

TEXAS AGRICULTURAL EXPERIMENT STATION

R. D. LEWIS, Director, College Station, Texas

761-769

Bulletin 761

LIBRARY
A. & M. COLLEGE OF TEXAS

**Comparative Morphology
of the
American Maydeae**

.72
52
161

April 1953



The TEXAS AGRICULTURAL AND MECHANICAL COLLEGE SYSTEM

GIBB GILCHRIST, Chancellor

DIGEST

The results of a comparative study of maize and its American relatives indicate that teosinte is within the combined range of variation of maize and *Tripsacum* in all of the 55 characters studied thus far, with two doubtful exceptions which should be disregarded. These results agree with a revised hypothesis that teosinte originated as a hybrid between primitive types of maize and of *Tripsacum*, whose plant characters were similar to those of extant forms but whose chromosomes were more closely homologous than those of forms which have been tested.

In all the characters by which Mexican and Guatemalan teosintes were compared, the Mexican type was found to be the more maize-like; also, the North American varieties of maize were found to be more teosinte-like than those typical of the Andean region. Although a relatively small number of characters were used in comparing the various forms of maize and of teosinte, the results are in agreement with a current hypothesis that the teosinte of Mexico is further modified by introgression from maize, and that North American maize is likewise modified by introgression from teosinte.

CONTENTS

	Page
Digest.....	2
Introduction.....	3
Materials and Methods.....	3
Results.....	5
Paired and Single Spikelets.....	5
Compactness of Ear.....	7
Depth of Alveolus of the Ear.....	9
Branching Habit.....	9
Falling and Rooting of Culms.....	12
Adaptation to Poorly-drained Habitats.....	12
Anatomical Characters of Leaves.....	13
Toughness of Culms.....	17
Discussion.....	20
Acknowledgments.....	25
Literature Cited.....	26

S
117
E2.2

Comparative Morphology of the American Maydeae

R. G. Reeves, Professor,
Departments of Agronomy and Genetics

FOR MORE THAN A DECADE, students of the evolution of maize and its relatives have been interested in the apparent fact that most of the characters of annual teosinte are such that they could have been inherited from either *Tripsacum* or maize. Thirty four characters were tabulated by Mangelsdorf and Reeves (1939), in which teosinte was intermediate between the other two or indistinguishable from one of them. This was regarded as evidence for the hypothesis that teosinte originated as a segregate from a hybrid between maize and *Tripsacum*, after the original hybrid had backcrossed to maize an indefinite number of times.

The main objective of the work reported in this bulletin was to collect and interpret additional data on this question. A secondary objective was to test the hypothesis that, in general, Mexican teosinte has more characters inherited from maize than has Guatemalan teosinte, and that Central and North American maize have more characters from teosinte, or indirectly from *Tripsacum*, than has Andean maize. If both of these hypothesis are valid, the five forms to be discussed—*Tripsacum*, Guatemalan teosinte, Mexican teosinte, North American maize and Andean maize—should fall into a series showing gradations from *Tripsacum* to Andean maize.

MATERIALS AND METHODS

Except when the contrary is stated in the text, the maize used as material was an open-pollinated North American variety and the teosinte was the Florida variety, the latter having come originally from Guatemala. The *Tripsacum* used included both diploid and tetraploid forms of *T. dactyloides*, but diploids were used consistently and tetraploids only as supplementary material. When the type of *Tripsacum* is undesignated in the text, it should be understood to be a diploid form of *T. dactyloides*.

It is desirable to delineate in some detail the premises adopted in selecting these particular forms and, for the study

of certain characters, only a few plants from each form. If it be assumed that maize and *Tripsacum* are parents of teosinte, only one form of maize and of *Tripsacum* would have been required to hybridize successfully to produce teosinte. For the results of this morphological study to be positive, therefore, it is only necessary for one form of maize and of *Tripsacum* to satisfy the requirements for the parents, and for one form of teosinte to satisfy the requirements for the offspring. If it were possible to choose the exact forms of teosinte, maize and *Tripsacum*, from all of those in existence, which would serve best on the basis of interfertility and cytogenetical relationships as the original teosinte and as possible parents of teosinte, it seems that such forms would also serve best as materials for the morphological study. But the information available does not permit such a choice to be made. A possibility exists, therefore, that combinations of forms other than those used might fulfill the theoretical requirements even better. On the other hand, the possibility is fully recognized that combinations of forms might be found which would give results much less positive than those obtained. It is obviously impracticable to make a detailed morphological analysis of a large proportion of the thousands of forms included in these three plant groups. Therefore, an analysis of a few forms must suffice for the present to give an indication of the morphological relationships.

Thus, the writer disclaims the assumption that the forms of maize, teosinte and *Tripsacum* included in the study are the most appropriate, except for the fact that those used consistently could be grown locally in the field with little risk of abnormal development due to poor adaptation.

Although North American maize, the principal type studied, is reputed to be tripsacoid, and therefore more similar to teosinte and *Tripsacum* than certain other types, it is sufficiently different from teosinte and *Tripsacum* to justify its use when the comparison includes only one maize variety. If North American maize really is tripsacoid, the results obtained probably are a little less positive than if only non-tripsacoid maize had been included.

According to conclusions of some investigators, Florida teosinte is one of the more "typical" teosintes known, the varieties from Northern Mexico being the results of recent introgression from maize. If this postulate is valid, Florida teosinte is a good choice of material for this study; if not, it might be regarded as having been taken at random.

Concerning the *Tripsacum* used as material, recognition must be made that according to Cutler and Anderson (1941), no form of *T. dactyloides* is known to occur naturally in Mexico or Central America, where teosinte is usually believed to have originated. For this reason, there is some doubt as to whether *T. dactyloides* should be considered as a possible parent of teosinte. However, the possibility is not completely excluded, because (a) our present conception of the place of origin of teosinte may be in error, and (b) the distribution of *T. dactyloides* at the time of origin of teosinte may have been very different from that known at the present time. Also, it may be noteworthy that published results of attempts to obtain fertile hybrids between maize and *Tripsacum* indicate that diploid *T. dactyloides* has given the most positive results of all forms tested thus far.

In the original plan of the work, no statistical treatment of the results was intended, because in the study of microscopic characters only 7 to 11 different clones of *Tripsacum* had been included. But later it appeared that such a treatment of data on characters listed in Table 1 might be useful. For each of them, analysis of variance was made, and the results obtained are indicated later.

RESULTS

Paired and Single Spikelets

Although the pistillate spikelets of teosinte and *Tripsacum* are borne singly, it is generally agreed that they originally were in pairs, as in maize, and became single by the abortion of one member of each pair. This is shown by the presence of the vestigial remains of a second spikelet accompanying each normal one.

It seems at first thought, therefore, that the three species represent two, and only two, distinct morphological classes with respect to this character. But evidence is available that teosinte actually constitutes a class intermediate between maize and *Tripsacum*, at least genetically. Maize-*Tripsacum* F₁ hybrids have single pistillate spikelets, while maize-teosinte F₁ hybrids have mainly paired spikelets; in fact, F₁ hybrids between Nobogame and New teosinte were found to have almost uniformly paired spikelets (Figures 1, 2). The facts stated here constitute fair evidence that teosinte is inherently between maize and *Tripsacum* in this character. As Nobogame-New hybrids have almost uniformly paired spikelets,

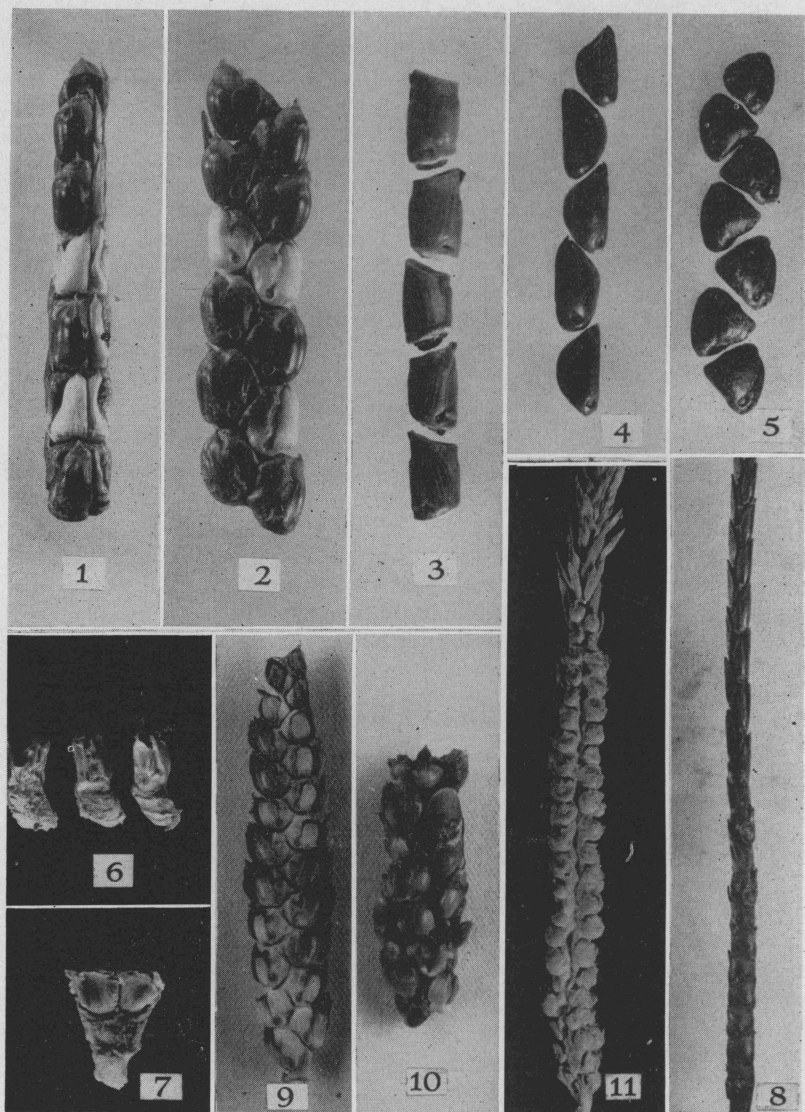


Fig. 1-11.—Fig. 1-2. Spike of F_1 hybrid of Nobogame X New teosinte.—Fig. 1. Edge view.—Fig. 2. Lateral view.—Fig. 3-7. Rachis segments.—Fig. 3. Diploid *Tripsacum dactyloides*; nodal parenchyma present.—Fig. 4. Florida teosinte.—Fig. 5. Mexican teosinte.—Fig. 6. Maize, lateral view.—Fig. 7. Maize, dorsal view.—Fig. 8-11. Spikes.—Fig. 8. Maize X diploid *T. dactyloides*, distichous.—Fig. 9. Maize X Jutiapa (Guatemalan) teosinte, distichous.—Fig. 10. Maize X Jutiapa teosinte, polystichous, the less common type.—Fig. 11. Maize X (maize X diploid *T. dactyloides*), distichous.

and hybrids of Florida teosinte with other varieties have few or none, a further suggestion is plausible that the Mexican varieties Nobogame and New, are intermediate between Florida teosinte and maize.

Thus, a series of forms is indicated, based on single and paired spikelets, the sequence being *Tripsacum*, Florida teosinte, Mexican teosinte and maize.

Compactness of Ear

Segments of the rachises of the plants studied here are homologous with the internodes of the vegetative culms, and may be compared with them. The internodes of the culms of all of them are commonly rectangular in lateral view but may be of various other forms.

The rachis-segments of *Tripsacum* are slightly trapezoidal in lateral view (Figure 3); those of Florida teosinte are more strongly so, in that their angles are more pronounced (Figure 4). In the Mexican teosintes and in the variety from San Antonio Huixta, Guatemala, the segments are triangular (Figure 5), an exaggeration of the trapezoidal form. Each degree of specialization from the rectangular form through the trapezoidal to the triangular gives an increase in compactness of the spike. The rachis with triangular segments normally produces twice as many grains per unit of length as if its segments were rectangular, and the number of its alicoles per unit of rachis-length is the maximum for the distichous spike. However, the number may be greater in the polystichous spike. The distichous spike with triangular segments, therefore, approaches the polystichous condition in compactness.

The segments of the polystichous maize rachis (Figures 6, 7) may be interpreted as being specialized along the same general pattern as those of *Tripsacum* and teosinte, but more strongly so. Here the segment is the unit of the cob to which a pair of spikelets is attached and which normally produces a pair of grains. It is so highly specialized in form and arrangement that it is scarcely recognizable as an internode, and sometimes is interpreted as a node with no accompanying internode. The segments are so shortened that they are wedge-shaped units never extending any farther inwards than the central axis of the cob, and therefore some of them may stand exactly opposite others. This specialization in arrangement is an integral part of the polystichous character, and it contributes toward a more compact ear.

Several types of observations give further support to these interpretations. The trapezoidal and triangular form of internode, as found in the rachises of *Tripsacum* and teosinte, are found also in the ear-shanks of maize and are especially pronounced in the culms of a brachytic form described by Kempton (1921). Distichous branches of maize ears have segments with approximately the same degree of compactness as those of teosinte spikes with paired spikelets (Figures 1, 2). Since the organs cited here are less compact than the maize cob but homologous with it, or in one instance a branch of it, the form of the ordinary cob-segment of maize is correlated with compactness of the ear. It follows also that the cob-segment is the result of a high specialization of the same kind observed, though not so highly developed, in both *Tripsacum* and teosinte. Thus in form of rachis-segment, a component of compactness of ear, teosinte is intermediate between maize and *Tripsacum*.

In number of rows of alicoles of the ear, teosinte and *Tripsacum* appear on casual examination to comprise one class and maize another, because spikes of both teosinte and *Tripsacum* are distichous and those of maize are polystichous. However, through studies of appropriate hybrids between the species, it was found that this character is multifactorial, that teosinte has more factors than *Tripsacum* tending to make it polystichous, and that certain of the varieties of teosinte differ from one another in genotype.

F₁ hybrids of maize with *Tripsacum* (Figure 8) and with Florida teosinte (Figures 9, 10) had almost uniformly distichous spikes, but the similarity ends here. The backcross progeny of (maize X *Tripsacum*) X maize also had almost uniformly distichous spikes (Figure 11), but the corresponding backcross progeny of (maize X Florida teosinte) X maize was variable, the mean number of rows of alicoles being 4.49. Only one plant in the population of 79 had ears with two rows of alicoles. It must be pointed out that the proportion of maize germplasm in the two backcross progenies is only approximately similar. The *Tripsacum* backcross progeny, which may be regarded as having the genomic composition MMT, is estimated to have approximately 67 percent of its genes from maize, and the teosinte backcross progeny an average of 75 percent. But the difference in number of rows of alicoles is out of proportion to the difference in percentage of maize germplasm. The comparable backcross progeny of maize with Nobogame teosinte, a Mexican variety, gave a mean of 4.80 rows of alicoles, and that with Durango teosinte, also a Mexican variety, a mean of 4.91. The differences between

the maize backcross progenies involving the Guatemalan variety and each of the two Mexican varieties were highly significant, but the backcross progenies involving the Mexican varieties were not significantly different from one another. The results given here on hybrids of maize with teosinte are in agreement with those of Rogers (1950b).

It is of incidental interest that the rachis-segments of *Tripsacum* have nodal parenchyma (Figures 3, 12), as described by Weatherwax (1926) in the Oriental genera *Polytoca*, *Sclerachne* and *Chicnachne*, of the Maydeae.

Depth of Alveolus of the Ear

This character is unique among those included in this study in that teosinte does not seem to come within the combined range of maize and *Tripsacum*. This conclusion was reached without the taking of quantitative data, but it seems to be justified on the basis of the examination of many specimens. The alveoli of teosinte are deeper in proportion to the diameter of the rachis-segment than those of *Tripsacum* (Figures 12, 13) and deeper than those of most varieties of maize. Apparently, therefore, teosinte could not have inherited its deep alveolus from either of the other two species. However, it is possible that the teosinte alveolus represents a combination of depth and compactness, because the alveolus of pod corn may vary greatly on a single ear. At the tip, where the rachis is elongated, the alveolus is a flat shield-like structure; but at the base, where the rachis is more compact, the alveolus may be a deep depression. An alternative explanation may have transgressive segregation as its basis, provided teosinte originated as a hybrid between maize and *Tripsacum*.

Branching Habit

The profuse tillering of *Tripsacum*, teosinte and certain varieties of maize have been observed and described many times previously. To make a fair comparison of the three groups, however, a study of the types and relative amounts of branching in general, rather than merely the amount of tillering, is the more instructive. In a study of this kind, the underground branching associated with the rhizomes of *Tripsacum* should not be overlooked, since this is fundamentally the same type of phenomenon as that associated with the production of tillers or of aerial branches. Bews (1929) has pointed out that it is but a step from the type of aerial culm which takes root at the nodes to the rhizome which pushes its

way through the soil. According to Bews, rhizome production is usually associated with the presence of extra-vaginal buds, which may be the principal character that initiates rhizome production. It seems pertinent, therefore, to consider the various types of branching, and to determine, if possible, whether teosinte occupies a position between maize and *Tripsacum*, both in the profusion of its branches and in the position of the branches on the culm.

The *Tripsacum* plant branches profusely at its base (Figure 14); probably most of its branching occurs beneath the

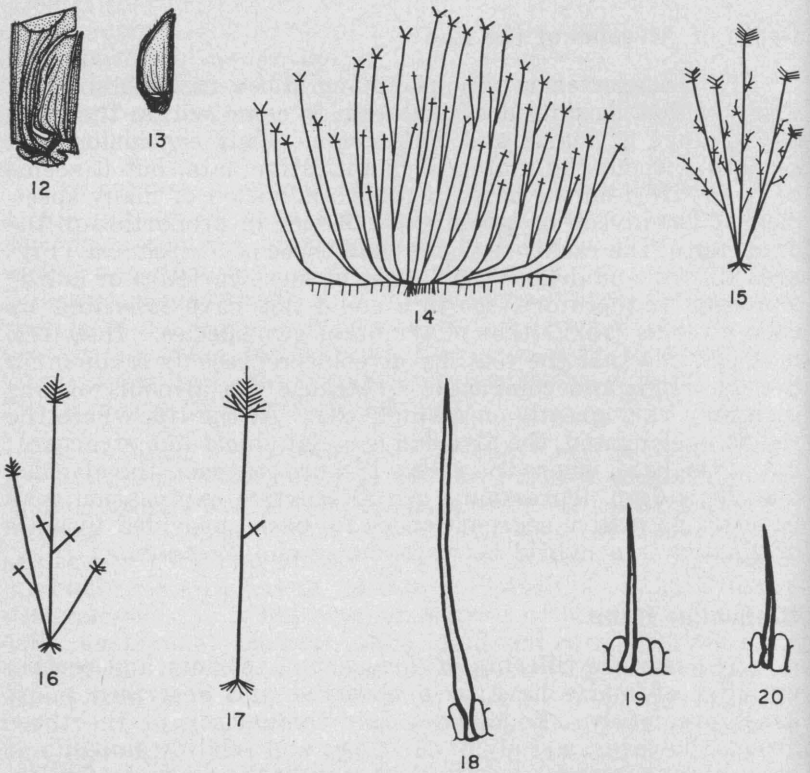


Fig. 12-20.—Fig. 12. Rachis segment of diploid *Tripsacum dactyloides*, showing depth of alveolus and nodal parenchyma. X 1.75—Fig. 13. Rachis segment of Florida teosinte, showing depth of alveolus. X 1.75.—Fig. 14-17.—Branching habits, diagrammatic.—Fig. 14. Diploid *T. dactyloides*.—Fig. 15. Florida teosinte—Fig. 16. A prolific type of North American maize.—Fig. 17. Typical Andean maize.—Fig. 18-20. Large leaf hairs. X 50.—Fig. 18. Maize.—Fig. 19. Teosinte.—Fig. 20. Diploid *T. dactyloides*.

surface of the soil. Also its aerial parts often give rise to branches, but these are relatively few. The inflorescence terminating each culm is either unbranched or sparingly branched. Therefore, two characters of the branching of *Tripsacum* may be noteworthy: (a) the branches are inclined to be basal; and (b) they are extremely abundant.

Florida teosinte (Figure 15), a Guatemalan variety, is also rather low-branching and more or less diffusely so. But most of its pistillate spikelets are borne on branches arising somewhat above the base, and its terminal inflorescences are much more elaborately branched than those of *Tripsacum*. In general, the branches of Florida teosinte depart at higher positions than those of *Tripsacum*. If only aerial branches were considered, it is possible that those of Florida teosinte would be more numerous than those of *Tripsacum*. However, the difference would evidently be small, and in the Mexican teosintes the aerial branches apparently are decidedly less numerous than in *Tripsacum*.

Therefore, Mexican varieties of teosinte are a step farther from *Tripsacum* than is Florida teosinte. Some of them are very maize-like, in that they have relatively few tillers and few branches of the terminal inflorescence. However, they do form tillers and more branches of other kinds than most varieties of maize.

North American maize supplies the fourth stage in the series (Figure 16). Some of its varieties actually have less elaborately branched tassels than the most maize-like varieties of teosinte, but this is not a common occurrence. This is to be expected in some fraction of the varieties, certain Mexican varieties for example, if they have a tendency not only to produce their branches higher on the plant than teosinte but also to produce fewer total branches. It may be explained that their tendency to produce tassel branches, which arise at high positions on the plant, is in part vitiated by their other tendency to produce but few branches. In its ears, this branching habit associated with the strong capacity for the production of grains contributes to compactness.

Andean varieties of maize produce the fewest tillers of all forms studied. Their tassels are branched, usually with secondaries. This is especially true of the tall varieties which are believed to be typical of that region (Figure 17). As compared with North American maize, the ears have shorter shanks and are borne higher on the culms.

Therefore, the groups of plants under consideration here, except the two types of maize, may be arranged in a series

showing progressively fewer total branches and progressively higher positions of the divergence of the branches. The sequence is *Tripsacum*, Florida teosinte, Mexican teosinte and maize. Although Andean maize produces its branches at higher positions on the plant than the North American, the two types have about equal numbers of branches.

Falling and Rooting of Culms

Weatherwax (1918) described the branches of teosinte and *Tripsacum* as having a tendency to become prostrate under certain conditions, and those of teosinte as taking root after becoming prostrate. These phenomena seem to be related to the branching habits already described. *Tripsacum* has underground branches, rhizomes, that regularly take root and enable the plant to live indefinitely as a perennial. Its aerial shoots also show a tendency towards this behavior, but in these shoots the mechanism is weak and belated. Annual teosinte shows the same tendency to an even greater extent in its aerial shoots, but to a less extent in general. It does not have true rhizomes, and its aerial shoots are intermediate between the aerial shoots and the rhizomes of *Tripsacum*; but they are more like aerial shoots, since they usually do not take root and relatively few of them actually become prostrate. Perhaps maize exhibits the same character to a negligible degree, for its culm sometimes takes root far above the base, especially if by chance it becomes prostrate. In this character we have a series of forms, the sequence being *Tripsacum*, teosinte and maize.

Adaptation to Poorly-drained Habitats

In so far as the writer has observed it in the wild condition, *Tripsacum dactyloides* often occurs in poorly drained soil, although it can be grown as a mesophyte. When grown with a medium amount of moisture, it becomes somewhat dormant in dry seasons and renews its growth in rainy seasons. Teosinte probably thrives best in poorly-drained locations and is reported to be able to survive with the bases of its culms in water. Its prostrate branches frequently take root in marshy soil. But it also thrives naturally under dry conditions, for Kempton and Popenoe (1937) described thousands of acres of teosinte along the ridge separating the Camoja Valley from that of Rio Huixta in Guatemala; and there is was regarded as the dominant vegetation.

It should be explained, therefore, that the observations in *Tripsacum* of tolerance to poorly-drained conditions apply only

to *Tripsacum dactyloides*. In addition, there are indications that both teosinte and *Tripsacum*, or at least various types of each, are more tolerant to drouth than maize. Thus it may be that the character to be observed in teosinte and *Tripsacum* generally, by which they differ from maize, is not simply tolerance to high humidity nor to drouth, but to a wide range of humidity conditions. In either case, they are somewhat similar to one another and different from maize.

Anatomical Characters of Leaves

A comparative study was made of seven measurable anatomical characters of the leaves of *Tripsacum*, teosinte and maize. These are enumerated, along with the means of their measurement, in Table 1. Observations were made on three additional leaf characters, the results of which are summarized in Table 2 and described briefly. All of the maize plants included, except those used for the study of thickness of leaf, were of White Surcopper, a North American variety. The forms of *Tripsacum* were diploids collected at Angleton, Texas and tetraploids collected at Nacogdoches, Texas and New Haven, Connecticut. The forms of teosinte studied were the Florida and San Antonio Huixta varieties. Only data from

Table 1.—Anatomical characters of the leaf and stem of maize and its relatives; means of measurements.

Character	<i>Tripsacum dactyloides</i> (2n)	Florida teosinte	North American maize
Large hairs on upper leaf surface, number per .45 sq. mm.	6.9	7.5	17.6
Length of epidermal cells, mm.	.095	.125	.116
Number of hygroscopic cells per row	3.6	2.6	2.5
Distance apart, strips of hygroscopic cells, mm.	.248	.443	.767
Distance apart, stomates in the row, mm.	.083	.114	.133
Distance apart, rows of stomates, mm.	.082	.110	.121
Length of stomates, mm.	.031	.045	.048
Diameter of vascular bundles of stem, mm.	.217	.292	.431

Angelton *Tripsacum*, Florida teosinte and White Surcropper maize were included in the statistical treatments.

In each of these forms, leaf hairs are of two distinct sizes, which will be designated for convenience as "large" and "small." The relative sizes of large hairs in maize, teosinte and *Tripsacum* are shown in Figures 18 to 20. For the study of frequency of large hairs, counts were made on units of leaf surface which were 0.45 square millimeter. This character was found to be more variable in *Tripsacum* than in either maize or teosinte, because of two exceptionally hairy plants of *Tripsacum*. They had a mean of 40.7 hairs per unit of leaf surface; whereas, nine other plants of this stock had a mean of only 0.13. When these two exceptionally hairy plants were

Table 2.—Summary of characters of American Maydeae showing the plant groups in ascending order of magnitude of each character

1. Paired spikelets—*Tripsacum*, Guatemalan teosinte, Mexican teosinte, maize.
2. Length of rachis-segments—Maize, Mexican teosinte, Guatemalan teosinte, *Tripsacum*.
3. Number of rows of alicoles—*Tripsacum*, Guatemalan teosinte, Mexican teosinte, maize.
4. Depth of alveolus—Maize, *Tripsacum*, teosinte(?).
5. Number of culm branches—Andean maize, North American maize, Mexican teosinte, Guatemalan teosinte, *Tripsacum*.
6. Concentration of culm branches below—Andean maize, North American maize, Mexican teosinte, Guatemalan teosinte, *Tripsacum*.
7. Falling of culms—Maize, teosinte, *Tripsacum*.
8. Adaptation to marshy habitat—Maize, (teosinte, *Tripsacum*).¹
9. Number of large hairs per unit of leaf surface—(*Tripsacum*, teosinte, maize.)
10. Number of small hairs per unit of leaf surface—*Tripsacum*, teosinte, maize.
11. Size of large hairs on leaf—*Tripsacum*, teosinte, maize.
12. Size of small hairs on leaf—(*Tripsacum*, teosinte), maize.
13. Length of epidermal cells of leaf—*Tripsacum*, (teosinte, maize).
14. Number of hygroscopic cells per row—(Maize, teosinte), *Tripsacum*.
15. Distance apart, strips of hygroscopic cells—*Tripsacum*, teosinte, maize.
16. Distance apart, stomates in the row—*Tripsacum*, teosinte, maize.
17. Distance apart, rows of stomates—*Tripsacum*, teosinte, maize.
18. Length of stomates—*Tripsacum*, teosinte, maize.
19. Total thickness of leaf blade—*Tripsacum*, (teosinte, maize).
20. Relative thickness of "rind" of culm—Andean maize, Guatemalan maize, Guatemalan teosinte, *Tripsacum*.
21. Size of vascular bundles of culm—*Tripsacum*, Guatemalan teosinte, Guatemalan maize, Andean maize.
22. Number of vascular bundles per unit of cross section area of culm—Andean maize, Guatemalan maize, Guatemalan teosinte, *Tripsacum*.
23. Development of sclerotic bundles sheaths—Andean maize, Guatemalan maize, Guatemalan teosinte, *Tripsacum*.

¹Groups whose names are enclosed in parentheses were indistinguishable.

included among the total of 11, the mean for the species was 6.9. No other extraordinary character of the two hairy plants was detected. In general, the form of *Tripsacum* from New Haven, Connecticut was more pubescent than the other two forms; but even in this form, no plant was found to be nearly so pubescent as the two exceptional ones from Angleton. In all of the forms of *Tripsacum* studied, hairs occurred near the midrib more frequently than elsewhere. In all three of the species included in the study, leaf hairs of all types seem to be restricted to the upper surface.

In reference to small leaf hairs, teosinte is intermediate between maize and *Tripsacum* in number per unit of surface and probably also in size. They are very scarce in *Tripsacum*, and so few were found that the study of their size was not completely satisfactory. The size of this type of hair in maize approaches that of the large type in *Tripsacum*.

For length of epidermal cells, approximately equal numbers of measurements were made on the upper and lower surfaces in each of the species, but the mean lengths of cells on the two surfaces were almost identical and the data taken from them were therefore combined. Specialized types of epidermal cells were not included in these measurements; such, for example, as those near vascular bundles, guard cells, cells adjacent to stomates, hygroscopic cells and cells giving rise to hairs. Mean length of epidermal cells are shown in Table 1. In actual means, maize is intermediate between *Tripsacum* and teosinte, but the difference between maize and teosinte was not significant. The differences between *Tripsacum* and each of the other two species were highly significant.

Other leaf characters are listed in Table 1 with the mean values for each species, and these require but little comment. The hygroscopic cells in all plants studied were localized in longitudinal strips usually several cells wide, and the measurements of width of the strips were recorded in number of cells. The differences found between *Tripsacum* and each of the other two species were highly significant, but the difference between maize and teosinte was not significant. In distance apart of the strips of hygroscopic cells, and distance apart of stomates in the row, each of the three species showed highly significant differences. In distance apart of the rows of stomates, the differences between *Tripsacum* and each of the other species were significant at the .01 level, and the difference between maize and teosinte was significant at the .02 level. In length of stomates the differences between *Tripsacum* and each of the other species were significant at the .01 level, and that between maize and teosinte at the .05 level.

The relative thickness of leaves of the three species is illustrated in Figures 21 to 23. No quantitative data were taken on this character, but all observations indicate that the leaves of maize and teosinte were thicker than those of *Tripsacum*. There was little or no difference between maize and teosinte, but according to most of the observations the leaves of maize are a little thicker than those of teosinte.

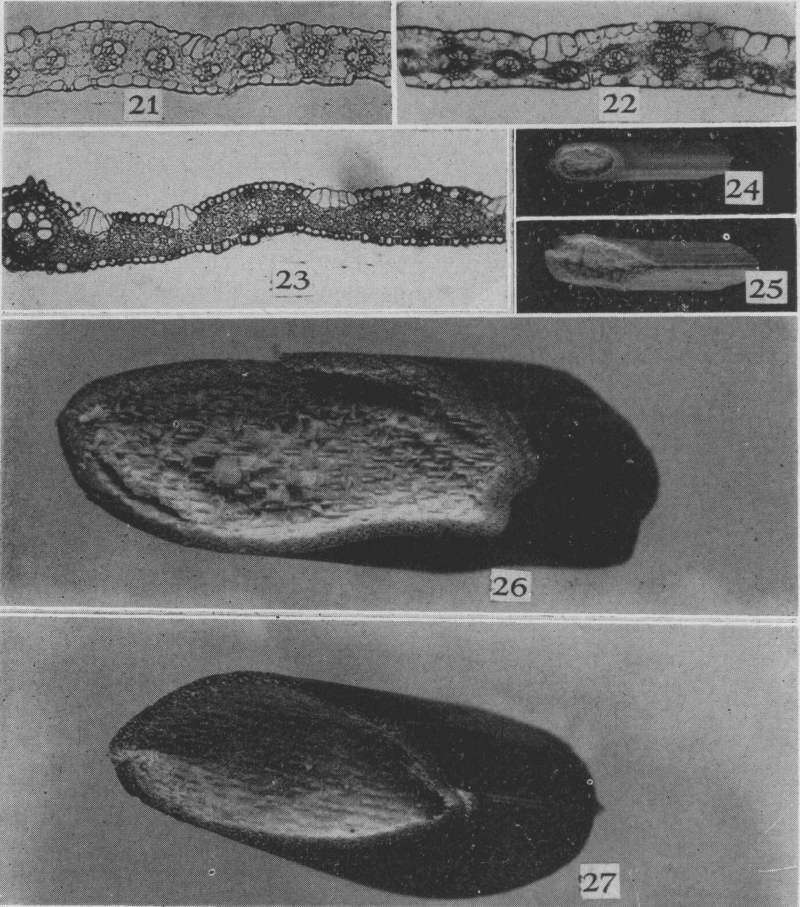


Fig. 21-27.—Fig. 21-23. Cross sections of leaves showing relative thickness.—Fig. 21. Maize.—Fig. 22. Florida teosinte. Fig. 23. Diploid *Tripsacum dactyloides*. Fig. 24-27. Segments of culms, showing relative thickness of “rind” and size of culm.—Fig. 24. Diploid *T. dactyloides*.—Fig. 25. Florida teosinte.—Fig. 26. Guatemalan maize—Fig. 27. Typical Andean maize.

Toughness of Culms

Observations indicate that the culms of *Tripsacum* are the most tenacious, in proportion to their size, of all of the species included in this study, and that those of Andean maize are the least so. Teosinte and North American maize are intermediate between the extremes. When plants of the various kinds of maize were grown under similar conditions in the field and subjected to strong winds, Andean maize was observed to break most readily. In one field under observation, more than 65 percent of the plants in the plots of Andean maize were broken, while North American maize growing in adjacent plots showed practically no broken plants. Guatemalan maize usually resembled North American maize in this respect. These observations refer to immature plants.

Such observations on toughness of culm were made through a period of 3 years, and a study of the anatomical characters accounting for the difference was finally undertaken. *Tripsacum*, Florida teosinte, Guatemalan maize and Andean maize were examined for four anatomical characters: (a) thickness of the woody peripheral region of the culm in relation to total size, (b) size of vascular bundles, (c) number of bundles per unit of area in cross section and (d) relative degree of development of the sclerenchymatous bundle sheaths.

Figures 24 to 27 show the relative thickness of the woody peripheral region, sometimes designated as "rind". Before being photographed, these specimens were allowed to dry so as to shrink the parenchyma and show the rind as clearly as practicable. An accurate study of the thickness of the rind in relation to size of culm is difficult to make, on account of a lack of sharp distinction between the rind and the central area, but the most satisfactory measurements indicate that the approximate ratios of thickness of rind to total diameter of culm in the various forms are *Tripsacum* 1:6, Florida teosinte 1:8 Guatemalan maize 1:11 and Andean maize 1:13.

In all of these forms, the epidermis and a few layers of subepidermal cells are small and thick-walled, and the number of these cell layers varies widely depending on the group of plants. The vascular bundles in the subepidermal region are relatively small and their sheaths very strongly developed. The sheaths of two or more adjacent bundles sometimes converge, so as to form a continuous, thick layer of sclerenchyma.

A gradual transition was found from subepidermal cells with extremely thick walls and no intercellular spaces to the

typical parenchyma cells of the central region. However, it was usually possible to distinguish the typical parenchyma of the central region from the transitional region external to it, and frequently the transitional region could be reasonably well distinguished from the subepidermal area of typical sclerenchyma.

In Andean maize, a subepidermal layer three to six cells in thickness was found to be made up of elements with strongly thickened walls. Beneath this, the transitional region was 25 to 30 cells thick. In Guatemalan maize, the strongly sclerified subepidermal layer was found to be of about the same thickness as that of Andean, but the transitional region was thicker, usually 35 to 50 cells. Florida teosinte has a subepidermal layer of sclerenchyma two to five cells thick and a transitional region 15 to 20 cells thick. However, the cells of the transitional region had thicker walls in proportion to the size of their lumina than was found in the corresponding region of either type of maize. These cells usually had little more than half the diameter of the typical parenchyma cells of the central region, and their walls were three to five times as thick, but intercellular spaces were not uncommon. In *Tripsacum*, the sheaths of the most peripheral bundles were so strongly developed that they usually converged with one another and with the fibers just beneath the epidermis. In this way the external fibrous region was about the width of one or two vascular bundles, and no distinction was seen between the subepidermal region of sclerenchyma and the fibrous sheaths of the bundles. Areas occurred within this circular zone, however, in which the bundles sheaths did not converge. Here the cells were thick-walled and small, but intercellular spaces sometimes occurred. Although this region is the homologue of the transitional region found in the other three forms, it is less genuinely transitional, because most of its cells have greatly thickened walls.

For the study of size of vascular bundles, measurements were made of the maximum diameter of bundles from plants of each of the four groups. Measurements were made only on bundles located in the central region of the culms, because these were differentiated from the tissue surrounding them. The measurements were recorded in tenths of a millimeter and the means from all except Andean maize are given in Table 1. The mean for Andean maize is 0.456mm. In this character, all the differences between North American maize, teosinte and *Tripsacum* were highly significant, and the difference between Andean and North American maize was significant at the .05 level. Figures 28 to 31 illustrate the size relationship

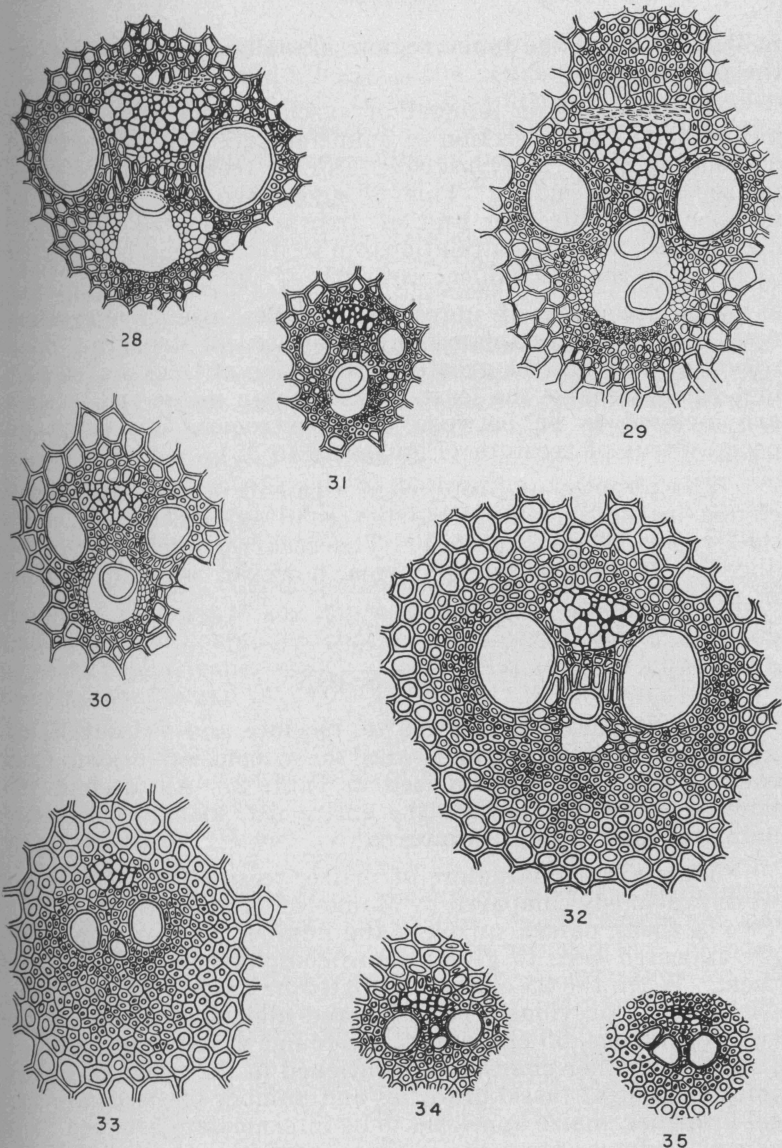


Fig. 28-35.—Fig. 28-31. Vascular bundles from the inner, parenchymatous region of culms. X 87.—Fig. 28. Typical Andean maize.—Fig. 29. Guatemalan maize.—Fig. 30. Florida teosinte.—Fig. 31. Diploid *Tripsacum dactyloides*.—Fig. 32-35. Vascular bundles from the peripheral zone, or "rind", of culms. X 132.—Fig. 32. Typical Andean maize.—Fig. 33. Guatemalan maize.—Fig. 34. Florida teosinte.—Fig. 35. Diploid *T. dactyloides*.

in bundles from the inner region, and Figures 32 to 35 from the peripheral.

Observations on number of vascular bundles per square millimeter of cross section of culm indicate that the series in descending order is *Tripsacum*, Florida teosinte, Guatemalan maize, Andean maize. This is suggestive that the greater number of bundles per unit of area is associated with their minuteness, and such a relationship in itself would be expected to increase the mechanical strength of the culm.

The structure of individual bundles also is interesting with respect to an explanation of mechanical strength. *Tripsacum* usually has the greatest proportion of thick-walled cells and Andean maize the least. Guatemalan maize and teosinte are inclined to be between these extremes, this being especially true of teosinte (Figures 28 to 35).

The absence of protoxylem elements and xylem parenchyma in the peripheral bundles is in agreement with a recent report of Sass (1951). The occurrence of bundles reduced to strands of sclerenchyma, however, was not included in the study.

DISCUSSION

The 23 characters of maize, teosinte and *Tripsacum* analyzed on preceding pages and the conclusion drawn from each of them are summarized in Table 2. An attempt will now be made to interpret the entire list, along with related data recorded in the literature.

Thirty-four characters of maize, teosinte and *Tripsacum* were previously compared by Mangelsdorf and Reeves (1939). Two of them, paired spikelets and number of rows of alicoles, are repeated here to give a more complete understanding of them. When the 23 characters listed in Table 2 are combined with the 34 previously reported and allowance made for the two repetitions, 55 characters are found to have been studied. In still two other characters mentioned in the previous report, total number of tassel branches and number of secondary tassel branches, maize appeared to be intermediate between *Tripsacum* and teosinte. Since the report was published, however, Reeves (1950, Figures 8 and 9) reported varieties of maize having numerous branches of both kinds; in fact, profusely branched tassels of maize, including those of varieties from the Andean region, now are commonly observed. It seems probable that maize should be regarded as essentially similar to teosinte in these characters.

Two of the 55 characters should be disregarded until studied more completely, because the bearing they may have on the problem is doubtful. In depth of alveolus, the evidence is not clear that the condition observed in teosinte could have descended from either of its putative parents, maize or *Tripsacum*, or from a hybrid between them. Frequency of large leaf-hairs is extremely variable, and although the mean of teosinte is between that of maize and *Tripsacum*, the results are not significant. According to the writer's observations and observations of colleagues, the other three characters of leaf hairs, numbered 10 to 12 (Table 2), are more variable within each of the three groups, North American maize, Guatemalan teosinte and diploid *T. dactyloides*, than the data indicate. However, the samples were chosen without prior knowledge of their minute characters, and, in fact, without regard to any of their special characters. It is believed, therefore, that the samples are fairly representative of their respective groups in the remaining 53 characters, even though an occasional plant or population may depart rather widely from them.

An apparent correlation between certain of the characters may give rise to the impression that in some instances a combination of correlated characters is controlled by a single gene with pleiotropic effects. Examples of such characters are those numbered 20 to 23 (Table 2), which contribute to toughness of culm. Martin and Hershey (1934-5) found that large culm in maize is correlated with large vascular bundles and with few bundles per unit of cross section; and such correlations seem to exist in some measure in the plants studied here. It may be that the characters of the stomates, numbers 16 to 18, are similarly correlated.

From the standpoint of the origin of these groups of plants, the number of genes controlling the characters, as well as the number of characters themselves, is important, because the genic differences indicate the number of mutations necessary for the direct descent of one group from another. Even if it be true that some of these combinations of characters are controlled by genes with manifold effects, there are at least three reasons for a suggestion that some of the single characters differentiating the plant groups are quantitative, or dependent on two or more genes.

First, it would be difficult to postulate three or more stable genetic classes based on differences in the same character, such as we have in many of these instances, as differing by a single mutation. Second, the analysis of variance on length of epidermal cells, distance apart of stomates in the row and length of stomates indicates that the differences be-

tween the three species are significant at the .01 level when tested with differences between plants within species. Third, the genetical work of Mangelsdorf (1947) and Rogers (1950a, b) on eight characters in which maize and teosinte differ show that each of those characters is controlled by genes on more than one chromosome. For paired *vs.* single spikelets, at least two chromosomes and possibly six others are involved; for tillering habit at least three. Other characters not included in the present study, such as glume development and distichous *vs.* polystichous ear, were found by Mangelsdorf and Rogers to be influenced by genes on at least 7 of the 10 chromosomes. In as much as the present study was not designed to determine the number of genes controlling the characters, there would be little value in further discussion of the question. It may be dismissed for the present with the assertion that in all probability the number of mutations necessary for the derivation of one of these species from another is much greater than the number of characters which separate them.

In all the 55 characters mentioned earlier in this discussion, teosinte is dissimilar to maize in 19 characters of the previous report and 19 of the present, which make a total, after subtracting the two repetitions, of 36. Indeed, this list is subject to revision and supplement by additional study, but it is indicative of the number of mutations necessary for the direct descent of maize from teosinte.

Further reference should be made to the eight characters listed in Table 1, for which small samples from only one or a few forms from each species were studied. Although the interpretation of results applies only to the restricted samples, if we add the assumption that the small samples are fairly representative of the original teosinte and its parents, the results take on a more positive meaning. Yet, the possibility remains that forms somewhat different from these might also fit the hypothesis of the hybrid origin of teosinte. It is unnecessary that the samples studied here be extremely similar to the original teosinte and its parents; it is of course necessary that any combinations of samples, from whatever source, representing the hypothetical parents, possess such characters that hybrids between them might be expected to bear a fairly close resemblance to some known form of teosinte.

It is now noteworthy that teosinte is intermediate between maize and *Tripsacum* or similar to one of them in all characters studied, with two doubtful exceptions. If the characters studied comprise a fair sample, the results impose a serious difficulty on the theory of Weatherwax (1918) that maize, teosinte and *Tripsacum* descended from a common an-

cestor by a series of mutations. Assuming that the origin of these mutant characters is a matter of chance, that theory would demand a series of coincidences, occurring against great odds.

But the results are in complete agreement with those expected if we adopt the hypothesis that teosinte originated as a segregate of a hybrid between maize and *Tripsacum*. The results are not finally conclusive on the problem of the degree of similarity of the maize and *Tripsacum* studied to the presumed parental types that gave rise to teosinte. They give no indication of the time when the hybridization might have occurred, and therefore none on the time of origin of teosinte. However, the literature contains a few facts and hypothesis on these interrelated questions.

From a study of the literature on archeology and plant geography, Mangelsdorf and Reeves (1938) estimated the time of origin of teosinte as about 600 A.D., and later (1939) revised this estimate to 900 A.D. Either of these relatively recent dates implies that the maize and *Tripsacum* postulated as parents of teosinte were recent, perhaps present-day, forms. Beadle (1939), Weatherwax (1950) and Randolph (1952) considered the difficulty in the hybridization of maize and *Tripsacum* to be a ruinous weakness of the hypothesis of the hybrid origin of teosinte. In the meantime, Mangelsdorf and Smith (1949) described archeological specimens of maize from Bat Cave, New Mexico, and some of the specimens showed evidence of contamination from teosinte. The specimens occurred in six strata, and Arnold and Libby (1951) estimated the ages of the various strata by the radiocarbon method. Specimens from the three lower strata, 3500 to 2249 \pm 250 years old, showed only doubtful evidence of contamination from teosinte. Specimens from Stratum IV, age 2239 \pm 250 years, and all higher strata showed unmistakable evidence of contamination. From these data, the inference is justified that teosinte was present in the vicinity of Bat Cave before the beginning of the Christian Era, possibly many centuries before. Mangelsdorf and Smith's publication (1949), issued before the radiocarbon technique was applied to the Bat Cave specimens, states that the hybridization between maize and *Tripsacum* which produced teosinte must have occurred no later than 500 B.C. and perhaps much earlier. This estimate and that of Arnold and Libby are in satisfactory agreement.

Stebbins (1950), recognizing that the genes of teosinte by which it resembles *Tripsacum* rather than maize are not distributed at random over the chromosomes but tend to be

grouped in a few segments of certain chromosomes (Mangelsdorf 1947), states that it is difficult to see how such a situation could have arisen except through hybridization. He also recognizes the weakness of that version of the hypothesis which requires the derivation of a fertile segregate from a hybrid between forms of maize and *Tripsacum* which thus far have been cross-pollinated experimentally. In an effort to explain these two apparently contradictory bodies of data, Stebbins adopts the view, which is well supported by facts, that the extant 18-chromosome (gametic number) forms of *Tripsacum* ordinarily designated as diploids are themselves really allopolyploids, and therefore of hybrid origin. He suggests that one, or conceivably both, of the extinct parents of *Tripsacum* contained forms which were more closely related to maize and more interfertile with it than is *Tripsacum* itself. Thus, he assumes that teosinte might have originated as a hybrid between ancient maize and a 9 or possibly a 10-chromosome parent of *Tripsacum*.

It should be pointed out that the possibility is not exhausted of finding combinations of modern maize and *Tripsacum* that are substantially more interfertile than those already tested. Also, it may be that fertile segregates eventually will be obtained from hybrids between the forms of maize and *Tripsacum* which thus far have shown only low interfertility. But in the absence of positive evidence on these possibilities, Stebbins' assumption of hybridization in a remote period must be viewed with favor as a provisional hypothesis.

However, Stebbins' explanation of teosinte as a hybrid between ancient maize and one of the 9-chromosome parents of *Tripsacum* apparently means that the genom brought into *Tripsacum* by its other parent accounts in large part for the strong barrier now observed between *Tripsacum* and maize. If this were true, we should expect more regular synapsis and gene exchange than has been reported between the modern maize genom and one of the 9-chromosome genomes of *Tripsacum*. Cytogenetical studies of hybrids between various combinations of modern maize and *Tripsacum*, reported by Mangelsdorf and Reeves (1939) and verified by Randolph (1952), show very little synapsis or exchange of genes. It seems, therefore, that if teosinte did originate as a hybrid between some ancient form of maize and an interfertile 9 or 10-chromosome parent of *Tripsacum*, the chromosomes of *Tripsacum* must have been more closely homologous with those of maize, and that maize and *Tripsacum* were more interfertile at that ancient time than now. This removes at least part of the necessity of Stebbins' assumption that the non-maize parent

of teosinte was also one of the parents of *Tripsacum*. Likewise, since *Tripsacum* is fairly satisfactory as a hypothetical parent of teosinte, from the standpoint of plant characters, the question might well be raised as to whether one of its own parents would be equally as satisfactory. This, of course, must remain an open question.

In view of all these facts and deductions, the suggestion seems justified that teosinte originated as a natural hybrid between a form of maize and an 18-chromosome *Tripsacum*, the hybridization having occurred at a remote time when maize and *Tripsacum* possessed somewhat the same plant characters as now but when they were more interfertile.

ACKNOWLEDGMENTS

During the preparation of the manuscript, many helpful suggestions were made by P. C. Mangelsdorf of Harvard University, H. C. Cutler formerly of the Chicago Natural History Museum, now of the Missouri Botanical Garden, and C. B. Godbey of the Agricultural and Mechanical College of Texas. The writer wishes to express his appreciation for this assistance.

LITERATURE CITED

- Arnold, J. R., and W. F. Libby. 1951. Radiocarbon dates. *Science* 113: 111-120.
- Beadle, G. W. 1939. Teosinte and the origin of maize. *Jour. Heredity* 30: 245-247.
- Bews, J. W. 1929. *The world's grasses*. Longmans, London.
- Cutler, H. C., and Edgar Anderson. 1941. A preliminary survey of the genus *Tripsacum*. *Annals Missouri Bot. Gard.* 28: 249-269.
- Kempton, J. H. 1921. A brachytic variation in maize. *U.S.D.A. Bul.* 925.
- _____, and W. Popenoe. 1937. Teosinte in Guatemala. *Carnegie Inst. Washington Pub. No.* 483: 199-218.
- Mangelsdorf, P. C. 1947. The origin and evolution of maize. In Demerec, M. *Advances in Genetics* 1: 161-207. Academic Press, New York.
- _____, and R. G. Reeves. 1938. The origin of maize. *Proc. Nat. Acad. Sci.* 24: 303-312.
- _____. 1939. The origin of Indian corn and its relatives. *Texas Agric. Expt. Sta. Bul.* 574.
- _____, and C. E. Smith, Jr. 1949. New archeological evidence on evolution of maize. *Harvard Univ. Bot. Mus. Leaflets* 13: 213-247.
- Martin, J. N., and A. L. Hershey. 1934-35. The ontogeny of the maize plant—The early differentiation of stem and root structures and their morphological relationships. *Iowa State College Jour. Sci.* 9: 489-503.
- Randolph, L. F. 1952. New evidence on the origin of maize. *Amer. Nat.* 86: 193-202.
- Reeves, R. G. 1950. Morphology of the ear and tassel of maize. *Amer. Jour. Bot.* 37: 697-704.
- Rogers, J. S. 1950a. The inheritance of photoperiodic response and tillering in maize-teosinte hybrids. *Genetics* 35: 513-540.
- _____. 1950b. The inheritance of inflorescence characters in maize-teosinte hybrids. *Genetics* 35: 541-558.
- Sass, J. E. 1951. "Reduced" vascular bundles in maize. *Iowa State College Jour. Sci.* 26: 95-98.
- Stebbins, G. L., Jr. 1950. *Variation and evolution in plants*. Columbia Univ. Press, New York.
- Weatherwax, P. 1918. The evolution of maize. *Bul. Torrey Bot. Club* 45: 309-342.
- _____. 1926. Comparative morphology of the Oriental May-deae. *Indiana Univ. Studies* 13, No. 73.
- _____. 1950. The history of corn. *Scientific Monthly* 71: 50-60.