THE INHERITANCE OF INFLORESCENCE CHARACTERS IN MAIZE-TEOSINTE HYBRIDS¹

JOHN S. ROGERS

Texas Agricultural Experiment Station, College Station, Texas

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THE realization near the end of the last century that a close relationship existed between maize and teosinte has resulted in an interest from that time to the present in the exact nature of the differences distinguishing the two species. The role that teosinte may have played in the origin and evolution of maize has been given particular attention. Some investigators have suggested that maize originated directly from teosinte by a series of mutations, while others have postulated that it may have arisen through hybridization of teosinte with some unknown species of the *Andropogoneae*. Hypotheses have also been advanced that teosinte is not directly concerned in the origin of maize, and is perhaps a descendant from a common ancestral form or a recent hybrid of maize with the related genus *Tripsacum*. All investigators, however, are in agreement that maize and teosinte are closely related, and that they had a common source of germplasm in a fairly recent phase of their evolution. A more thorough discussion of these theories concerning the relationship of maize and teosinte may be found in the work of MANGELSDORF and REEVES (1939) and MANGELSDORF (1947).

The most striking characteristic which distinguishes maize and teosinte is the extreme difference in structure of the pistillate spike of the two species. Although there is variation among different types of pistillate spikes within each of the two species, no types in one species approach any of the types found in the other species. Maize and teosinte represent two strongly discontinuous classes for this particular characteristic. Of the differences between the pistillate spikes of the two species the primary ones are paired versus single spikelets, many-ranked versus two-ranked arrangement of the spikelets and inconspicuous soft glumes versus prominent horny glumes. Several studies have been previously conducted to determine the genetic nature of these differences and, although the results have not always been in complete agreement, the conclusion in most instances has been that several factors determine the inheritance of these characters.

COLLINS and KEMPTON (1920) were the first to make a detailed inheritance study of characters in maize-teosinte hybrids. They measured 33 plant characters in an F_2 population of a cross between Tom Thumb popcorn and Florida teosinte, but found none in which a strictly Mendelian inheritance occurred. The only approach to a simple Mendelian inheritance was found in the arrangement of the spikelets in the pistillate inflorescence; the double spikelets of maize appeared to be a simple dominant over the single spikelets of teo-

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sinte. KEMPTON (1924) in a further study of hybrids between Florida teosinte and maize determined the inheritance of the recessive maize characters crinkly, ramose and brachytic. In some instances there was a correlation between the quantitative characters distinguishing the two species and the qualitative marker genes. KEMPTON called attention to the blending of characters in the F_2 as further proof of the close relationship between maize and teosinte.

MANGELSDORF and REEVES (1939) in a study of the backcross (Florida teosinte $\times$ maize) $\times$ maize reported a strong linkage of inflorescence characters differentiating maize and teosinte with marker genes on chromosome 4. However, they found little evidence of linkage with marker genes on chromosomes 2 and 6, and only a slight evidence of linkage with a marker gene on chromosome 9. LANGHAM (1940) studied the inheritance of paired versus single spikelets and many-ranked ear versus two-ranked ear in Durango teosinte-maize hybrids and their segregating populations. He concluded that maize was dominant to teosinte for these characters, and that both were inherited in a simple Mendelian fashion. MANGELSDORF (1947) made a further study of the inheritance of several inflorescence characters differentiating the two species in F_2 populations of Nobogame teosinte-maize and Durango teosinte-maize hybrids. These included the characters earlier studied by LANGHAM (1940), as well as two quantitative characters "glume score" and "disarticulation score," which were both measured in a wholly empirical fashion. None of the characters segregated as simple Mendelian recessives and linkages were detected on several chromosomes for most of them. MANGELSDORF concluded that chromosomes 1, 3, 4, 8, 9 and 10 carry more than their proportionate share of the genes differentiating the two species.

The present study was undertaken to obtain further information on the inheritance of the inflorescence characters, and in addition to determine the chromosomes on which genes affecting these characters are located.

MATERIALS AND METHODS

The inheritance of the inflorescence characters was studied in several F_1 , F_2 and maize backcross populations involving six different varieties of teosinte. These latter included the Nobogame, Durango and Chalco varieties from Mexico, and the El Valle, Huixta and Jutiapa varieties from Guatemala. The common maize parent, which was used in all crosses with the exception of those involving Jutiapa teosinte, was quite uniform as a result of inbreeding and carried homozygous marker genes on nine of the ten chromosomes. The marker genes were *bm₂*, *P*, *lg₁*, *a₁*, *su₁*, *Y*, *gl₁*, *j₁*, *wx* and *g₁*. Progenies used for this study were grown in the spring and summer of 1948 at College Station, Texas. A more complete discussion of this same material, as well as a description of the conditions under which the experimental material was grown, is given in a recent paper by ROGERS (1950). The same progenies used in this previously reported study on photoperiodic response were also utilized for this study of inflorescence characters.

The two-ranked pistillate inflorescence bearing single spikelets, which is

FIGURE 1.—From left to right. Pistillate spike of 1) maize parent, 2) Durango teosinte-maize F_1 hybrid, showing both many-ranked and two-ranked spikes, and 3) Durango teosinte.

characteristic of teosinte, offers a marked contrast to the many-ranked pistillate inflorescence bearing paired spikelets, which is found in maize. This difference is well illustrated in figure 1, where pistillate spikes of both parental types and the F_1 hybrid are shown. The spike illustrated is of the Durango variety of teosinte, and is rather typical of the pistillate spikes found in all varieties of teosinte. Examples of both many-ranked and two-ranked spikes of the F_1 hybrid are shown, since both types occur, even in crosses of maize

FIGURE 2.—Segregates from the Durango teosinte-maize F_2 population, showing range in type of pistillate spike. A. Two-ranked, single spikelets. B. Two-ranked, paired spikelets. C. Many-ranked, single spikelets. D. Many-ranked, paired spikelets, intermediate. E. Many-ranked, paired spikelets, resembling maize.

with a single variety of teosinte. Ordinarily in Guatemalan teosinte-maize F_1 hybrids a high proportion of the ears are two-ranked, while in Mexican teosinte-maize F_1 hybrids a high proportion of the ears are many-ranked. In all crosses studied in this experiment the F_1 hybrids have paired pistillate spikelets.

The pistillate inflorescences of both the Nobogame teosinte-maize and

FIGURE 3.—Segregates from the El Valle teosinte-naize F_2 population, showing many-ranked central spike (left) and two-ranked central spike (right).

FIGURE 4.—Selected sample of each of the five ear grades from the cross (Nobogame teosinte $\times$ maize) $\times$ maize (above), and the cross (El Valle teosinte $\times$ maize) $\times$ maize (below).

Durango teosinte-maize F_2 populations were classified on the basis of two-ranked versus many-ranked arrangement of the spikelets and paired spikelets versus single spikelets. A representative sample of ears from the maize-Durango F_2 population may be seen in figure 2, which shows the range from that type resembling the typical two-ranked teosinte spike to that resembling the many-ranked maize ear. An attempt was made to classify these characters in crosses of the Guatemalan teosintes, but so few of the plants produced ears that very little information was obtained. In the F_2 of El Valle teosinte $\times$ maize approximately one-fourth of the progeny produced pistillate spikes, and these were classified for the above mentioned characters. Practically no pistillate spikes were produced in either the maize-Huixta or maize-Jutiapa F_2 populations. In those F_2 progenies where analysis of the pistillate inflorescence was impossible, the central spike of the tassel was studied to obtain information on the inheritance of the two-ranked versus many-ranked character. For this character all teosinte varieties possess a two-ranked central spike, while maize has a many-ranked central spike. Segregates of both the many-ranked and two-ranked type of central spike from the maize-El Valle F_2 population are shown in figure 3.

The backcrosses to maize offered more favorable material for obtaining information on characters of the pistillate inflorescence than did the F_2 progenies, since practically all plants in each of the maize backcross populations produced ears. These progenies exhibited a range in ear type from that of the maize parent to that resembling the F_1 . Although the F_1 varied somewhat in appearance depending upon the type of teosinte, it produced in all instances a very small spike quite unlike the maize parent. In order to determine whether linkage existed between any of the marker genes and quantitative factors affecting the ear, all backcross progenies were classified by ear grade. This was an arbitrary designation into five classes made according to the appearance of the ear, 0 resembling the maize parent and 4 the F_1 . The intermediate grades 1, 2 and 3 represent a successive trend from the maize-like segregates to those like the F_1 hybrid. Selected samples of the various ear grades from the Nobogame and El Valle backcross populations are shown in figure 4. There was a considerable difference in appearance of the ears in the various backcrosses, and of those populations studied the one involving Nobogame teosinte had the most maize-like segregates, while the El Valle population was one of the least maize-like. This fact may be readily determined by an examination of the representative ears of the two populations.

CLASSIFICATION OF EAR AND TASSEL CHARACTERS

F_1 and F_2 Populations

The results from a classification of the F_1 hybrids given in table 1 show that the various teosintes differ in the strength of their expression on both ear and tassel characters. The varietal name of each teosinte is used in this table, as in all later tables, to designate the indicated generation of a cross involving that particular teosinte and maize. No data are shown for the Chalco teosinte-

maize F_1 , since plants of this hybrid were not available for classification. The many-ranked pistillate and staminate inflorescence of maize is completely dominant in the F_1 cross with Nobogame teosinte. In the Durango hybrids both many-ranked and two-ranked pistillate spikes occur, although all tassels possess a many-ranked central spike. Apparently the genetic complex of the maize-Durango hybrid is of such an intermediate nature that either the maize or teosinte form of pistillate spike may result, depending perhaps on the environmental conditions at the time of development.

TABLE 1
Classification of characters in maize-teosinte F_1 populations.

CHARACTERS	NUMBER OF INDIVIDUALS				
	NOBOGAME	DURANGO	EL VALLE	HUIXTA	JUTIAPA
Many-ranked pistillate spike	14	5	0	0	0
Two-ranked pistillate spike	0	9	8	6	2
Total	14	14	8	6	2
Many-ranked central spike	14	15	10	4	14
Two-ranked central spike	0	0	4	7	1
Total	14	15	14	11	15
Paired pistillate spikelets	14	15	8	6	2
Single pistillate spikelets	0	0	0	0	0
Total	14	15	8	6	2

All of the Guatemalan teosinte-maize F_1 plants developing pistillate spikes produced the two-ranked type of the teosinte parent. However, both many-ranked and two-ranked central spikes occur in tassels of each of these same F_1 populations. The development of both types of central spikes in these F_1 hybrids involving a particular Guatemalan teosinte again illustrates the flexible nature of maize-teosinte crosses. The differential response of these Guatemalan teosinte-maize hybrids also indicates that the Huixta variety exerts the strongest effect on rank of the central spike. Of the three Guatemalan teosinte hybrids, the maize-Huixta F_1 has the highest proportion of two-ranked central spikes, followed in order by the maize-El Valle and maize-Jutiapa F_1 hybrids.

The maize-teosinte F_1 hybrids were consistent in their behavior for one character; all plants produced paired pistillate spikelets.

The data on ear and tassel characters of the F_2 populations, with the exception of the Chalco teosinte-maize progeny, are presented in table 2. In those populations classified for rank of pistillate spike, the frequency of two-ranked spikes is lowest in the Nobogame cross. The Durango hybrid has a somewhat higher proportion than the Nobogame hybrid, and the El Valle cross exceeds

both of the Mexican teosinte hybrids in frequency of two-ranked pistillate spikes. It is quite likely that the frequency of two-ranked spikes in the El Valle population would have been even higher, if a larger proportion of the later, more teosinte-like plants in the population had produced ears.

The same tendency exhibited in the F_1 hybrids for rank of the central spike persists in the F_2 progenies classified for this character. The greatest frequency of two-ranked central spikes is found in the Huixta hybrid, lower frequencies occurring in the El Valle and Jutiapa hybrids respectively. The failure of a

TABLE 2

Classification of characters in maize-teosinte F_2 populations.

CHARACTERS	NUMBER OF INDIVIDUALS				
	NOBOGAME	DURANGO	EL VALLE	HUIXTA	JUTIAPA
Many-ranked pistillate spike	223	130	25		
Two-ranked pistillate spike	103	184	70		
Total	326	314	95		
Many-ranked central spike			204	91	128
Two-ranked central spike			122	96	54
Total			326	187	182
Paired pistillate spikelets	248	188	56		
Single pistillate spikelets	78	126	39		
Total	326	314	95		

large number of the late plants to produce tassels probably resulted in a lower frequency of two-ranked central spikes in the Huixta population.

The paired pistillate spikelets of the maize parent predominate in all populations classified for this character. However, there is a definite increase in proportion of single spikelets from the Nobogame hybrid to the Durango hybrid, and from the Durango hybrid to the El Valle hybrid. Again, the frequency of teosinte-like segregates in the El Valle progeny in all likelihood would have been greater had more of the late plants produced ears.

The behavior of these ear and tassel characters in the F_1 hybrids, as well as their segregation in the F_2 populations, does not indicate a simple Mendelian type of inheritance. Although the segregation of paired versus single spikelets approximates a 3:1 ratio in the Nobogame teosinte-maize F_2 , it cannot be assumed that the character is controlled by a single gene. Depending upon the variety of teosinte used in a hybrid with maize, almost any type of segregation may occur in the F_2 . Apparently it is by chance that the segregation in the Nobogame hybrid is such that it approaches a simple Mendelian ratio.

The behavior of the characters for both pistillate and staminate spikes obviously varies with the variety of teosinte used in the cross. Results in both

the F_1 and F_2 populations are consistent in showing that fewer teosinte-like segregates for these characters occur in the Mexican teosinte populations than in the Guatemalan. In a comparison between the two Mexican hybrids, it is at once apparent that the Durango variety exerts a more pronounced effect on the ear characters than does the Nobogame variety. Among the Guatemalan teosintes, the Huixta variety influences the ear and tassel characters in both F_1 and F_2 populations to a greater extent than do the other varieties studied. El Valle teosinte is in turn more effective than the Jutiapa variety in controlling characteristics of the ear and tassel.

Maize Backcross Populations

The results from a classification of the (teosinte $\times$ maize) $\times$ maize populations for ear grade and glume score are presented in table 3. As mentioned previously, these classes for both ear grade and glume score represent arbitrary

TABLE 3
Classification of characters in (maize $\times$ teosinte) $\times$ maize populations.

CHARACTER AND CLASS NUMBER	NUMBER OF INDIVIDUALS					
	NOBOGAME	DURANGO	CHALCO	EL VALLE	HUIXTA	JUTIAPA
Ear Grade						
0	11	8	4	5	12	3
1	42	19	33	12	29	16
2	100	50	77	46	77	67
3	40	80	62	54	53	44
4	2	28	11	10	11	14
Total	195	185	187	127	182	144
Glume score						
0	6	7	6	6	13	3
1	64	22	43	18	39	24
2	77	68	76	49	82	60
3	48	88	62	54	48	57
Total	195	185	187	127	182	144

groupings which have been made for the purpose of studying linkage relations of marker genes with these characters. The distribution of individuals in the various classes, therefore, does not represent an exact segregation that occurs for these characters. This grouping by classes, however, does furnish an index to the general nature of the segregates in a particular population. The populations with the higher frequencies in classes 0 and 1 for either character are more maize-like than those populations with lower frequencies in these classes.

An almost continuous range of ear types from one parental type to the other occurs in all of these maize backcross populations. Also there are very few segregates in any of the crosses that are approximate duplicates of the original

parental types. Therefore, ear grades 0 and 4 represent the two extremes of a population rather than the parental types, and grades 1, 2 and 3 include the various intermediate types. In a comparison of effects of the various teosintes on these characters, grade 1 is considered to include maize-like segregates and grade 3 to include F_1 -like segregates. In the classification for glume score, the 0 class includes those segregates with a very light glume similar to that of the maize parent, and class 3 includes all segregates with a strongly developed horny glume. Class 1 approaches the maize type rather closely, and class 2 includes those ears with moderate glume development.

This study of the maize backcrosses again demonstrates that the various teosintes differ in their effect on morphological characters of the pistillate spike in hybrids with maize. Those crosses with the greatest frequency of F_1 -like segregates for ear grade also show a high frequency of F_1 -like segregates for glume score. In other words, there is a strong correlation between ear grade and glume score, and any teosinte variety exerting a strong effect on one also exerts a strong effect on the other.

Nobogame teosinte again exhibits the weakest effect of any of the teosinte varieties. The segregates of this cross are definitely more maize-like than those of the other crosses. However, it is interesting to note that the Huixta teosinte cross most closely approaches that of the Nobogame hybrid in frequency of maize-like segregates. This represents a definite reversal of the tendency displayed by this variety for those characters previously discussed, in which the Huixta variety exerted the most extreme effect of any of the teosinte varieties. The backcross population involving Chalco teosinte resembles that of the Huixta backcross in its proportion of maize-like segregates, indicating that these two varieties are somewhat similar in their effect on the two characters studied. The high frequency of F_1 -like segregates in the Durango, El Valle and Jutiapa hybrids definitely show that these varieties have a more pronounced effect on ear characteristics of the backcross populations than do the other varieties studied.

The behavior of the different teosintes in their effect on characters studied in the backcross progenies differs somewhat from their behavior for the characters observed in the F_1 and F_2 populations. In this study of ear grade and glume score, Durango, one of the Mexican teosintes, produces a stronger effect than the Guatemalan variety, Huixta. However, for the inflorescence characters studied in the F_1 and F_2 progenies, there is a marked contrast in the behavior of the Mexican and Guatemalan teosintes, the latter group always exhibiting the most pronounced effect. It is felt that these results obtained in the maize backcross progenies represent a more accurate analysis of the different teosinte varieties in their effect on ear characters, since development of the pistillate inflorescence in both the F_1 and F_2 populations is definitely affected by response to photoperiod. In the maize backcross progenies these differences among the teosintes in photoperiodic response are minimized, and each variety has an opportunity to produce its effect on the inflorescence characters without appreciable influence from other factors.

The reaction of the Mexican teosintes in these maize backcross populations

shows conclusively that the Durango variety carries more effective factors influencing these ear characters than do the other Mexican varieties studied. Also, the rather high frequency of F_1 -like segregates occurring in the Durango hybrid suggests that this variety actually possesses more factors than either the Nobogame or Chalco varieties. These results agree with those of MANGELSDORF (1947) on the comparative effect of Durango and Nobogame teosinte, as he also reports that Durango is the more potent of these two varieties. In fact, there is every indication that the Durango variety is just as potent as the El Valle and Jutiapa varieties in affecting ear structure and glume development in these maize backcrosses. Among the Guatemalan teosintes, it seems obvious that the Huixta variety possesses fewer and less effective factors influencing these characters than either the El Valle or Jutiapa varieties.

LINKAGE RELATIONS OF MARKER GENES WITH INFLORESCENCE CHARACTERS

A study of linkage relations between the marker genes and quantitative inflorescence characters serves to identify, at least in part, the chromosomes on which genes affecting these characters are located. Results of such a study also provide information as to whether the genes differentiating the inflorescences of maize and teosinte are scattered at random throughout the chromosomes, or occupy only a few sections of certain chromosomes.

A chi-square test for independent assortment was used to test for linkages between the marker genes and inflorescence characters. Comparisons involving each of the characters studied were made between those segregates carrying the maize allele and those carrying the teosinte allele, for each of the marker

TABLE 4

Linkage relations of ear grade and glume score with each other and with marker genes on nine chromosomes of maize, for each (maize×teosinte)×maize population.

CHROM.	CHAR- ACTER	NOBOGAME		DURANGO		CHALCO		EL VALLE		HUIXTA	
		EG	GS	EG	GS	EG	GS	EG	GS	EG	GS
1	<i>Bm₂</i>	I	—	+	—	+	I	—	—	—	—
1	<i>P</i>			I	—	—	—				
2	<i>Lg₁</i>	—	—	+	—	—	—	+	—	—	—
3	<i>A₁</i>	+	—	—	—	—	—	+	I	I	I
4	<i>Su₁</i>	++	++	++	++	++	++	—	—	++	+
6	<i>Y</i>	—	—	—	—	—	—	I	+	—	I ^s
7	<i>Gl₁</i>	++	—	—	—	—	—	I	+	—	—
8	<i>J₁</i>	—	—	—	—	—	—	—	—	—	—
9	<i>Wx</i>	—	—	—	—	I	—	+	I	—	—
10	<i>G₁</i>	—	—	—	—	I ^s	—	—	I	I	—
	<i>EG</i>		++		++		++		++		++

EG=Ear grade.

++=Strong linkage, $P < .01$.

+ = Linkage, $P = .05 - .01$.

I = Indication of linkage.

GS=Glume score.

— = Independent inheritance.

I^s = Deviation not due to linkage, $P = .05 - .01$.

TABLE 5

Linkage relations of two-ranked spikes and paired spikelets with each other and with marker genes on nine chromosomes of maize, for each maize-teosinte F₂ population.

CHROM.	CHARACTER	NOBOGAME		DURANGO		EL VALLE			HUIXTA
		TR	PS	TR	PS	TR	TR ^t	PS	TR ^t
1	<i>Bm</i> ₂	—	—	++	—	I	—	I	—
1	<i>P</i>	I ^s	—	—	—	—	—	—	—
2	<i>Lg</i> ₁	—	—	++	—	I	—	I	—
3	<i>A</i> ₁	++	—	—	+	++	I	I	—
4	<i>Su</i> ₁	—	—	—	—	—	—	—	—
6	<i>Y</i>	+	—	—	—	I	—	—	—
7	<i>Gl</i> ₁	—	+	—	+	—	—	—	—
8	<i>J</i> ₁	—	—	—	—	I	++	I	+
9	<i>Wx</i>	—	—	—	—	—	I	I	—
10	<i>G</i> ₁	—	—	—	—	—	+	I	—
	<i>TR</i>		—		—		++	+	
	<i>TR</i> ^t							++	

TR=Two-ranked pistillate spikes.

++=Strong linkage, $P < .01$.

+ =Linkage, $P = .05 - .01$.

I=Indication of linkage.

TR^t=Two-ranked central spike of tassel.

PS=Paired spikelets.

— =Independent inheritance.

I^s=Deviation not due to linkage, $P = .05 - .01$.

genes individually. A linkage was considered as established if the distribution of individuals within the various classes was significantly different from that expected by chance, and the deviation was in the proper direction to indicate a linkage.

A summary of the linkage relations of the marker genes with the various inflorescence characters in the maize backcross and F₂ populations is shown in tables 4 and 5. No linkage data are available for the Jutiapa populations, since the multiple tester stock was not used as the maize parent in these crosses. The certainty of the linkage relationships between the marker genes and inflorescence characters has been designated for both the .05 and .01 levels of significance. Strong indications of linkage, as evidenced by the distribution of segregates in the various classes, have also been included in these tables for linkage relations. This latter type occurs most frequently for the ear grade and glume score characters, where a definite trend indicating linkage is sometimes exhibited, although it does not always prove to be statistically significant.

The most effective gene (or genes) acting upon ear structure occurs on chromosome 4, as ear grade shows a strong linkage with the marker gene on chromosome 4 in all but one of the progenies studied. This one exception is the progeny involving El Valle teosinte, and a satisfactory linkage test for chromosome 4 in this cross was impossible because of the extreme shortage of *su*₁ segregates. This pronounced effect on ear structure exhibited by chromosome 4 agrees with the results obtained by MANGELSDORF and REEVES (1939) and MANGELSDORF (1947) in studies of this same nature.

Several other genes also affect ear structure, but their location on the chromosomes varies with the variety of teosinte. Genes influencing ear structure are found on chromosome 1 of Durango, Chalco and possibly Nobogame teosintes, and on chromosome 3 of Nobogame, El Valle and possibly Huixta teosintes. Genes also occur on chromosome 2 of Durango and El Valle, on chromosome 9 of El Valle and possibly Chalco, on chromosome 7 of Nobogame and possibly El Valle, and perhaps on chromosome 6 of El Valle and chromosome 10 of Huixta.

The linkage data for glume score show that chromosome 4 of each teosinte, excluding the El Valle variety, carries the most effective gene (or genes) responsible for glume development. In fact, chromosomes 6 and 7 of El Valle teosinte are the only other chromosomes on which genes for this character definitely occur. Genes affecting glume development are also indicated on chromosome 1 of Chalco teosinte, chromosome 3 of Huixta teosinte and chromosomes 3, 9 and 10 of El Valle teosinte. These results on glume development agree only in part with those obtained by MANGELSDORF (1947), who reported genes for this character not only on chromosome 4 of Nobogame and Durango teosintes, but also on several other chromosomes of the two varieties.

Genes producing the two-ranked condition of the pistillate spike in teosinte are found on chromosomes 3 and 6 of Nobogame teosinte and on chromosomes 1 and 2 of Durango teosinte. LANGHAM'S (1940) data also strongly indicate that a gene (or genes) governing the two-ranked condition of Durango teosinte occurs on chromosome 1. MANGELSDORF'S (1947) results show that a situation similar to that reported for glume development prevails for the two-ranked condition, as genes for this latter character were also found to occur on several chromosomes of both Nobogame and Durango teosintes.

The data for two-ranked condition of the pistillate spike in the El Valle maize-hybrid show that genes occur on chromosome 3 and possibly on chromosomes 1, 2, 6 and 8 of this variety. The additional data obtained on the central spike of the tassel in the Guatemalan teosinte-maize hybrids show that genes controlling the two-ranked condition occur on chromosome 8 of El Valle and Huixta, on chromosome 10 of El Valle and possibly on chromosomes 3 and 9 of El Valle.

Genes responsible for single spikelets of the teosinte pistillate spike are found on chromosome 7 of Nobogame and Durango teosinte, on chromosome 3 of Durango teosinte and possibly on chromosomes 1, 2, 3, 8, 9 and 10 of El Valle teosinte. The failure to obtain statistically significant linkages in the maize-El Valle hybrid is probably due to the fact that only a small proportion of the individuals in this population could be classified for the single versus paired spikelet condition. LANGHAM'S data (1940), which indicate a linkage of the single spikelet condition in Durango teosinte with the marker gene *Lg₂* on chromosome 3, corroborate the present findings that a gene (or genes) for this character occurs on chromosome 3 of Durango teosinte. However, the present results do not agree with those of MANGELSDORF (1947), who reports that genes governing the single spikelet character are found on chromosomes 4

and 8 of Durango and on chromosome 4 and possibly chromosome 8 of Nobogame teosinte.

Ear structure and glume development are consistently correlated with each other in all populations studied. This strong correlation between the two characters indicates that the same genes or group of genes are largely responsible for both ear structure and glume development.

The linkage studies definitely show that several of the teosinte chromosomes may carry genes affecting the inflorescence characters which differentiate the two species. Although the particular chromosomes which are involved may vary somewhat among the different varieties, genes governing these characters are found on chromosome 4 of all varieties, with the possible exception of El Valle, and on chromosomes 1 and 3 of most varieties.

Genes responsible for the distinguishing ear characteristics of the two species are found on most of the chromosomes of El Valle teosinte, while only a few of the chromosomes of the other teosintes carry genes which strongly affect these characters. It is also significant that within this latter group the chromosomes exhibiting these strong effects vary to some extent with the variety. Genes with a strong effect on the ear characters occur on chromosome 1 of Durango and Chalco, on chromosome 3 of Nobogame and Huixta, on chromosome 7 of Nobogame and on chromosome 2 of Durango. These results strongly suggest, that for the ear characteristics, the El Valle variety differs from maize by genes distributed upon most of the chromosomes, while the other teosintes represent types which differ from maize by genes of a more localized nature on a few chromosomes.

DISCUSSION

As additional information is obtained from the study of maize-teosinte hybrids, it becomes evident that most of the ten chromosomes carry genes distinguishing the pistillate inflorescence of the two species. The data from the present experiment show that while the same chromosomes are often involved regardless of the teosinte variety studied, there are certain rather definite exceptions. The chromosomes carrying genes strongly affecting the ear characters sometimes differ from one variety to another.

These results, which show that genes affecting ear characters may occur on different chromosomes of the various teosintes, support the hypothesis that the more maize-like teosintes represent the original teosinte with a substitution of maize germplasm on various chromosomes. However, genes strongly affecting the ear characters occur on chromosome 4 of all varieties, which suggests that this chromosome in particular carries genes which are essential to development of the teosinte type of pistillate spike. The particular chromosomes on which the maize germplasm has been substituted may differ with the variety, since this introgression of maize germplasm has undoubtedly occurred at different locations. In fact, according to MANGELSDORF (1947) the transfer of maize genes to teosinte is still occurring at localities in Mexico today, and these teosintes are acquiring the characteristics of the surrounding corn. It is

probable that some of the Mexican varieties such as Nobogame have only a sufficient amount of teosinte germplasm to enable them to retain those characteristics necessary for survival in their present state of existence. The substitution of 3 or 4 sections of maize chromatin in some of these teosintes might actually result in the development of a maize-like type of pistillate inflorescence in these varieties.

The results of this experiment agree with previous findings by MANGELSDORF and REEVES (1939) and MANGELSDORF (1947) that the genes or groups of genes affecting structure of the pistillate spike tend to have similar effects. In the El Valle teosinte-maize hybrid, as indicated by the number of linkages of ear characters with the marker genes, it appears that the genes on different chromosomes have similar effects. There is no tendency for a pronounced linkage of these characters with marker genes on any chromosome as is so often the case in the other maize-teosinte hybrids, but rather an indication of linkage with the marker genes on several chromosomes. The more maize-like teosintes retain the essential characteristics of the teosinte spike, even though they possess genes on different chromosomes governing ear characters. This suggests that the particular chromosomes on which the maize germplasm has been substituted, with the exception of chromosome 4, are not too important, as long as a sufficient amount of the teosinte germplasm is retained to effect the teosinte type of pistillate spike. It seems that the El Valle variety functions more as a complete gene complex to produce the characteristic spike of teosinte, while the other teosintes studied are differentiated from maize by groups of genes at a limited number of locations on the chromosomes.

The strong correlation between ear grade and glume score in the present study strongly suggests that the same genes influence both ear structure and glume development. In previous studies of several ear characters, MANGELSDORF (1947) has also found that genes responsible for a particular character are frequently involved in some of the others. Apparently those genes or groups of genes responsible for the teosinte type of pistillate spike act in a general manner, rather than each gene or group of genes affecting only a particular character such as glume development.

Several differences exist among the teosinte varieties for the genes controlling ear characteristics. The El Valle variety carries genes affecting ear characters on most of the chromosomes, in contrast to the other varieties studied which carry genes responsible for these characters on only a few chromosomes. MANGELSDORF's (1947) report that the appearance of teosinte-like plants in a Florida teosinte-maize cross is more frequent than in crosses involving either Nobogame or Durango teosinte tends to substantiate these results. Since the El Valle and Florida teosintes are of southern Guatemalan origin, apparently the teosintes of southern Guatemala differ genetically from maize to a greater extent than do the teosintes of either northern Guatemala or Mexico so far as characteristics of the pistillate spike are concerned. The fact that each teosinte variety has retained the essential characteristics of the pistillate spike, although genes controlling the character may occur on different chromosomes of each variety, suggests that the more extreme form of teosinte, from which

these varieties have been derived, carried approximately the same kind of germplasm on different chromosomes.

In considering the present data, as well as those recently reported by ROGERS (1950) on the inheritance of photoperiodic response and tiller number in maize-teosinte hybrids, it becomes evident that the different teosinte varieties have retained varying amounts and types of germplasm affecting the various teosinte characters. None of the Mexican varieties possess the extreme response to short-day or high capacity for tillering found in the Guatemalan varieties. However, Durango teosinte has retained more effective genes controlling ear characters than the other Mexican or northern Guatemalan teosintes so far studied. The Huixta variety possesses an extreme response to photoperiod, but has apparently had some of the genes influencing the ear characters replaced by maize genes. Among the Mexican teosintes the Chalco variety shows the strongest response to photoperiod, yet exhibits one of the weakest effects of any of the varieties on ear characters, and has practically lost the ability to produce tillers. Nobogame represents a teosinte variety which has been so contaminated with maize that it probably has only the minimum amount of original teosinte germplasm necessary to enable it to retain those features of teosinte which clearly distinguish it from maize.

MANGELSDORF and REEVES (1939) have suggested that teosinte is a hybrid of maize and *Tripsacum*, and that teosinte is essentially maize on which four principal blocks of *Tripsacum* germplasm have been superimposed. The data from these recent experiments give no conclusive evidence as to the original relationship of maize and teosinte, nor do they render untenable the hypothesis that teosinte originated as a cross of *Tripsacum* and maize. The fact that genes affecting ear characters occur on most chromosomes of El Valle teosinte, as well as on most of the chromosomes of the Mexican teosintes when they are considered as a composite, indicates that if this hypothesis is correct, the *Tripsacum* germplasm is distributed throughout the chromosomes to a greater extent than originally suggested by MANGELSDORF and REEVES.

These results do emphasize the complex genetic differences between the two species, and lead to the conclusion that teosinte is not the progenitor of maize. At least it does not seem possible that maize could have originated from teosinte as the consequence of a small number of mutations. It does seem certain that in the original form of teosinte the genes distinguishing maize and teosinte were located on most of the ten chromosomes, and in the evolution of the present forms of teosinte each variety has retained some portion of the germplasm responsible for these distinguishing characteristics.

SUMMARY

Inflorescence characters were studied in several maize-teosinte hybrid populations involving a common multiple gene maize parent and six different varieties of teosinte. The maize parent carried marker genes on nine of the ten chromosomes. Teosinte varieties from three sources each in Mexico and Guatemala were used in the experiment.

None of the inflorescence characters studied exhibit a simple Mendelian

type of inheritance. The variety of teosinte has a pronounced effect on the proportion of teosinte-like segregates appearing in all of the segregating populations.

The linkage studies show that most of the ten chromosomes may carry genes distinguishing the pistillate inflorescence of maize and teosinte. Genes governing the ear characters are found on chromosome 4 of all varieties, with the possible exception of El Valle, and on chromosomes 1 and 3 of most varieties. However, other chromosomes exhibiting a strong effect on the ear characters may vary to some extent with the variety. Genes responsible for the teosinte type of pistillate spike occur on most of the chromosomes of El Valle teosinte, while only a few of the chromosomes of the other teosintes carry genes which strongly affect this character. The present results indicate that these genes or group of genes affecting structure of the pistillate spike tend to have similar effects.

The data now available from studies of maize-teosinte hybrids show that pronounced differences exist among the various teosintes in those characters which differentiate the two species. Since no single variety is least maize-like in all of the characters studied, it seems reasonable to conclude that all of the known teosintes represent varieties with some degree of admixture with maize, and they differ according to the type and amount of maize germplasm which each has acquired.

There is still no conclusive evidence on the original relationship of maize and teosinte, although the results of recent studies emphasize the complex genetic differences between the two species and tend to weaken the hypothesis that maize originated from teosinte.

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