Pollen samples from both types of plants are shown in Figure 1. It was evident from this examination that the Nobogame teosinte used as a parent was segregating for some factor causing small or empty pollen. A reciprocal translocation would behave in this manner; however, no cytological evidence has been obtained on these semi-sterile plants which might verify this possibility. The average pollen fertility in the normal F_1 plants of this cross, although higher than that of the maize-Chalco hybrid, is still lower than the fertility of the maize-Durango hybrid. Apparently the Nobogame variety is somewhat intermediate between the Durango and Chalco varieties on the basis of their chromosomal homology with respect to maize.

In addition to the F_1 hybrid, two backcross progenies of (Nobogame teosinte x maize) x maize were examined for pollen sterility. All plants of the first progeny examined were normal in pollen fertility. Evidently a normal F_1 plant had been used in making this backcross to the maize parent. The other Nobogame teosinte-maize backcross examined, however, showed a segregation for normal and semi-sterile plants. Of the 50 plants examined, 20 were of the normal type and 30 were semi-steriles. The former group averaged 96.2 percent fertile pollen, while the latter averaged 59.4 percent. This behavior indicates that a semi-sterile plant was used in making this backcross, and that the semi-sterile condition is inherited as a dominant character. The ratio of normal to semi-sterile plants does not depart significantly from a 1:1 ratio, so it is entirely possible that one factor, such as a reciprocal translocation, is responsible for this condition.

The results obtained in this study with the Mexican teosintes corroborate the findings of previous investigators. All Mexican varieties so far studied, when crossed with maize, produce F_1 hybrids with a high degree of fertility. This indicates that the chromosomes of these teosintes and maize are quite similar, and that normal pairing ordinarily occurs at meiosis. This latter fact has been established by all cytological studies made on hybrids including any of the Mexican teosintes and maize. The semi-sterile condition noted in this experiment in certain plants of the Nobogame teosinte-maize F_1 hybrid is apparently an exception to the general condition, and resulted from the use of a particular plant which was not representative of the variety.

Guatemalan Teosinte-Maize Hybrids

Samples from 17 plants of a Huixta teosinte-maize hybrid revealed an average pollen fertility of 89.7 percent. This percentage is definitely below that ordinarily found in either corn or teosinte, and indicates there is sufficient difference between the parental chromosomes to cause some sterility. Although no cytological studies of Huixta teosinte-maize hybrids have been conducted, O'Mara (10) reported constant and regular pairing in a hybrid of maize with a variety from Nojoya in northern Guatemala which is quite similar to Huixta. This indicates the sterility of the maize-Huixta hybrid does not occur as a result of irregularities at meiosis, but is caused by gene differences between the two parental forms. It is possible that segregation in this F_1 hybrid results in a few disharmonious gene combinations which bring about abnormal pollen development and consequent sterility. Certainly, this lower fertility in the Huixta teosinte-maize hybrid indicates that chromosomes of the Huixta variety differ from maize chromosomes to a greater extent than do those of the Mexican varieties studied.

The Florida teosinte-maize hybrid was the only one of the crosses studied to exhibit a consistently high degree of sterility. The average pollen fertility for the 15 plants examined was 49 percent, and fertility among individual plants varied from 37.0 to 60.0 percent. Pollen samples from both parents and the F_1 hybrid are shown in Figure 2.

The nine backcross populations involving Florida teosinte show that an extreme amount of variability in pollen sterility exists among the various crosses. The classification of all progenies, according to the percentage of plants in each population which occurs at different fertility levels, is shown in

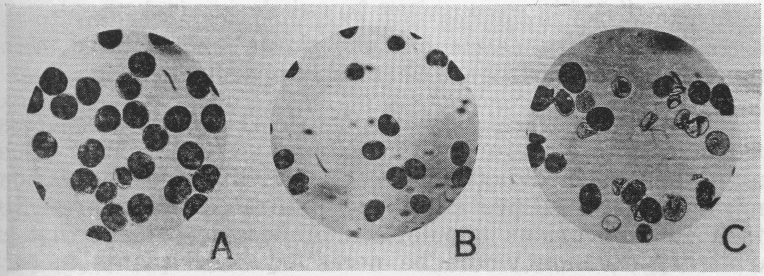

Figure 2. Pollen from plants of A. maize, B. Florida teosinte and C. Florida teosinte x maize.

Table 1. In some progenies, more than half the population is above the 90 percent level of fertility, while practically no plants aproach the 50 percent level. On the other extreme, one of the crosses has practically no plants above 90 percent fertility, while almost half of the population is either approaching or below the 50 percent level. Other progenies are intermediate between these types.

These observations indicate clearly that the maize stocks have a decided effect upon the amount of sterility in the backcross population. These populations show that in most cases there is a very small number of plants with as great an amount of sterility as is found in the F_1 hybrids, which indicates that more than one factor, as well as an interaction of factors, may be the cause of this sterility produced between hybrids of the two species. Because of the continuous distribution, as shown in Table 1, it has been impossible to divide

Table 1. The percentage of plants in each (Florida teosinte x maize) x maize progeny at different pollen fertility levels

Total plants	103	74	54	131	68	77	335	162	86
Percent pollen fertility	Percentage of plants								
95-100	38.8	5.4	0	12.2	36.7	9.1	14.6	14.8	22.1
90-95	24.3	12.2	5.6	20.6	30.8	20.7	18.8	21.6	30.1
85-90	11.7	21.6	9.2	32.8	13.2	16.9	21.5	29.6	18.6
80-85	10.7	14.9	13.0	14.5	10.3	11.7	20.0	19.2	19.8
75-80	6.8	10.8	13.0	9.9	3.0	11.7	11.9	8.0	1.2
70-75	2.9	5.4	11.1	6.1	1.5	11.7	4.2	3.1	3.5
65-70	1.9	8.1	3.7	.8	3.0	7.8	3.6	2.5	1.2
60-65	1.0	6.8	7.4	.8	1.5	3.9	1.5	0	2.3
55-60	0	4.0	7.4	0	0	0	.6	0	0
50-55	1.9	4.0	9.2	0	0	1.3	.9	1.2	0
Below 50	0	6.8	20.4	2.3	0	5.2	2.4	0	1.2

these backcross progenies into exact classes according to the degree of fertility, as most of the plants are clustered in the upper range of fertility without an apparent dividing line.

It was the original intention to classify these backcross progenies into certain fertility groups, so that linkage values might be obtained between pollen sterility and the various marker genes. However, as no natural division presented itself in the various populations, it became evident that an arbitrary division would be necessary. All plants in each population were first arranged in descending order according to their percent fertility. Each population was then divided into five groups of equal size, the first group containing the plants with the highest fertility, the second group those with the next highest fertility, and so on. By making these divisions it was possible to determine whether any linkages existed between sterility and the marker genes; for if such a linkage existed, the teosinte allele of the marker gene exhibiting the linkage would be expected to appear less frequently in the upper fertility groups and more frequently in the lower fertility groups. If no linkage existed, the marker genes would be expected to occur with approximately the same frequency at each of the five fertility levels.

The results of the division of these different progenies are shown in Table 2. Tests for linkage were made by calculating chi-square values on the basis of independent assortment of the marker genes within the five fertility levels. The P values obtained by this method for each of the progenies studied are also included in Table 2.

The gene *Tu* on chromosome 4 is the only marker gene studied which exhibits a highly significant deviation from the values expected by independent assortment. This deviation is in the direction expected if a linkage exists between this gene and sterility. As there is an indication of linkage with the su_1 and gl_3 genes, also on chromosome 4, it seems certain that this chromosome is involved with some sterility factor. There is a definite tendency for the plants carrying the teosinte alleles of these two genes to appear in the lower fertility levels more often than would be expected by chance, and significant deviations would in all probability have been obtained if larger populations in which these genes were segregating had been grown.

No marker genes on the other chromosomes show deviations which are significantly different from those expected by random assortment. The gene lg_2 exhibits a deviation

Table 2. Linkage relations of marker genes with pollen sterility

Chrom.	Marker gene	Number of plants in each of five fertility levels: 1	2	3	4	5	Total	P Value
1	P	50	50	53	61	48	262	
	p	50	49	46	38	51	234	
							496	.37
1	bm_2	8	7	6	5	5	31	
	Bm_2	3	4	5	6	5	23	
							54	.70
3	a_1	14	14	16	12	13	69	
	A_1	12	12	10	14	12	60	
							129	.90
3	lg_2	11	5	15	14	12	57	
	Lg_2	15	21	11	12	13	72	
							129	.05
4	su_1	7	7	4	2	2	22	
	Su_1	7	7	10	11	11	46	
							68	.11
4	gl_3	7	5	2	2	3	19	
	Gl_3	7	9	12	11	10	49	
							68	.19
4	Tu	6	6	0	1	0	13	
	tu	12	11	17	16	17	73	
							86	.01
5	bm_1	8	8	7	8	7	38	
	Bm_1	8	8	8	7	8	39	
							77	.99
6	Y	17	26	14	15	18	90	
	y	24	15	26	25	21	111	
							201	.08
6	Pl	74	76	64	60	58	332	
	pl	52	50	61	65	66	294	
							626	.10
8	j_1[1]	1	2	1	4	1	9	
	J_1	10	9	10	7	9	45	
							54	.36
9	wx	3	2	5	4	2	16	
	Wx	8	9	6	7	8	38	
							54	.60
10	g_1	5	6	3	3	6	23	
	G_1	6	5	8	8	4	31	
							54	.41

[1]Segregating in 3:1 ratio.

which approaches significance, but its distribution in the various fertility levels does not show the definite trend that might be expected if a linkage existed, and the deviation which does occur is in the wrong direction to indicate linkage. There is a slight indication of linkage between sterility and the genes *Y* and *Pl* on chromosome 6. However, as the populations in both crosses are quite large, and the distribution of the marker genes in the five fertility levels does not show a strong trend suggesting linkage, if a linkage does exist it is certainly very slight.

Another striking feature concerning the genes on chromosome 4 is the marked deficiency of the maize alleles exhibited by the backcross populations. Only 15.1 percent tunicate, 30.7 percent glossy and 33.3 percent sugary segregates were recovered. Similar results were obtained by Mangelsdorf and Reeves (9) when they recovered 15.1 percent tunicate and 38.7 percent sugary segregates in the same type of backcross populations. Although the cause of these deficiencies cannot be determined from these data, it seems reasonable to conclude that they are related to the sterility which is found in these maize-teosinte hybrids. Certainly, the discovery of a linkage between sterility and these genes on chromosome 4 lends credence to this supposition.

Inter-Varietal Teosinte Hybrids

In addition to the pollen sterility studies of various maize-teosinte hybrids, a study was made of F_1 hybrids between several varieties of teosinte. The varieties used in this study were New, Florida, Durango, Nobogame and Chalco. The last three are Mexican teosintes and the Florida variety is of Guatemalan origin. The native habitat of the New teosinte is unknown, as it was originally obtained from the U. S. Department of Agriculture without any data on this point. In gross morphology and appearance, however, it resembles a great deal the Mexican teosinte varieties.

It was originally intended to make all possible crosses between these varieties, but due to differences in blooming dates it was possible to make only a part of them. Relatively few seed were obtained from each cross, and as all of these did not germinate successfully, only a few hybrid plants were obtained. All were examined for pollen fertility, and the results are given in Table 3.

The pollen sterility in these hybrids suggests that the Nobogame, Durango and New varieties are very similar in

Table 3. Percent pollen fertility for all plants of inter-varietal teosinte hybrids

Percent fertility of individual plants							
	Nobogame	Nobogame	Durango	New	Nobogame	Florida	Florida
	New	Durango	New	Chalco	Chalco	Chalco	New
	97.0	93.9	96.0	95.3	94.7	83.8	61.5
	96.7	93.8	95.2	95.1	94.1	79.5	55.5
	95.9	93.3	93.8	92.8	91.2	66.7	50.8
	95.7	93.1	92.9	90.8	89.9	55.0	50.7
	95.6	92.5	49.2	85.4	88.6	48.9	48.5
	95.5	92.1		82.4	85.1	39.0	46.6
	95.0	91.1		78.0	81.7	37.5	31.4
	94.2	87.7		62.3	79.3	28.9	28.9
	92.7				72.2	20.0	
	92.4				68.9		
	89.9						
	85.4						
Ave.	93.8	92.2	85.4	85.3	84.6	51.0	46.7

chromosome structure. All hybrid plants involving only these three strains, with one exception in the New x Durango cross, show a rather high degree of fertility. The Chalco variety seems to be somewhat different from these three varieties, as in hybrids of Chalco with either New or Nobogame teosinte, the pollen fertility is inclined to be lower than in crosses where the others alone are involved. Those hybrids with the Florida variety exhibit the greatest amount of sterility; hybrids of both the Chalco and New varieties with Florida show an average pollen fertility of approximately 50 percent. It should be noted, however, that there is a great range in fertility among plants of these last two crosses, indicating that the degree of sterility must be controlled by some easily changeable mechanism.

This study indicates that the Mexican teosinte varieties, as well as New teosinte, are similar in chromosomal constitution, although the Chalco variety differs slightly from the other three. This finding is also in agreement with the results from the maize-teosinte hybrids, as in these crosses the Chalco variety apparently differed from maize slightly more than either the Nobogame or Durango varieties. Both Chalco and New teosinte differ in some manner from Florida teosinte, as is shown by the high degree of sterility in hybrids of these two with the Florida variety. Durango is also known to differ from the Florida variety, as Beadle (2) reports an average pollen sterility of 66.8 percent, as well as irregular behavior at meiosis, in a hybrid of Durango x Florida teosinte. As Nobogame teosinte is known to be similar to the three varieties which differ in some manner from Florida teosinte, it seems certain that the Nobogame variety also differs from the Florida variety, although no hybrids between the two have actually been studied. It may be concluded, therefore, since the Mexican teosintes produce partially sterile hybrids when crossed with Florida teosinte, that in gross chromosomal morphology they resemble maize more closely than they do Florida teosinte.

Discussion

The pollen sterility studies conducted in this experiment corroborate previous findings on fertility relationships in maize-teosinte hybrids. Apparently all Mexican varieties are similar to maize in chromosomal structure, because their hybrids with maize show regular behavior at meiosis and a normal degree of fertility. Although one exception was noted in this study, when a high degree of sterility appeared in certain hybrids involving Nobogame teosinte, this behavior is not characteristic of the Mexican varieties. It is also evident that the Mexican varieties, as well as maize, differ from the southern Guatemalan varieties in chromosome structure. The cytological investigations of Longley (6, 7) and O'Mara (10), in addition to the pollen sterility studies, show that a difference in chromosomal homology exists between the teosintes of northern Guatemala and those of southern Guatemala. It may be concluded, therefore, that teosinte varieties of southern Guatemala possess a particular chromosome structure which differentiates them not only from maize, but from all other teosinte varieties which so far have been studied.

Although the various teosinte varieties differ somewhat in gross plant morphology, they are all quite similar in the characteristic features which distinguish them from maize. However, within this morphologically similar group of varieties, there exists a difference in chromosome structure which is greater than that found between most of the teosinte varieties and maize. In other words, if fertility of the F_1 hybrid is used as a basis of relationship, many of the teosinte varieties might be considered more closely related to maize than to certain other teosinte varieties. A comparison of inflorescence characters, however, leaves no doubt but that all known forms of teosinte may be placed in the same species, and that the species should probably, as suggested by Reeves and Mangelsdorf (11), be made congeneric with maize. The group of teosintes from southern Guatemala represents a variation in type from the remainder of the species and, perhaps, differs in chromosome structure as a result of isolation from maize and other teosinte varieties for a long time.

The exact nature of the chromosome structure of the southern Guatemalan teosinte varieties, as well as the cause for sterility in hybrids involving this group of varieties, is not yet fully understood. In any attempt to arrive at an explanation of the distinctive behavior of these particular varieties, however, it is essential to consider all pertinent facts now available on hybrids involving representative varieties of this group. In all instances, these hybrids show irregular chromosome behavior at meiosis, and two or four univalents are frequently present. Pollen sterility in these hybrids is always quite pronounced, and usually approaches 50 percent.

In all backcross populations involving Florida teosinte, in which marker genes on chromosome 4 are segregating, there is a marked deficiency of the maize alleles. A definite linkage has been established between sterility and the marker genes on the fourth chromosome. It is of especial interest that the *Tu* gene shows not only the greatest deficiency of any of the fourth chromosome genes so far studied, but also the strongest linkage with sterility. Mangelsdorf and Reeves (9) and Mangelsdorf (8) showed conclusively that chromosome 4 carries many of the genes responsible for the morphological differences observed between maize and teosinte. In addition, O'Mara (10) reported that in respect to maize, there is a rearrangement on chromosome 4 of the southern Guatemalan varieties. Certainly, there is now a considerable body of evidence indicating that differences on the fourth chromosome are of primary importance in distinguishing the southern Guatemalan teosintes from maize, and to some extent from the other teosinte varieties.

The occurrence of the gene *Tu* in only 15 percent of the backcross population, rather than in the 50 percent which might be expected from a random segregation, is apparently due to the low proportion of viable gametes which carry the maize allele. In fact, it would be necessary to assume a sterility of 41.1 percent, on the basis of the data in the present experiment, to account for the distribution of *Tu* and *tu* plants in the backcross population. As the segregation in this particular population is 73 non-tunicate to 13 tunicate, 60 inviable gametes carrying the *Tu* gene would be required to maintain an equality in number of gametes carrying the two alleles.

Assuming that this particular population affords a representative sample of the gamete production of the F_1 hybrid, it may be seen that the number of required inviable gametes (60), divided by the total gametes in the sample (73 + 13 + 60), gives the percentage (41.1) of sterility necessary to account for the distribution of the *Tu* and *tu* genes. This, of course, is the minimum sterility required for such a distribution, and each time that *tu* occurs in a non-functional gamete there would be an increase in the sterility required to account for the abnormal ratio of tunicate and non-tunicate plants. Therefore, since the fourth chromosome is apparently involved in a minimum of 41.1 percent of the sterility, and the observed sterility in these hybrids is approximately 50 percent, practically all of the sterility may be accounted for by the abnormal behavior of the fourth chromosome.

The relative deficiencies of the fourth chromosome genes in the backcross populations, as well as the linkages of these same genes with sterility, suggest that the factor or factors leading to this sterility are located very close to *Tu*, and between *Tu* and su_1. There is apparently some lack of homology between maize and Florida teosinte in this particular section of the fourth chromosome. And not only is this lack of homology found between maize and Florida teosinte, but also between the southern Guatemalan varieties and all other varieties of teosinte and maize so far studied. Apparently this lack of homology between the two types of parental fourth chromosomes leads to sterility in the F_1 hybrids, and the mechanism causing this sterility results in the formation of non-functional gametes which carry a certain segment near the *Tu* locus of the maize fourth chromosome.

Further genetical and cytological studies of these hybrids, with particular emphasis on the fourth chromosome, should provide a better understanding of this characteristic chromosome structure of the southern Guatemalan varieties, and perhaps determine in what manner the chromosomes of these varieties differ from the chromosomes of both maize and other teosinte varieties.

Summary

Hybrids of the Mexican teosinte varieties with maize exhibit approximately normal fertility. However, the percentage fertility of the Mexican teosinte-maize F_1 hybrids increases slightly with the use of the Chalco, Nobogame and Durango varieties, respectively. One exception in the be-

havior of the Mexican teosintes is found in the F_1 hybrid involving the Nobogame variety; semi-sterile plants are sometimes observed. A segregation of normal and semi-sterile plants in a 1:1 ratio occurs in one of the (Nobogame teosinte x maize) x maize backcross populations, and it is suggested that a reciprocal translocation may be responsible for this condition.

Hybrids of maize with the Huixta variety of northern Guatemala exhibit relatively normal fertility, although the percentage is somewhat below that found in the Mexican teosinte-maize hybrids. In contrast, the F_1 hybrid of maize with the Florida variety of southern Guatemala shows an average pollen fertility of 49 percent. A study of nine backcross populations involving the Florida teosinte variety reveals that the maize parent has a pronounced effect on the degree of sterility. Linkage studies show that a definite linkage exists between sterility and marker genes on chromosome 4. There is a marked deficiency in the backcross populations of the maize alleles of all fourth chromosome marker genes.

The behavior of the inter-varietal teosinte hybrids shows that Florida teosinte produces hybrids of approximately 50 percent fertility in crosses with the Mexican varieties, but that hybrids involving only the Mexican varieties are relatively normal in fertility.

A consideration of all present information on maize-teosinte and inter-varietal teosinte hybrids indicates that the southern Guatemalan teosinte varieties differ from the other teosinte varieties and maize in chromosomal homology. The results of the sterility studies show that some factor or factors on the fourth chromosome, located very close to *Tu*, and between *Tu* and su_1, account for most of the sterility in hybrids involving these southern Guatemalan varieties. Apparently the mechanism causing this sterility results in the formation of non-functional gametes, which carry a certain segment of the maize fourth chromosome near the *Tu* locus.

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