UNITED STATES DEPARTMENT OF AGRICULTURE

BULLETIN No. 925

Contribution from the Bureau of Plant Industry
WM. A. TAYLOR, Chief

Washington, D. C. | PROFESSIONAL PAPER | February 18, 1921

A BRACHYTIC VARIATION IN MAIZE

By

J. H. KEMPTON
Assistant in Crop Acclimatization

CONTENTS

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CONTENTS.

DEFINITION OF BRACHYSM.

Practically all the organs of maize are subject to profound modification, with heritable variations the rule rather than the exception. Many of these variations are undesirable abnormalities, and a knowledge of their origin and inheritance is of practical importance chiefly as an aid to their elimination. Among the many variations, however, one has appeared which gives promise of becoming of agricultural value, since it possesses several highly desirable features advantageous for dry-land and irrigated conditions.

This variation consists of a shortening of the internodes without a corresponding reduction in their number or in the number and size of other organs. (Pl. I.) Variations of this nature are found in many agricultural plants, as, for example, the "bush" varieties of peas, beans, squashes, and tomatoes, and are popularly known as dwarfs. The distinction between this type of dwarfing and that in which many if not all of the organs have suffered a reduction in size has been pointed out by Cook (4),[1] who studied similar variations in cotton and suggested the term brachysm for that type which involves a shortening of the internodes only.

[1] Serial numbers in parentheses refer to "Literature cited" at the end of the bulletin.

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REVIEW OF THE LITERATURE.

Brachysm and true dwarfing, or nanism, are variations which have recurred in maize in widely divergent and wholly independent stocks. In addition to the case of brachysm here described, Emerson (6) records the origin of a dwarf which has a brachytic stalk, short broad leaves, staminate flowers scattered throughout the pistillate inflorescence, few branches in the male inflorescence, and it sheds little, if any, pollen (Pl. II). This variation appeared simultaneously in three progenies grown from self-pollinated ears. Two of these progenies were closely related, but the third had an entirely different ancestry. A third independent origin of this anther-ear dwarf was reported by Montgomery (14), who received the seed ear from C. P. Hartley.

A fourth independent origin of this same peculiar variation is reported by East and Hays (5), who found it in a commercial strain of the Stowell's Evergreen variety of sweet corn. While the dwarf found by Emerson and that of East and Hays have not been compared by crossing, there can be little doubt that the three variations involve a similar genetic change.

Emerson (7) also records the origin and inheritance of still another type of dwarf which, in addition to reduced stature, produces most of the seeds in the terminal inflorescence. This variation has been designated "tassel ear."

Hartley (9) records the origin of a brachytic dwarf, the leaves of which were shorter and broader than those of the parental variety. When the dwarf plants were crossed among themselves they were found to breed true.

Gernert (8) found a dwarf plant in a plat of Leaming Yellow Dent. The plant was less than one-third the height of normal plants of the parental variety, but produced as many nodes. The leaves were as long as those of the variety mentioned, which would seem to establish it as a true case of brachysm. The plant produced no ear, but was used as the male parent in crosses with plants of normal stature. There was no report on the progeny of these crosses.

In addition to the brachytic variation to be discussed later, other brachytic plants have appeared in two instances in our breeding block, but, contrary to the usual behavior, the brachysm in these cases did not behave as a simple Mendelian character. The inheritance of these variations is considered briefly on pages 6–7.

ORIGIN AND DESCRIPTION OF THE VARIATION.

The brachytic strain of maize under consideration arose in a hybrid between the Algerian pop-corn and the Chinese waxy varieties (No. Dh 416). The second generation, in which the brachytic plants appeared, was the result of self-pollinating a first-generation plant which was being grown for seed characters (10). Approximately one-quarter of the plants were brachytic, the actual numbers being 5 brachytic and 21 normal (11).

The appearance of brachytic plants in the second generation of this hybrid may be explained by assuming that the Chinese parent was heterozygous for brachysm. The reasons for this assumption will appear later. On this hypothesis one-half of the F_1 plants when self-pollinated should give progenies having one-quarter of the plants brachytic, and if the Chinese parent had been self-pollinated, one-quarter of its progeny also should be brachytic. The Chinese plant, unfortunately, was not self-pollinated, so that the possibility of its having been heterozygous for brachytic culms can not be tested directly. However, many hundred progenies and several large bulk plantings of this waxy variety have been grown without brachytic plants having been found. It would seem, therefore, not unreasonable to conclude that this variation is the result of a relatively recent genetic change and is not the result of bringing into expression a recessive variation which has been masked by the dominance of normal culms.

The brachytic plants might also be accounted for by assuming that a single gamete of the Chinese parent mutated and was fertilized by a normal gamete of the Algerian variety, but since only three second generation progenies of the hybrid Dh 416 have been grown, there is a possibility that more than one gamete of the Chinese parent of this hybrid had mutated.

One of the brachytic plants was self-pollinated and the resulting progeny were all brachytic. At the present time 16 progenies, derived from self-pollination or crosses between sister brachytic plants, have been grown. These progenies without exception have produced nothing but brachytic plants.

In addition to these 16 progenies several crosses have been made between plants of normal stature and brachytic plants. The first generations of such crosses were all as tall as or taller than the normal parent, while the second generations show a segregation into normal and brachytic plants closely approximating the Mendelian 3 to 1 ratio.

Both parents of the hybrid from which the brachytic plants arose may be considered of the pop-corn type and bear several small ears. The brachytic plants are in no sense inferior to their parents in leaf area or yield of grain. A comparison of normal and brachytic progenies is shown in Table I. These progenies were grown from self-pollinated ears of sister plants.

TABLE I.—*Measurements of maize plants of two sister progenies, one of which was brachytic and the other normal in stature.*

Plant character.	Brachytic.	Normal.
Height of plant .... decimeters	8.66±0.10	14.40±0.24
Number of leaves:		
Above the upper ear	3.20±0.08	3.37±0.09
Total	22.90±0.19	20.80±0.27
Number of branches in the tassel	15.30±0.64	25.90±1.01
Ear length:		
Upper ear .... centimeters	14.20±0.27	16.40±0.23
Total .... do	27.60±0.98	28.10±0.71
Number of rows on upper ear	16.30±0.26	21.20±0.30
Diameter of stalk .... $\frac{1}{16}$-inch	20.50±0.35	12.40±0.21
Fourth leaf from top:		
Length .... centimeters	62.60±6.20	64.40±8.90
Width .... do	9.20±1.40	12.30±1.50

The range in height of the brachytic plants was from 6 to 10 decimeters with a coefficient of variability of 10.1±0.81. Nine hand-pollinated ears were obtained from these brachytic plants, from which progenies were grown the following season (Table II). In five cases colored and white seeds were planted separately, making 14 progeny rows. Since no differences were found between the plants grown from seed of the two colors, they may be considered as single populations. The progenies from seeds of different colors of the same ear are grouped together in the table. In each pair the progeny grown from white seeds appears first. The differences in height between the progenies were for the most part insignificant, and while the measurements are given separately in Table II, it would seem not unfair to consider them as a single population. The number of individuals is then 286 with a mean height of 8.81±0.046. The range in height is from 5 to 13 decimeters with a coefficient of variability of 13.1±0.37.

The progenies differed somewhat in appearance, some having stiff erect leaves while in others the leaves were long and drooping, like those of the plant shown in Plate I. They differed also in productivity, the best-yielding progeny exceeding the poorest by more than 100 per cent. The diversity among the progenies, however, was no greater than is ordinarily found among sister progenies of normal stature.

All but one progeny had about 25 per cent of the plants with aborted male inflorescences (Pl. III). The degree of abortion varied from plants having a few of the branches aborted at the tips or perhaps several short naked branches to those which aborted all the tassel branches or bore only undeveloped spikelets. The progenies also varied in the percentage of affected plants, but for the 274 plants involved 27±1.81 per cent showed this abnormal behavior.

The abortion of the male inflorescence did not affect the female inflorescence, and the yield of such plants was as great as that of unaffected plants. The fact that one progeny was free from this undesirable characteristic affords evidence that it is inherited and that strains free from this defect can be grown.

TABLE II.—*Measurements of maize plants of 14 brachytic progenies directly descended from the original variation.*

Designation of the progeny.	Height (dm.).	Length (cm.).		Number of nodes above the ear.	Total number of leaves.	Longest leaf (cm.).	
		Longest tassel branch.	Ear stalk.			Length.	Width.
Dh 416 L2 L1	8.7±0.16	15.4±0.72	....	3.1±0.03	19.4±0.21	66.4±0.88	5.8±0.02
Dh 416 L2 L1 L3–3.	8.3±0.23	14.0±1.13	....	4.1±0.06	21.5±0.49	71.1±2.2	7.0±0.15
Dh 416 L2 L1 L3–4.	7.5±0.31	12.3±1.99	....	4.0±0.17	22.7±0.50	71.2±1.89	7.5±0.32
Dh 416 L2 L1 L4–3.	9.6±0.28	15.7±2.35	....	2.1±0.04	20.9±0.30	74.8±1.53	7.8±0.33
Dh 416 L2 L1 L4–4.	9.2±0.23	15.7±0.93	....	1.9±0.04	20.9±0.18	72.9±0.82	7.0±0.17
Dh 416 L2 L1 L5	9.2±0.17	18.8±0.72	5.8±0.16	2.1±0.06	20.6±0.40	67.8±1.26	7.5±0.17
Dh 416 L2 L1 L6–3.	8.7±0.11	18.8±0.55	10.0±0.28	3.5±0.13	21.4±0.15	69.5±0.74	8.2±0.15
Dh 416 L2 L1 L6–4.	8.1±0.15	17.2±0.79	10.0±0.24	3.6±0.11	....	69.8±0.68	8.7±0.08
Dh 416 L2 L1 L7	8.0±0.14	17.8±0.59	7.9±0.21	2.7±0.07	....	75.4±0.59	7.6±0.09
Dh 416 L2 L1 L9–3.	8.9±0.18	15.8±1.56	10.9±0.62	3.7±0.12	....	73.5±1.44	7.8±0.17
Dh 416 L2 L1 L9–4.	8.7±0.27	19.3±1.18	10.2±0.34	3.8±0.12	....	74.2±0.61	7.7±0.13
Dh 416 L2 L1 L8	9.0±0.17	18.6±0.76	8.6±0.34	3.1±0.08	....	71.1±0.86	8.4±0.16
Dh 416 L2 L1 L11–3	9.6±0.09	22.7±0.54	9.4±0.26	3.1±0.08	....	70.7±0.52	8.1±0.11
Dh 416 L2 L1 L11–4	9.2±0.12	17.7±0.75	8.9±0.31	3.0±0.14	....	68.5±0.79	7.6±0.13

Designation of the progeny.	Length (cm.).		Number of tassel branches.	Length of ear (cm.).		Number of rows.	Diameter of stalk ($\frac{1}{16}$ inch).
	Branching space of tassel.	Central spike.		Upper.	Total.		
Dh 416 L2 L1	4.0±0.26	19.9±0.71	13.3±0.58	11.5±0.23	12.3±0.34	15.5±0.17	....
Dh 416 L2 L1 L3–3	3.5±0.17	19.4±1.77	15.0±0.86	12.3±0.34	22.0±0.51	16.3±0.16	....
Dh 416 L2 L1 L3–4	2.7±0.60	17.0±1.86	12.4±0.68	11.5±0.44	18.5±1.64	16.0±0.25	....
Dh 416 L2 L1 L4–3	2.4±0.25	21.9±2.35	15.3±1.59	10.3±0.63	27.7±0.96	16.0±0.20	....
Dh 416 L2 L1 L4–4	3.3±0.19	24.5±1.08	14.0±0.64	9.2±0.30	18.6±0.59	14.7±0.18	....
Dh 416 L2 L1 L5	3.2±0.16	28.3±0.69	10.5±0.59	10.1±0.30	18.7±0.75	14.9±0.23	16.2±0.44
Dh 416 L2 L1 L6–3	2.9±0.08	26.2±0.70	13.5±0.36	10.7±0.21	18.3±0.78	16.8±0.23	16.2±0.24
Dh 416 L2 L1 L6–4	3.3±0.19	24.7±1.1	14.3±0.31	10.4±0.18	20.5±0.59	17.3±0.24	17.3±0.25
Dh 416 L2 L1 L7	4.3±0.24	25.5±0.94	14.5±0.46	11.8±0.27	23.1±0.75	15.3±0.21	18.0±0.34
Dh 416 L2 L1 L9–3	3.9±0.42	21.8±2.32	13.9±0.84	12.8±0.34	25.5±1.05	16.5±0.21	18.1±0.29
Dh 416 L2 L1 L9–4	4.4±0.31	27.5±1.26	14.3±0.47	13.5±0.24	23.6±0.81	15.9±0.15	15.9±0.22
Dh 416 L2 L1 L8	4.3±0.45	26.5±0.80	16.3±0.55	12.9±0.26	27.6±0.82	15.8±0.10	17.9±0.26
Dh 416 L2 L1 L11–3	6.4±0.37	31.3±0.41	16.4±0.36	12.4±0.39	26.4±0.83	16.5±0.13	18.3±0.22
Dh 416 L2 L1 L11–4.	4.4±0.24	25.5±1.51	14.2±0.46	11.7±0.40	21.1±1.00	16.8±0.22	17.6±0.31

Designation of the progeny.	Height of ear from ground (dm.).	Number of nodes.		Length of the longest leaf sheath (cm.).	Number above the longest—		Length of internode (cm.).	
		Without roots.	With roots.		Leaf sheath.	Internode.	Longest.	Uppermost.
Dh 416 L2 L1	4.3±0.10	....	....	....	....	....	....	....
Dh 416 L2 L1 L3–3	3.3±0.11	....	....	....	....	....	....	....
Dh 416 L2 L1 L3–4	3.5±0.19	....	....	....	....	....	....	....
Dh 416 L2 L1 L4–3	4.9±0.10	....	....	....	....	....	....	....
Dh 416 L2 L1 L4–4	4.5±0.10	....	....	....	....	....	....	....
Dh 416 L2 L1 L5	4.0±0.07	12.3±0.26	8.4±0.18	21.1±0.18	10.2±0.20	7.4±0.19	4.2±0.10	7.3±0.21
Dh 416 L2 L1 L6–3	3.6±0.08	12.8±0.09	7.8±0.16	19.5±0.16	10.8±0.14	8.5±0.21	3.9±0.09	7.5±0.21
Dh 416 L2 L1 L6–4	3.7±0.07	13.6±0.12	....	19.6±0.16	11.8±0.13	9.4±0.29	3.6±0.09	6.6±0.21
Dh 416 L2 L1 L7	3.1±0.04	12.7±0.22	....	19.4±0.14	10.3±0.17	7.5±0.30	3.5±0.12	7.7±0.18
Dh 416 L2 L1 L9–3	4.5±0.14	13.7±0.15	....	21.2±0.45	11.7±0.25	7.8±0.38	5.8±0.20	....
Dh 416 L2 L1 L9–4	4.1±0.05	12.7±0.10	....	21.2±0.16	11.0±0.14	9.0±0.15	5.6±0.15	....
Dh 416 L2 L1 L8	3.9±0.03	13.2±0.18	....	19.9±0.22	11.4±0.20	7.9±0.26	4.0±0.08	....
Dh 416 L2 L1 L11–3	3.5±0.10	13.9±0.09	....	20.0±0.13	12.6±0.17	9.4±0.32	4.3±0.08	....
Dh 416 L2 L1 L11–4.	3.8±0.05	13.4±0.21	....	19.6±0.22	11.9±0.19	8.8±0.31	4.5±0.14	8.5±0.29

Brachytic plants are of two general types with respect to the shape of the internodes. The most common type has internodes of the familiar cylindrical form. A longitudinal section through the long axis of the other type of internode is almost triangular, the internode being in the shape of an obliquely truncated cylinder. This form of internode is due to the position of the node, which in these cases instead of being horizontal and at right angles to the main axis is borne obliquely (Pl. IV). This character of the node does not always extend throughout the entire plant, the upper nodes tending to assume the horizontal position. A tendency toward such a difference in the position of the nodes probably exists also in plants of normal stature, but has escaped detection until accentuated by brachysm. The alteration in the position of the node seems to be unaccompanied by other changes, and whether it will be inherited remains to be seen. The buds are borne in the leaf axils on the long side of the internodes and seem to be entirely normal.

The internodes of brachytic plants differ also in the shape of the sides, which in some cases are convex and in others concave. This difference seems irrespective of the length of the internode in brachytic plants, although in normal plants short internodes are frequently convex, indicating a partial compensation in girth for the loss of height.

INHERITANCE OF OTHER BRACHYTIC VARIATIONS.

In one other instance brachytic plants have appeared in the progeny of a hybrid of which one of the parents was Chinese (Pl. V). In all probability the brachytic characteristic in both these cases is derived from the Chinese parent, since this variety produces a rather large number of nodes for the height of the plant. The usual number is about 19, with an average height of 135 cm. as compared with the well-known Boone County White variety, which produces about 20 nodes, with an average height of 240 cm., indicating an internode length of about 12 cm. for Boone and of 7 cm. for the Chinese.

The hybrid in question was between a white dent variety from Kansas and Chinese, grown from original seed. The first generation was of normal stature, and no evidences of brachysm appeared in numerous progenies until the fourth generation. In the fourth generation, however, two brachytic plants were found in a progeny of only 20 individuals. One of these plants was self-pollinated, and its progeny offers a striking contrast to those derived from the Chinese-Algerian hybrid. Only 10 plants were grown from this self-pollinated ear and 9 of them were of normal stature, the other being brachytic. This latter plant has been self-pollinated, but a progeny has not yet been grown. The pedigree of this hybrid is shown in figure 1.

A brachytic plant appeared also in a progeny of the Esperanza variety of *Zea hirta* (Pl. VI). This plant was not self-pollinated, but was crossed with a normal plant of the Chinese waxy variety.

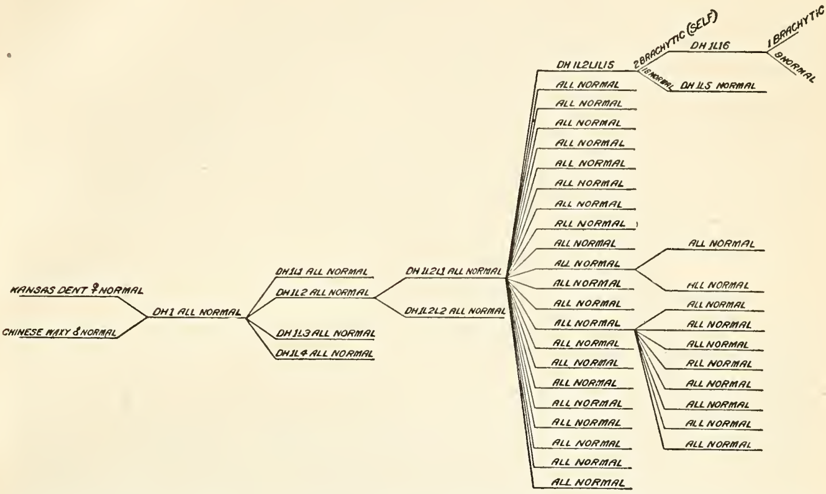


Fig. 1.—Pedigree chart of a brachytic strain which does not breed true. None of the progenies shown in this chart were the result of self-pollination except Dh1L16, the progeny of a brachytic plant.

The hybrid has been designated Mh 17 by Collins (1). The first-generation plants were all much taller than either parent. Three plants were hand-pollinated, but not selfed. The second-generation progeny of these plants gave no evidence of brachysm, as is shown by the frequency distribution for plant height (fig. 2). The modal height of the second-generation plants was 190, which is the average height of normal Esperanza plants. The brachytic Esperanza parent of this hybrid was 105 cm., while the Chinese parent was but 167 cm. high. Succeeding generations have continued normal in stature, although progenies differing widely in height have been isolated. It is hoped that crosses between some of these progenies and true-breeding brachytic strains will explain the complete disappearance of this variation in the Mh 17 hybrid.

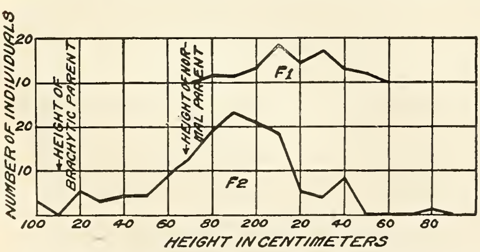


Fig. 2.—Frequency distributions of height of plant of the first and second generation hybrid between the brachytic Esperanza plant shown in Plate VI and a Chinese waxy plant of normal stature.

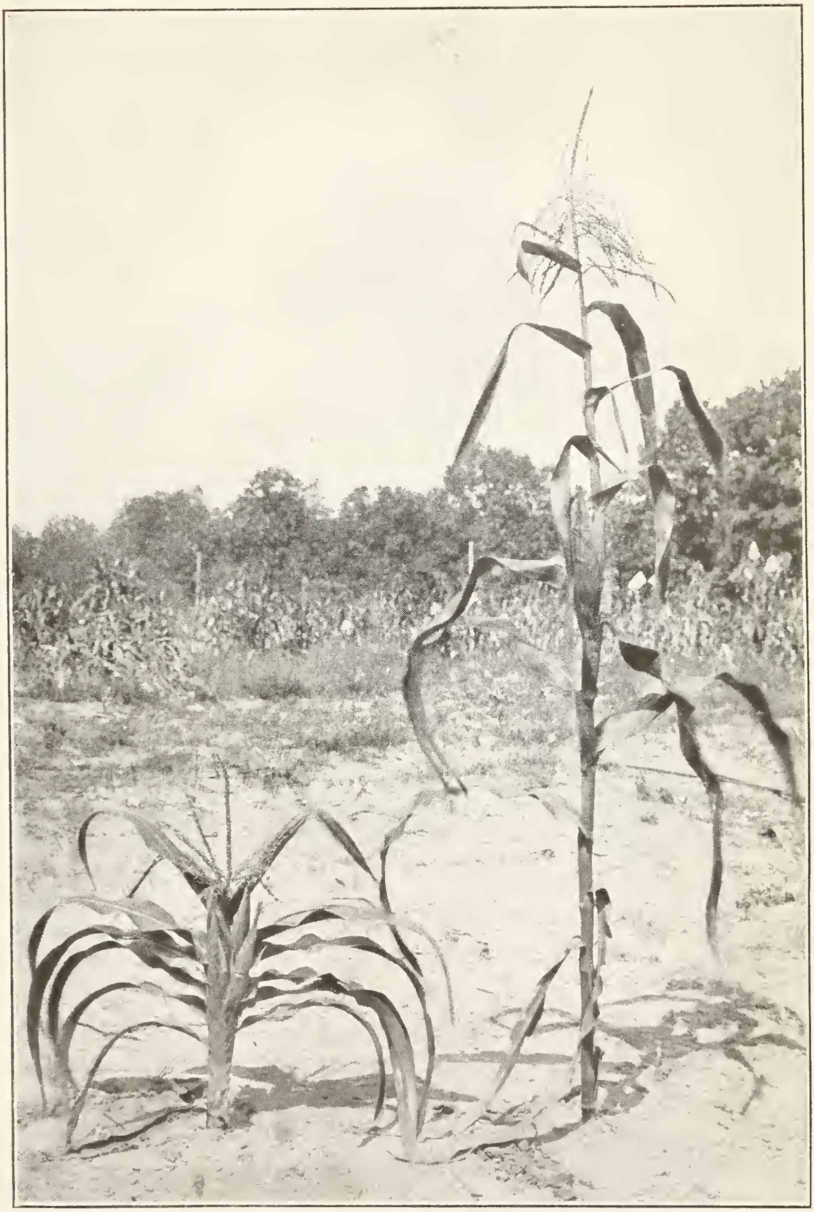
MORPHOLOGICAL SIGNIFICANCE.

The recurrence of brachysm in maize is perhaps to be understood from the normal presence of this characteristic in both staminate and pistillate inflorescences. In cotton it appears as a lack of differentiation between the floral parts and the internodes of the fruiting branches, and not only are the internodes reduced but the floral bracts are modified, becoming leaflike while the leaves become bractlike (4). In maize, however, there is no indication of changes on the main culm other than the shortened internodes, and the leaves are normal.

The most striking example of brachysm in maize is the normal pistillate inflorescence. Here a lateral branch has suffered so extensive a reduction in the length of the internodes that even the lower leaf sheaths of the branch inclose the terminal inflorescence. In this respect the brachysm of the pistillate inflorescence resembles that found in cotton, since the leaf blades have become much reduced or more frequently lost and only the sheath remains. This is an approach to the floral condition where the glumes of the spikelets are homologous with the leaf sheaths, and in this respect the brachysm may be said to represent an intermediate condition between floral and vegetative parts belonging to that class of variations designated by Cook (4) as metaphanic. This brachytic tendency is usually confined to the branches from the upper nodes, while those produced at nodes near but not necessarily below the surface of the ground have internodes of normal length. In some tropical varieties of maize the brachytic specialization of the upper branches has been lost, and the result is a grotesque plant with one or two ears borne at the ends of enormously lengthened ear stalks which frequently exceed the main culm in height (Pl. VII).

When accidents force into growth the branches below the ear, which ordinarily remain dormant, they increase in length, or, in other words, reduce in specialization, progressing toward the base of the plant. The place where these branches change from having pistillate to staminate terminal inflorescences is usually marked by a more complete abortion of the buds, leaving an unbranched section of two or three internodes. Thus the brachysm of the lateral branches is an excellent illustration of a graded specialization, indicating gradual development, but, although there are all stages of branch brachysm on an individual plant, the advanced stages, as found on ear stalks, are little affected by environment.

Euchlaena, the nearest relative of maize, has no such specialization, and, although all of the nodes except the uppermost produce a branch, the apices of these branches are usually about the same height from the ground. This results from the fact that in progressing toward the apex of the plant each succeeding branch has one less node than the



A BRACHYTIC CORN PLANT COMPARED WITH A PLANT OF NORMAL STATURE.

The brachytic plant produced two leaves more than the normal plant.

A BRACHYTIC CORN PLANT COMPARED WITH A PLANT OF THE DWARF VARIATION FOUND BY R. A. EMERSON.

Anthers are always found interspersed among the seeds on the ears of the Emerson dwarf, and because of this fact it has been designated "anther ear."

TWO SISTER BRACHYTIC CORN PLANTS FROM THE SAME PROGENY ROW, SHOWING AN EXTREME EXAMPLE OF ABORTED TASSEL.

The plant with the aborted tassel bore ears which were broken off in dissecting.

TWO TYPES OF BRACHYTIC CULMS.

The buds are borne on the node at the long side of the internode. (Natural size.)

A BRACHYTIC CORN PLANT WHICH APPEARED IN THE FOURTH GENERATION OF A HYBRID BETWEEN THE CHINESE WAXY MAIZE AND A VARIETY OF WHITE DENT CORN FROM KANSAS.

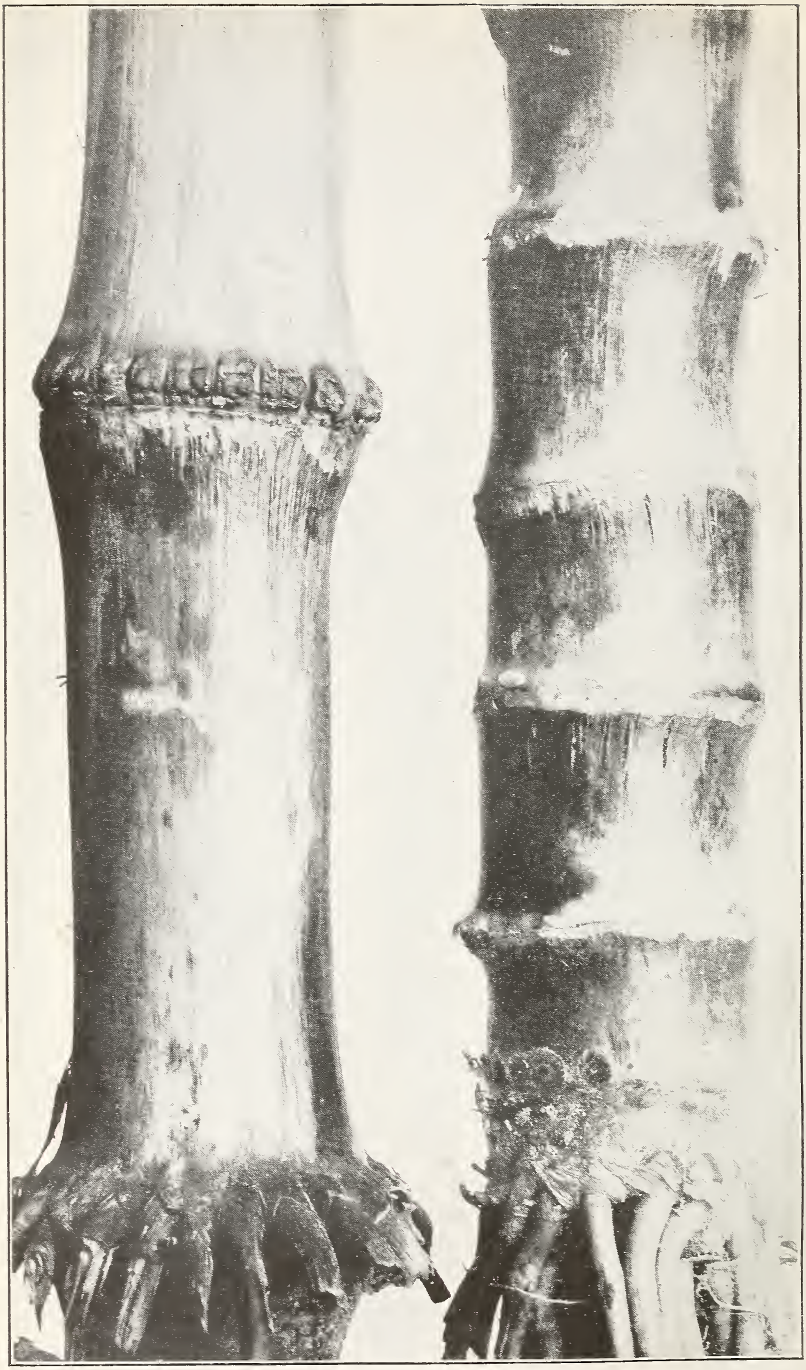
When this plant was self-pollinated it did not breed true, but its progeny included a few brachytic plants.

A BRACHYTIC CORN PLANT FOUND IN A STRAIN OF THE ESPERANZA VARIETY OF ZEA HIRTA.

Progenies of this plant failed to show any evidences of brachysm. This plant is 105 centimeters tall.

A MAIZE PLANT WHICH HAS LOST THE BRACHYTIC SPECIALIZATION OF THE EAR STALK.

This plant was grown at Chula Vista, Calif., from seed obtained in Bolivia.



BASAL SECTIONS OF NORMAL AND BRACHYTIC STALKS OF MAIZE, SHOWING THE NODES JUST ABOVE THE SURFACE OF THE GROUND.

This illustrates the increase in root-producing nodes which could be obtained on the brachytic plants by a cultural method which would cover this section of the stalk with soil. (Natural size.)

branch immediately below until the uppermost branch, borne in the axis of the second leaf from the top, has but two nodes. Thus each branch has one more internode than has the portion of the main culm, which is immediately above it. Contrary to Montgomery (13), this does not hold true for maize, but the relation may have been modified through brachysm. There is some evidence to show that the total number of nodes is increased when the main culm is brachytic, and if this fact held true for lateral branches it would account for the difference between maize and teosinte in this respect. When the ear stalk is lengthened, as in the tropical varieties previously mentioned, it becomes possible to ascertain the number of nodes with accuracy. In these cases it has been found that there are 15 or more nodes, while only 5 or 6 nodes of the main stalk are above the ear-bearing branch.

Although the pistillate inflorescence of maize affords the most striking example, there are indications of brachysm in the formation of the male inflorescence. If it is assumed that the internodes of the main axis are shortened and the terminal spike is formed through a reduction of lateral branches, this would constitute a still further stage of brachysm.

Brachysm of the main culm might be considered an example of homoeosis (12), but on this hypothesis it is difficult to understand the absence of any tendency for the brachysm of the upper branches to become transferred to lower ones, a step much more direct than that involved in transferring this characteristic to the main culm. There is, however, some support for this view in that several of the brachytic plants developed pistillate flowers in the otherwise unaltered staminate inflorescence, and although none of these pistillate flowers developed seed this fact suggests that an association exists, however slight, between bracytic internodes and the development of female flowers.

ASSOCIATED CHANGES.

Mutations in most organisms are not confined to single characters, but alter the expression of many and frequently unrelated parts. Usually a particular character is changed greatly, serving to divert attention from minor changes in other characters. Careful examination of many characters of an individual which has mutated obviously in a single one often reveals the presence of the other changes.

With the intention of determining whether other characters than internode length had undergone alteration in the original brachytic plants, careful measurements were made of other organs. Only two other changes were observed. The ears were flattened somewhat, doubtless due to the mechanical pressure of the large number of leaf sheaths. Such an alteration can not be considered as mutative, since it is an indirect manifestation of the brachytic condition. The other character affected is the length of the ear stalk, which shows a reduction in internode length similar to that of the main culm. While this may be considered simply as the general extension of the brachytic tendency to all the lateral branches, as indicated also by the condition of the suckers, it must be remembered that the brachytic nature of the ear stalk on plants of normal stature is not ordinarily reflected in the main culm.

This further shortening of the ear stalk on brachytic plants indicates that the brachytic stalks of normal ears are the result of a genetic change separate from that which caused brachytic internodes on the main culm.

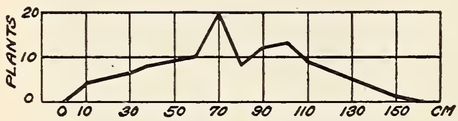


FIG. 3.—Frequency distribution for the length of the third branch in an F_2 of Tom Thumb pop corn × Florida teosinte.

Support for this latter contention is derived from a hybrid between Florida teosinte and Tom Thumb pop corn (3). If the ear stalk is an example of brachysm similar to that of the main stalk, the second generation of the hybrid between teosinte and maize should give the same evidence of segregation of this character as is found with the internodes of the main culm when plants with brachytic culms are crossed with those of normal stature.

With the second-generation plants, the third branch from the top on the main culm is assumed to be homologous with the ear stalk of normal maize, since it is borne at approximately the same node as the ear of maize. The frequency distribution for the length of this branch on second-generation plants of the Tom Thumb × Florida hybrid is shown in figure 3.

It is apparent that there is no bimodality in the distribution of branch lengths, and it must be concluded that the brachysm of the ear stalk of normal maize does not behave as a simple Mendelian character in crosses with teosinte.

Slight evidence for the discontinuous nature of the brachysm of ear stalks is to be found in the second generation of a cross between Boone County White and the brachytic strain. The frequency distributions for the length of the ear stalk on brachytic plants directly descended from the original variation and on the first and second generation plants of the brachytic-Boone cross are shown in figure 4. While the brachytic plants had shorter ear stalks than normal plants, the frequency distribution for this character on the normal segregates of the second generation of the hybrid suggests a bimodality that is most easily explained by assuming an independent inheritance of the ear-stalk character. Too much confidence must not be placed in results of this sort, as it is obvious that at least one other factor besides length of internode is involved in the length of the ear stalk. This factor is the number of nodes. The actual number of nodes can not be determined with accuracy, and an estimate is likely to give very misleading results.

Further evidence for the independent inheritance of the brachysm of ear stalks and that of the culm is to be found in an analysis of the correlations of these characters.

In the normal plants of the second generation of the brachytic-Boone hybrid there was a correlation of 0.295±0.06 between the length of the longest internode on the main culm and the length of the ear stalk. This correlation is reversed in the brachytic plants of the same hybrid, but the coefficient of 0.09±0.09 is not a significant deviation from no correlation. These low correlations indicate an

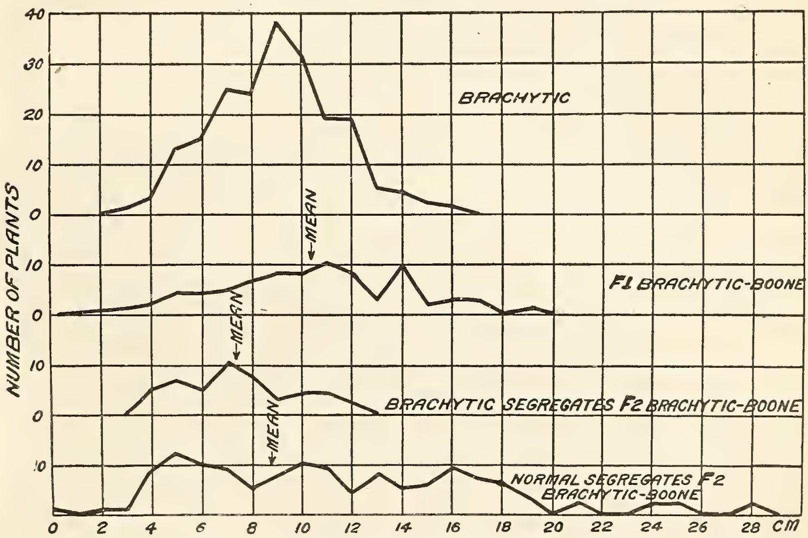


FIG. 4.—Frequency distribution of length of ear stalk on brachytic, brachytic × Boone F_1, and brachytic and normal plants segregated in the F_2 of brachytic × Boone.

almost complete independence of the factors which affect the internode length of the culm and those which affect the ear stalk.

AGRICULTURAL ADVANTAGES.

Brachysm in maize produces a form of plant which seems admirably adapted to meet the unusual requirements of dry land and irrigated regions. The chief obstacles to the utilization of such variations lies in the numerous defects which commonly accompany them (Cook, 4), but the present brachytic strain is relatively free from undesirable corollaries.

The striking characteristics of this brachytic type of plant are its reduced height and sturdy erectness. There are many situations in which these features might prove to be of paramount value. It is hard to conceive of brachytic plants breaking down or lodging either when exposed to severe winds or when grown in soil that becomes very soft when wet.

While it may not be worth while to consider the substitution of brachytic varieties for the ordinary varieties in situations where the latter do well, there are many situations in which the normal height of the maize plant and its tendency to lodge in soft ground or wilt down in drying winds place it at a decided disadvantage. For such situations it would seem to be worth while to select progenies in which this brachytic character is combined with other characters adapted to the region.

In addition to these two very obvious advantages there is another which might be fully as important in certain dry-land situations. This latter advantage lies in the fact that because of the shortened internodes more nodes are in contact with the soil and develop roots.

With the exception of the Navajo or Hopi type of maize the roots which appear at germination serve only to establish the young seedling. Subsequent growth and development depend upon the roots produced from nodes. In most varieties of maize grown under common cultural methods, from four to eight nodes remain in contact with the ground and produce roots. The uppermost node which produces roots is usually somewhat above the surface of the soil. At this node in the Boone County White variety the number of primary roots is about 20. The young roots are covered with a sticky, transparent gelatinous substance which affords protection from the dry atmosphere and permits them to reach the soil from a height of about 10 cm. Maize plants are capable of producing roots at practically every node below the ear and possibly even above the ear, provided these nodes are brought in contact with the ground or otherwise kept abnormally moist. Some tropical varieties have been observed with roots at 15 nodes above the surface of the ground, and these roots have attained a length of 8 or 10 cm. before finally drying. The highly specialized commercial varieties have not lost their ability to produce roots from the upper nodes, and within 24 hours after lodging such plants will be found to have started roots from all nodes which are in contact with the ground.

In brachytic plants the reduction in the length of the internodes results in more nodes coming in contact with the ground, thereby increasing the production of roots. If it were found to be desirable, the root-producing nodes could be increased as much as 40 per cent over the common dent varieties by a proper system of culture, and even greater increases are possible by listing, a practice much in vogue in certain sections of the West. The possibilities in this respect are graphically shown in Plate VIII. In addition to the increase in the number of roots due directly to the shortened internodes, there is a further increase of about 15 per cent, due to the fact that the reduced height is accompanied by an increase in the diameter of the culm, thus increasing the periphery of the nodes from which the roots arise.

This increased root system obtained under ordinary conditions of flat surface tillage is of no mean advantage. In irrigated regions where the flooding system is practiced or even under most furrow systems the taller varieties of maize lodge badly following an irrigation, especially if there is a moderate wind. The brachytic plants are thoroughly anchored and by reason of their greatly reduced height would be able to withstand such conditions and remain erect.

In addition to the increased root system, brachytic plants offer another character that may be of advantage for dry-land culture. The reduction in internode length brings the leaves close together, thus effecting a partial shade at the time when the sun is at its height. In this manner transpiration may be reduced at the critical period, and if this reduction is appreciable it should result in a lower water requirement for brachytic plants. The feature of partial shade may be desirable also for irrigated regions where, during the bright days of summer, the plants frequently are unable to obtain water from the soil with sufficient rapidity to supply the heavy demands of midday transpiration, even though the soil is thoroughly wet.

It remains to be determined just how far farm practice can be made to comply with the requirements of harvesting such a crop. Where the practice of hogging off is followed, the brachytic plants are ideal, since the ears are brought within easy reach of the animals and little waste should occur.

As a general rule, the commercial varieties of corn are taller than is necessary to satisfy the physiological requirements for yield of grain. This increased height is due almost entirely to the elongation of the internodes and not to an increase in the number of nodes. An increase in the height of the culm would seem to be a disadvantage unless it is the result of an increase in the number of nodes, as otherwise no additional leaf area results. The brachytic variation affords a means of reducing the stature, with no corresponding reduction in leaf area.

There is, of course, a physiological limit to the production of grain upon small plants, beyond which it is impossible to proceed. This limit is obviously dependent upon the leaf area available for purposes of photosynthesis. The reduction in internode length does not reduce the number of nodes, nor is it accompanied by a reduction in the size of the leaves, and the total leaf area therefore remains the same. The leaves, however, are brought closer together, and possibly the area available for photosynthesis has been reduced somewhat. The degree of this reduction is yet to be determined, but with the exception of this reduction which, under certain conditions, may be beneficial, there should be no other physiological difficulties in combining high productivity with brachytic stature.

Genetically, however, more difficulties are to be expected. Yield of grain, like most quantitative characters, is one of those relatively unstable characters difficult to recover from hybrids involving small-eared varieties. If only 10 factors are involved in maximum grain production, all 10 of these would be expected to occur in homozygous combination with brachytic culms in an F_2 hybrid only once in 4,195,304 plants. To be reasonably certain of securing the combination in an F_2 hybrid, at least 12,585,912 plants should be grown. It is, however, an unfortunate fact that probably many more than 10 factors are involved. The form of the inflorescence alone can be resolved into several component parts, such as length, diameter, number of seeds, size of seeds, number of rows, volume, and weight of seeds, all of which are known to be inherited separately, and even these subdivisions are far from being simple characters.

With the several advantages, the commercial value of the brachytic variation depends upon the success with which the shortened internodes may be combined with the grain production of the standard dent varieties. It is not unlikely that if such a combination were effected the value of the strain would be appreciated in areas outside the regions of extreme climatic conditions. The brachytic character is one which reappears in the perjugate generation of hybrids, and the possibility of combining the dwarf stature with the high productivity of commercial varieties will be considered.

INHERITANCE OF BRACHYSM IN HYBRIDS WITH COMMERCIAL VARIETIES.

BRACHYTIC × BOONE.

In an effort to combine the brachytic character of the culm with the high productivity of commercial varieties, several crosses have been made. Two crosses were made with the Boone County White variety, and a few first-generation plants of each cross were grown in the greenhouse and self-pollinated. Three ears resulted, and a progeny of each of these, as well as a large population of the first generation, was grown in the field at Lanham, Md. The first-generation plants grown in the field were fully as large as the Boone parent and remarkably uniform. A number of characters were measured, as shown in Table III.

The three second-generation progenies segregated into normal and brachytic plants, with well-defined classes closely approximating the 3 to 1 monohybrid ratio. The actual number was 234 normal and 74 brachytic, the percentage of the recessive class being 24.0 ± 1.7. The measurements of these second-generation plants also are given in Table III.

TABLE III.—*Measurements of maize plants of the first and second generations of the brachytic × Boone hybrid.*

[The ears had dark and pale colored seeds, and the number 11 following the progeny designation indicates that the color of the seed planted was dilute. Figures in the last two columns in black-face type indicate the characters in which the brachytic plants exceeded the plants of normal stature.]

Character.	First generation.				Second generation.			
	Dh 435.	Dh 435–11.	Dh 436.	Dh 436–11.	Normal.	Brachytic.	Difference.	Difference ÷ probable error.
Height of plant, decimeters	27.2±0.25	26.8±0.36	26.0±0.22	26.1±0.37	29.7±0.19	10.4±0.12	19.3±0.17	114.0
Height of upper ear from the ground . decimeters	13.0±0.25	12.4±0.28	12.3±0.19	11.7±0.26	12.0±0.12	3.9±0.06	8.1±0.13	62.2
Length of branching space . . . . . centimeters	19.5±0.27	19.0±0.37	18.2±0.34	17.1±0.54	15.1±0.16	12.2±0.22	2.9±0.27	10.7
Length of central spike, centimeters	32.0±0.67	30.0±0.50	30.7±0.61	32.7±0.71	30.0±0.28	30.7±0.56	**0.7±0.63**	**1.1**
Length of longest tassel branch . . . centimeters	29.1±0.50	27.0±0.46	27.7±0.51	28.2±0.40	24.3±0.43	24.4±0.29	**0.1±0.48**	**.2**
Number of tassel branches	37.8±1.24	34.0±1.21	29.3±1.33	24.2±1.34	31.7±0.46	36.4±0.72	**4.7±0.77**	**6.7**
Longest leaf:								
Length . centimeters	103.5±0.57	91.5±1.24	86.5±0.87	85.8±1.28	95.2±0.42	90.2±0.62	5.0±0.75	6.7
Width . . . . do	9.9±0.15	9.1±0.15	8.7±0.12	8.9±0.12	8.9±0.06	8.9±0.07	**0.0±0.09**	**0**
Length of longest internode . . . . . . centimeters	16.8±0.34	18.2±0.13	17.8±0.29	17.5±0.16	16.8±0.12	5.4±0.12	11.4±0.17	67.0
Number of internodes above longest	9.9±0.29	7.7±0.18	7.4±0.21	7.3±0.15	7.5±0.09	7.1±0.18	0.4±0.20	2.0
Diameter of stalk, $\frac{1}{16}$ inch	16.9±0.29	13.8±0.39	13.1±0.18	13.1±0.31	14.2±0.12	16.0±0.23	**1.8±0.26**	**6.95**
Number of ears	. . . .	. . . .	. . . .	. . . .	1.25±0.02	1.5±0.05	**0.25±0.05**	**4.6**
Ear length:								
Upper ear, centimeters	23.2±0.53	21.4±0.55	18.8±0.41	20.2±0.38	16.2±0.20	14.0±0.21	0.22±0.29	.76
Total . . . centimeters	26.8±1.25	22.2±0.54	22.2±0.90	24.3±0.94	20.7±0.40	20.6±0.57	0.1±0.7	.1
Number of rows on upper ear	18.2±0.11	16.6±0.24	17.7±0.11	16.2±0.11	18.2±0.12	17.0±0.13	1.2±0.17	7.13
Length of staminate spike on upper ear, centimeters	. . . .			. . . .	5.5±0.30	4.8±0.46	0.7±0.55	1.3
Number of leaves:								
Above the upper ear	5.7±0.09	5.2±0.08	5.0±0.06	5.0±0.08	4.9±0.03	4.8±0.04	0.1±0.05	2.0
Total	22.3±0.20	20.3±0.25	21.0±0.21	21.9±0.75	21.7±0.09	22.3±0.12	**0.6±0.15**	**4.0**
Number of nodes:								
With roots	7.5±0.14	. . . .	. . . .	. . . .	7.3±0.07	8.5±0.05	**1.2±0.08**	**15.5**
Without roots	14.7±0.25	14.4±0.22	14.1±0.14	13.6±0.17	. . . .	. . . .	. . . .	. . . . . .
Length of longest leaf sheath . . . . centimeters	23.6±0.29	22.6±0.25	20.9±0.20	20.0±0.43	22.7±0.13	22.4±0.19	0.3±0.2	1.5
Number of leaf sheaths above longest	13.0±0.27	12.4±0.42	12.0±0.27	11.4±0.24	11.3±0.09	11.6±0.14	**0.3±0.16**	**1.8**
Length of upper ear stalk . . . . . centimeters	12.7±0.46	10.2±0.56	9.6±0.40	9.5±0.70	8.7±0.23	7.4±0.23	1.3±0.31	4.2

While no difficulty was encountered in classifying the plants as to stature, a closer examination showed that several plants, classed as normal, in reality had one or more shortened internodes. The actual number was 14 plants with one or two shortened internodes in a population of 130 otherwise normal plants. These brachytic internodes were located either near the base or near the top of the plant. (Pls. IX and X.) Such plants may be heterozygous for the brachytic character with a partial failure of dominance or they may be considered as instances where the segregation has been incomplete.

In either event the well-defined difference between these brachytic internodes and the adjoining normal nodes emphasizes the individuality of the node and internode as a metamer. If these cases are looked upon as partial failures of dominance, it is significant that instead of a general shortening of internode length throughout the entire plant single internodes only are affected and become abruptly and decidedly shorter than their mates. This fact indicates that no general lengthening of the internodes is to be expected as the result of contamination by repeated "back crosses" on plants of normal stature.

These cases would seem to offer some support for the hypothesis of somatic segregation or perhaps bud variation. If such an explanation is adopted, a question arises whether an ear borne on a node subtended by a brachytic internode would behave in heredity as a true brachytic. No such cases have arisen as yet, and there would be some difficulty in distinguishing them unless the brachysm was pronounced, as in the case shown in Plates IX and X.

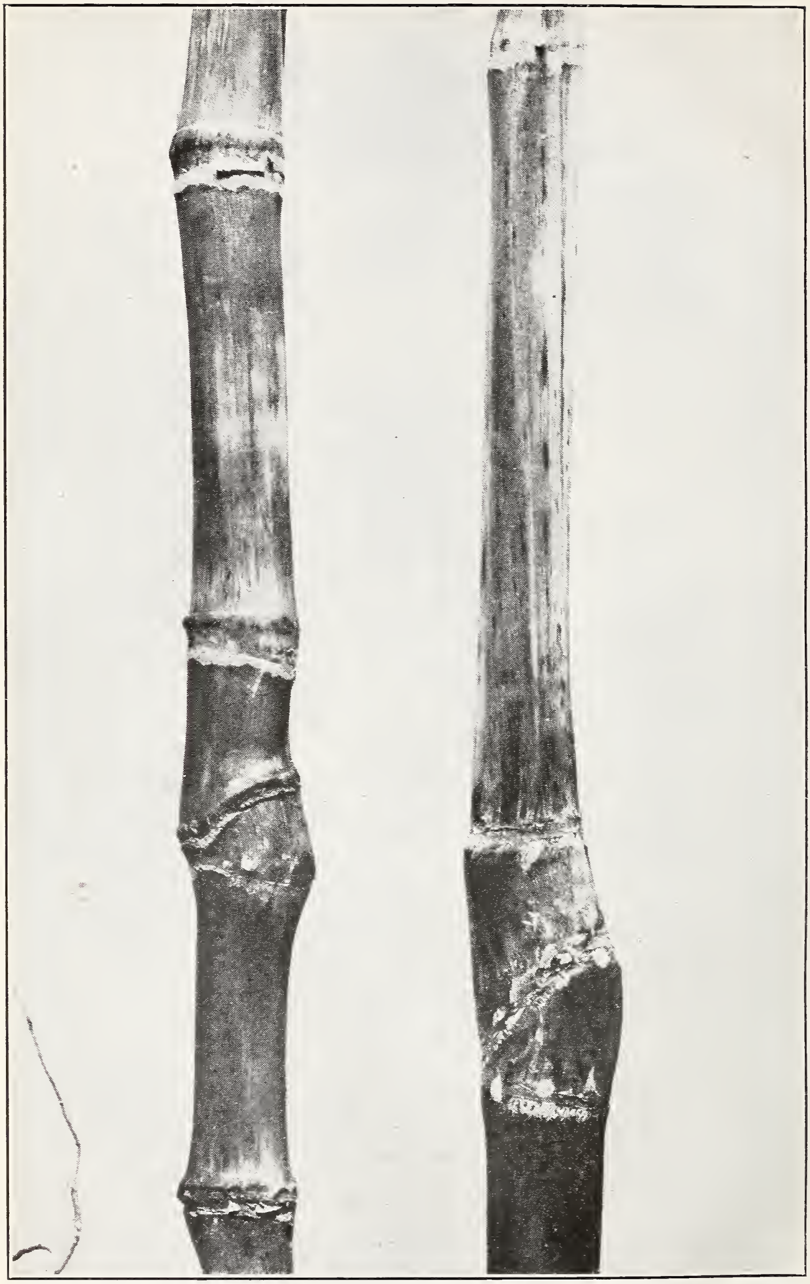
The internode borne on the same node with the ear is almost invariably shorter than the internodes immediately above and below, so that to be detected brachysm of the internode at this point must of necessity be pronounced.

Although an ear borne on a brachytic internode might be germinally brachytic, it of necessity must be fertilized by male gametes from an inflorescence produced from a normal node. The resulting seeds, therefore, would give rise either to plants of normal stature only, or, if the parental plant had been heterozygous for brachysm, one-half of the progeny could be brachytic. The point is of interest in connection with the sudden appearance of brachysm in the two Chinese hybrids.

The brachytic segregates in the F_2 of Boone-brachytic hybrids had a mean height in decimeters of 10.42 ± 0.112, with a coefficient of variability of 14.3 ± 0.79 and a range of 7 to 15 decimeters. The coefficient of variability of the brachytic segregates compared with that of the 14 brachytic progenies shows that there was no significant increase in variation in the segregates, the increase being only 1.2 ± 0.87. A somewhat larger increase is obtained if the coefficient of variability of the brachytic segregates is compared with that of the brachytic progeny grown in 1918; the difference then becomes 4.2 ± 1.13, or 3.7 times the probable error, but since these progenies were not grown the same year the propriety of comparing their variability is questionable. While the average height of the brachytic segregates was greater than that of brachytic plants directly descended from the original variety, the difference of 1.61 ± 0.87 is

TWO BRACHYTIC INTERNODES ON A CORN PLANT THE OTHER INTERNODES OF WHICH WERE OF NORMAL LENGTH.

This plant was found in the second generation of the brachytic-Boone hybrid. (Natural size.)

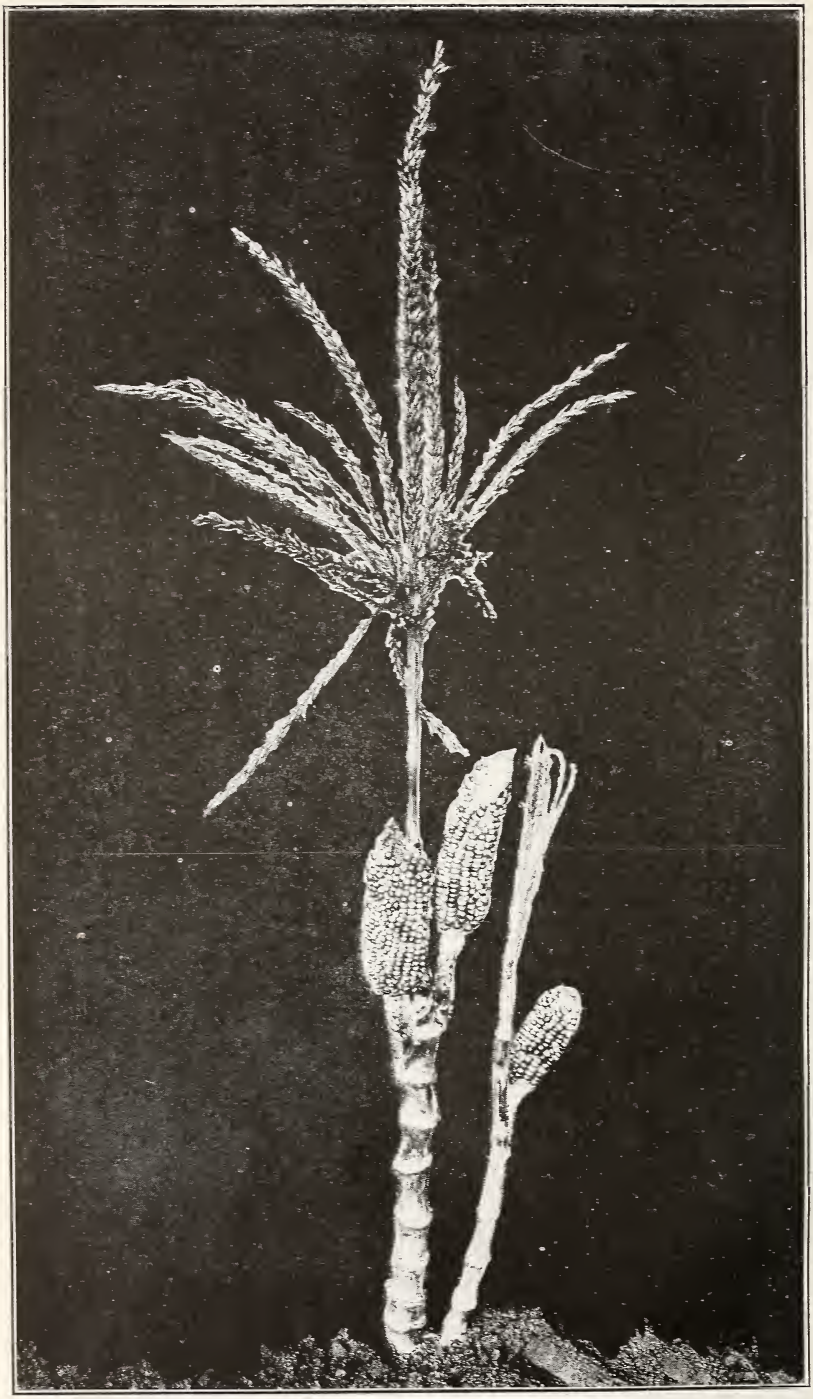


TWO CULMS OF MAIZE, EACH SHOWING TWO BRACHYTIC INTERNODES, THE OTHER INTERNODES BEING OF NORMAL LENGTH.

These plants were segregated in the second generation of the brachytic-Boone hybrids. The portion shown at the left is from the base of the plant. (About one-half natural size.)

A BRACHYTIC CORN PLANT FROM THE SECOND GENERATION OF THE BRACHYTIC-BOONE HYBRID.

This plant produced the longest leaves of any brachytic plant. In length of leaf it exceeded the average of the normal plants and is among the 30 plants which produced the longest leaves in any of the progenies.



THE SAME CORN PLANT SHOWN IN PLATE XI WITH THE LEAVES AND HUSKS REMOVED TO SHOW THE CHARACTER OF THE INTERNODES.

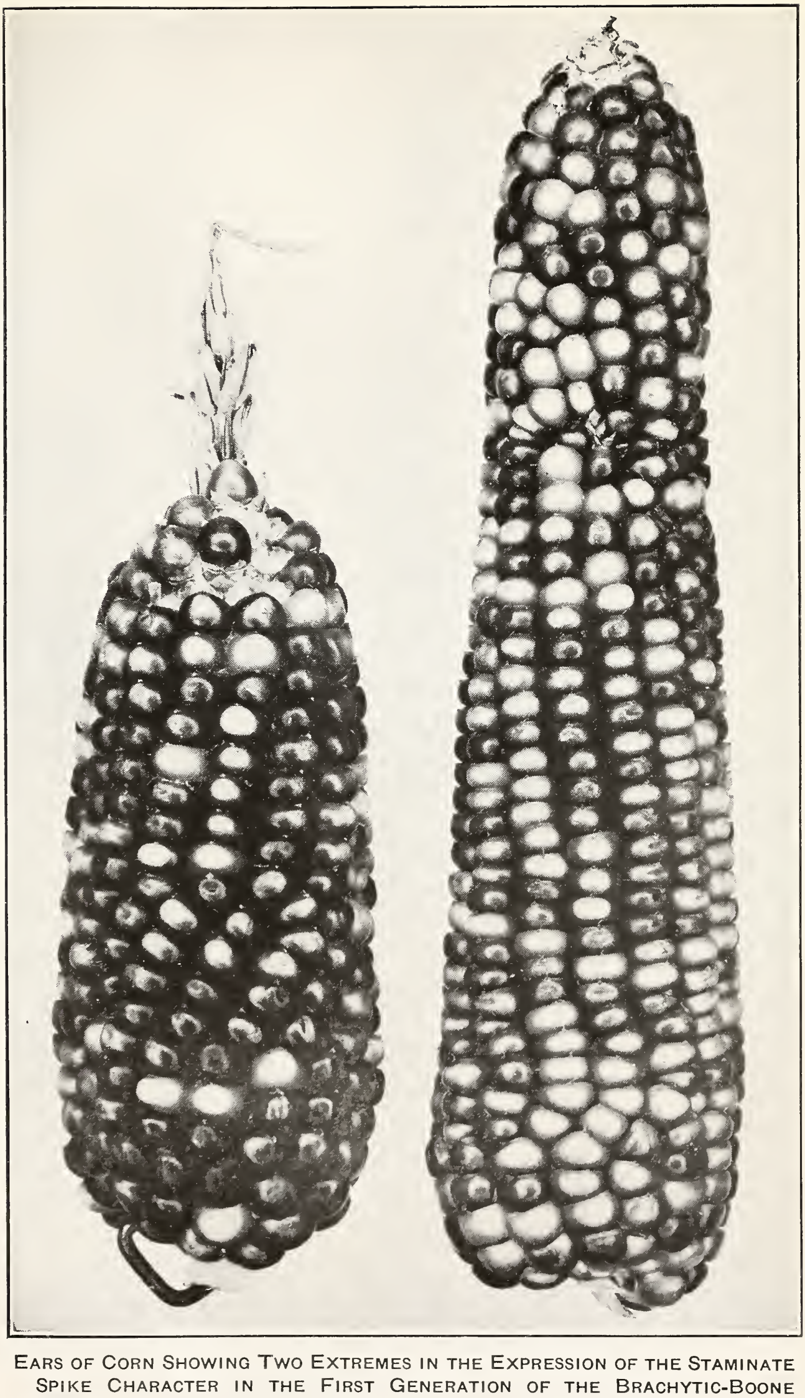
Note the brachytic tiller.

AN "ADHERENT" VARIATION OF MAIZE WHICH APPEARED IN THE SECOND GENERATION OF THE BRACHYTIC-BOONE HYBRID.

The upper leaves of such plants adhere as if glued, and the branches of the tassel are compacted into a hardened mass. This variation has been found on plants of normal stature only.

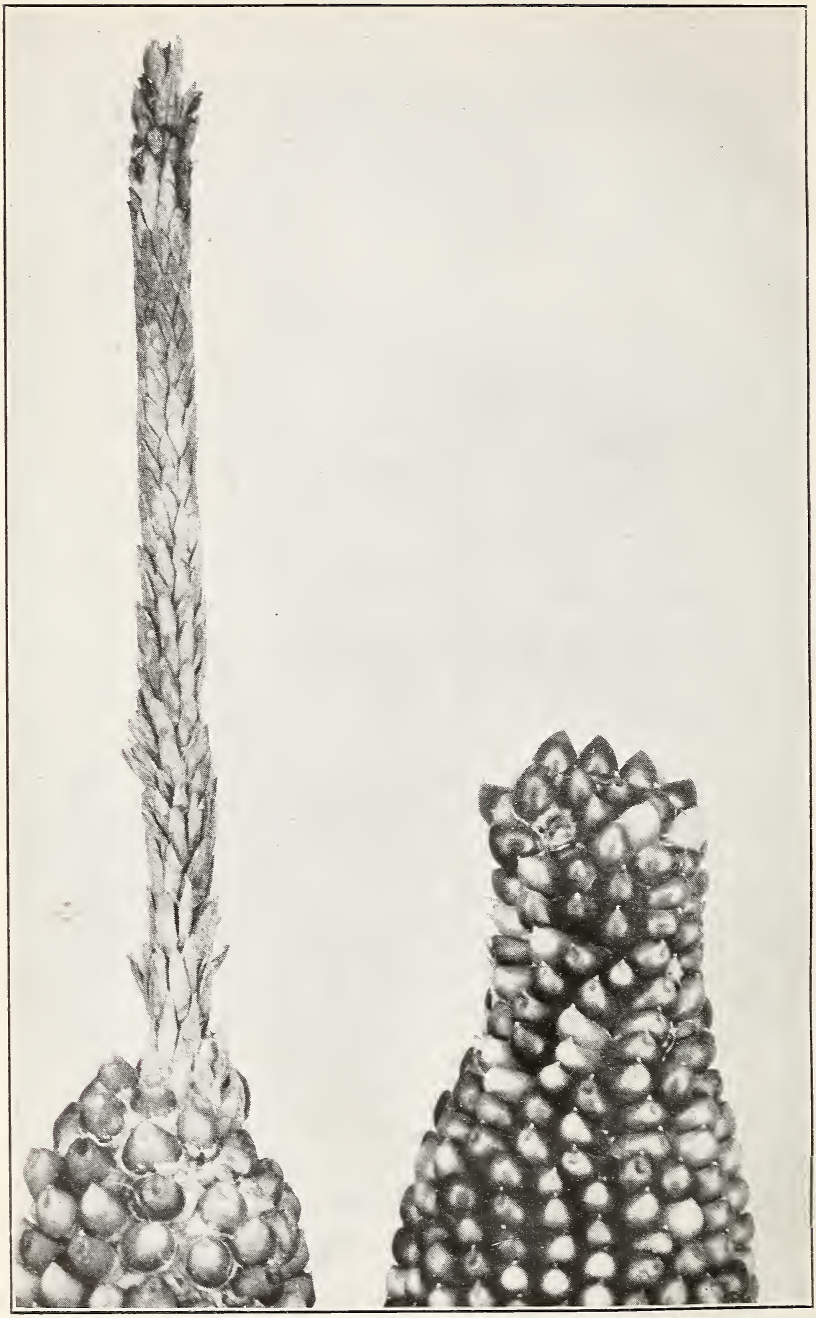
UPPER SECTION OF AN ADHERENT CORN PLANT.

The tassel, the silks of the upper ear, and the contortions of the culm are shown. (Nearly natural size.)



EARS OF CORN SHOWING TWO EXTREMES IN THE EXPRESSION OF THE STAMINATE SPIKE CHARACTER IN THE FIRST GENERATION OF THE BRACHYTIC-BOONE HYBRID.

Note the few staminate spikelets about 6 centimeters from the tip on the ear at the right. (Slightly reduced.)



TIPS OF EARS OF CORN SHOWING THE EXTREMES IN THE EXPRESSION OF THE STAMINATE SPIKE CHARACTER.

These ears are from the second generation of the brachytic-Boone hybrid. (Nearly natural size.)

not significant. The frequency distribution for height of plant is shown in figure 5.

In yield, as measured by the total ear length, neither the normal nor the brachytic F_2 plants equaled the first generation, but individual plants were obtained which yielded fully as well as the best

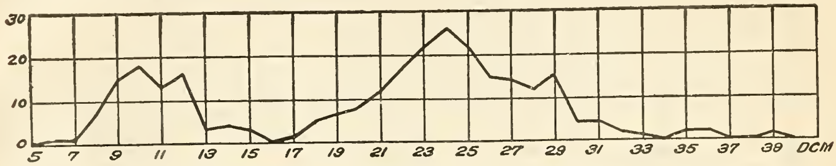


FIG. 5.—Frequency distribution of height of plant in brachytic × Boone, second generation.

of the F_1. With a sharp segregation into normal and brachytic plants and a failure to increase the variability of height in the segregated brachytic plants, the procedure to be followed in securing the desired combination of brachytic stature with high yield becomes greatly simplified and eventual success becomes more certain. It is necessary only to back cross the best yielding of the segregated brachytic plants upon the high-yielding commercial varieties and repeat the procedure until the desired combination is obtained.

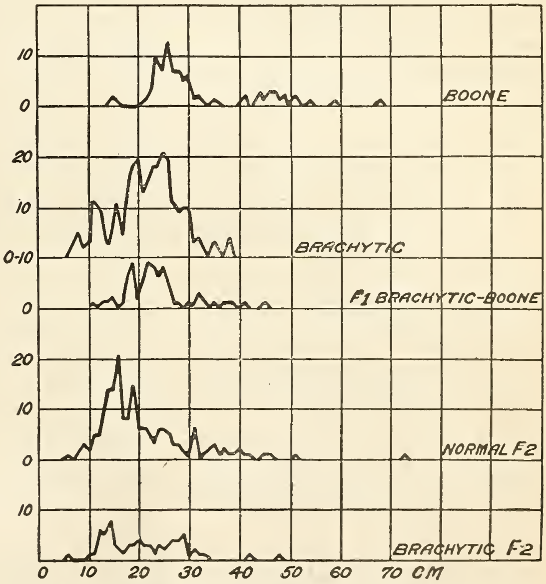


FIG. 6.—Frequency distribution for total length of ears on Boone, brachytic, Boone × brachytic F_1, and the normal and brachytic plants segregated in the brachytic × Boone F_2.

While the mean length of ear of the brachytic segregates in the second generation of the brachytic-Boone hybrids is little, if any, greater than that of the 14 brachytic progenies, several plants were obtained which greatly exceeded in length of ear the directly descended brachytic plants (Pls. XI and XII). The frequency distributions for ear length are shown in figure 6.

The normal plants of the second generation exceed the brachytic plants not only in stature but also in the length of the longest leaf, in the number of rows on the upper ear, and in the length of the ear stalk. The brachytic plants, on the other hand, exceed the plants of normal stature in the number of branches in the tassel, the diameter of the culm, the total number of leaves, and the number of nodes that produce roots. The frequency distributions for the total number of nodes for the Boone, brachytic, and first and second generation hybrids are shown in figure 7.

The reduced length of the branching axis of the tassel of the brachytic plants clearly indicates that brachysm includes the terminal inflorescence. Although the length of the rachis from which branches arise is reduced, the total number of branches is increased. This increase is comparable to the increase in the number of nodes on the culm, which is coincident with reduced stature.

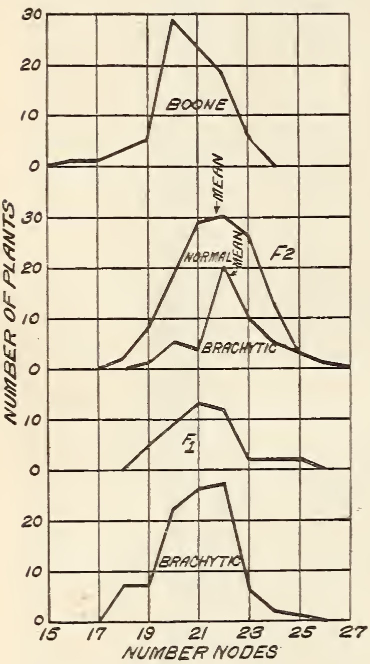


Fig. 7.—Frequency distribution for total number of nodes in Boone, brachytic, Boone × brachytic F_1, and the normal and brachytic segregates in the F_2 of brachytic × Boone.

The abortion of the terminal inflorescence discussed on page 4 did not appear in the progeny of the brachytic-Boone hybrid. As the evidence available thus far for this character indicates a Mendelian behavior, it would seem that the brachytic-Boone combination will be free from this defect.

It is an interesting fact that, although the longest internodes on brachytic plants are less than one-third the length of the longest internodes on normal plants, the length of the longest leaf sheath is not reduced on the brachytic plants, nor is the position of the sheath altered.

There is a correlation of 0.434±0.047 between the length of the leaf sheath and the length of the internode on normal plants, indicating a definite tendency for the sheaths to cover the internodes. Curiously enough, however, the longest leaf sheath does not inclose the longest internode, but on the contrary is produced, on the average, four internodes below the longest internode. That the correlation is no closer than 0.434 is not surprising, since the length of internodes on plants of normal stature is so largely determined by environmental conditions and may be altered at a comparatively late date, while the dimensions of the sheath are relatively constant.

While there is a definite relation between the length of internodes and sheaths on normal plants, this relationship is not found on brachytic plants. On these plants the coefficient of correlation between these characteristics is but 0.036 ± 0.097, indicating complete independence in the size of these two organs.

Since the length of the longest sheath has the same range and variability in both brachytic and normal plants, the absence of a correlation with length of internode on the brachytic plants indicates that the variability in internode length on these plants is due to environmental rather than inherited differences.

TERATOLOGICAL VARIATIONS.

Although brachysm is commonly accompanied by other abnormal manifestations, only two teratological forms have been observed in the progenies of brachytic-normal maize hybrids. One of these abnormalities is ears which end in staminate spikes. This abnormality has been observed frequently in strains not involving brachysm and therefore may be considered as having appeared incidentally in these hybrid progenies, with no direct relation to the brachysm of the culm.

The other variation is entirely new in our experience, and while there is no evidence to indicate that it is caused by brachysm it seems desirable to record briefly the more general features of its inheritance. In this variation the leaves adhere to one another as if glued (Pl. XIII). With many plants the upper leaves are affected most severely, but the seedling leaves also are subject to the abnormality.

Seedlings in which this peculiarity is pronounced fail to develop, and even those plants which exhibit the character in a minor degree produce but little seed. When the variation makes its appearance relatively late in the life of the plant the upper leaves adhere so firmly that the culm is forced into many contortions in attempting to elongate. In some instances the ear-bearing node is involved, in which case the ear also is contorted. The branches of the tassel are compacted into a solid structure which in expanding bursts through the confining blades and sheaths (Pl. XIV). The spikelets are adversely affected and become shortened and twisted. In view of the nature of this variation it has been designated "adherence."

The variation appeared in two second-generation progenies of the brachytic-Boone hybrid, but in none of the other progenies involving brachytic. In these two progenies the percentage of total plants that were adherent was 19.1 ± 1.85. The adherent variation was, however, confined to plants of normal stature, and the percentage of adherent among the nonbrachytic plants was 23.9 ± 2.1. The nature of the abnormality was such that the stature of the adherent plants was reduced, but there can be no question that the variation appeared only on plants genetically of normal stature. This is well demonstrated in figure 8, which shows frequency distributions of the three types of plants for the length of the longest internode. The longest internode, disregarding the very uppermost, which is sometimes difficult to differentiate from the rachis of the tassel, is found almost always well below the ear, and hence below the area affected in the adherent plants.

If the adherent variation is considered as being due to a single factor, completely coupled or linked with normal stature, then the adherent plants should be 25 per cent of the total, while the observed percentage is 19±1.85. While this deviation seems large, the nature of the variation is such that many of the plants must be eliminated in the seedling stage and doubtless escape notice. The percentage of adherent plants necessitates the assumption that this variation is recessive to the normal condition, and if the above hypothesis of perfect linkage with normal stature is correct, self-pollinated adherent plants should produce nothing but adherent plants of normal stature. The F_1 of a brachytic adherent cross should be normal with respect to both characters, and in the second generation there should be three classes of plants in the proportion of one normal in stature and adherent, two normal in stature and nonadherent, and one brachytic and nonadherent. The Boone plant which was crossed with brachytic must have been heterozygous for adherence, or otherwise it would have exhibited this character. Therefore, the progenies of one-half of the F_1 plants should have 25 per cent of the plants adherent. As yet only three progenies have been grown and two have exhibited the variation, but 30 additional hand-pollinated ears remain to be tested.

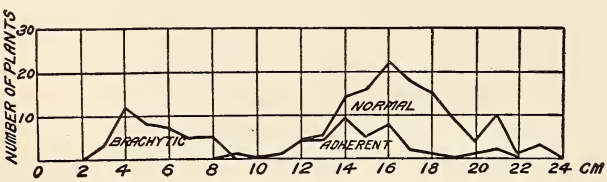


FIG. 8.—Frequency distribution of the length of the longest internode on brachytic, adherent, and normal plants from the second generation of brachytic × Boone.

EARS ENDING IN STAMINATE SPIKES.

The staminate spike variation was found not only in the Boone-brachytic hybrid but also in some of the other brachytic-normal hybrids. The ears in this variation terminate in single spikes bearing several rows of paired staminate spikelets. The number of rows of these staminate spikelets, in the cases where they can be determined with reasonable accuracy, is usually less than the number of rows of seeds upon the ear.

The character is extremely variable in expression, especially in the second generation of the Boone-brachytic hybrid. In this hybrid, ears were found with staminate spikes ranging from 15 cm. in length to those with just a few scattered spikelets near the tip or with only a disorganized area where spikelets failed to develop, leaving a bent and deformed ear. The range of variation in the Boone-brachytic hybrids is shown in Plates XV and XVI.

The variation is one which is found frequently in maize in several forms. The nature of its inheritance has not been reported, but that it is heritable seems certain.

While neither the Boone nor the brachytic parent plants produced ears with staminate spikes, many plants of the first generation produced such ears. The exact ratio in the F_1 was 17 with staminate tips to 63 normal. This is a very close approximation to a Mendelian monohybrid ratio, where the variation is recessive to the normal form of the ear. To secure such a ratio in an F_1, it may be assumed that both parents were heterozygous for the character involved. The same result would be obtained if normal ear form were the result of two dominant independent factors with the brachytic parent heterozygous for both of these factors and the Boone parent homozygous for one dominant factor and heterozygous for the other. On this latter hypothesis the progeny of the self-pollinated brachytic parent would have 43.75 per cent of the plants bearing ears terminating in staminate spikes, while the self-pollinated Boone parent would give 25 per cent of the progeny with such ears.

Of the nine hand-pollinated ears obtained from brachytic plants, six were the result of self-pollination, the other three representing crosses between sister plants. Only one progeny grown from these nine ears exhibited the staminate spike character. This progeny was from a self-pollinated ear. Ears were produced by 36 plants, 20 of which had staminate spikes that ranged in length from 2 to 12 cm. The average length was 6.55 ± 0.52 cm. The percentage of plants having staminate spikes (55.5 ± 5.6) is very close to that for a Mendelian dihybrid, where the character is the result of the combination of two dominant factors and the parent plant is heterozygous for both of them. As in all the second-generation progenies in which this character reappeared it behaved as a recessive character, the percentage of 55.5 may be considered a chance departure from 43.75. With the small number involved (only 36), the deviation of 11.75 per cent above the 43.75 is less than three times the probable error.

If the above explanation is correct, self-pollinated F_1 plants should give the following progenies: One all normal, three with 25 per cent of the plants with staminate spikes, two with 43.75 per cent of the plants with staminate spikes, and two with all the plants with staminate spikes. The last two, of course, would be recognized in the first generation, since they would result from self-pollinating plants exhibiting the variation.

If the hypothesis is correct that both the Boone and the brachytic parents were heterozygous for the variation, three classes of progeny should be obtained from self-pollinated F_1 plants, one class producing nothing but normal-eared plants, one with 25 per cent of the plants with staminate-spiked ears, and one with all the plants having ears with staminate spikes. The ratio in which these progenies should appear would be the familiar 1:2:1.

As in the other hypothesis, the F_2 progenies which would have all the plants exhibiting the variation would be recognized in the F_1, since they would show the variation in that generation. Since only three self-pollinated progenies have been grown thus far, it is not possible to test crucially the two hypotheses. The F_1 progenies which furnished seed for the second generation were grown in the greenhouse. The ears produced by these plants gave no indication of staminate spikes, and it was only in the larger planting in the field that the variation appeared in the first-generation plants.

The three second-generation Boone-brachytic progenies were fairly consistent with respect to the percentage of plants that produced the variation, all three closely approximating 25 per cent with staminate tips. The variation obviously is detrimental, since the ears affected are reduced in length. Although the staminate spike is not developed entirely at the expense of the pistillate portion, the evidence from the Boone-brachytic hybrid indicates that the length of the ear is reduced about one-half the length of the staminate spike.

It is of practical interest, therefore, to determine whether this undesirable variation is associated with stature. In this respect the three Boone-brachytic progenies differ somewhat. All three progenies show that the gene, or at least one of the genes for staminate spikes, is located in the same chromosome with the gene for stature. In the present hybrid, staminate spikes are associated with normal stature, so that the improvement in yield of the brachytic variation is not threatened in these cases. It must not be overlooked, however, that by suitable crosses these correlations could be reversed, thereby increasing the percentage of brachytic plants with the undesirable staminate spike variation.

The three progenies exhibit varying degrees of closeness of the relationship of stature to staminate spikes on the ear, with an average correlation of 0.37 ± 0.112. Such a correlation coefficient indicates a rather loose linkage, but it is apparent that in some progenies this relationship might be very much closer. That such cases may be expected is shown by the F_2 of the brachytic-Hopi hybrid where the brachytic plants appeared in combination with the staminate spike character in half the cases. In this particular cross also the spikes were unusually well developed. (See Table IV.)

BRACHYTIC × HOPI.

The Hopi variety, in common with other varieties grown by the Indians of the Southwestern States, possesses the long mesocotyl, which permits deep planting. An attempt was made by crossing brachytic and Hopi to combine the brachytic stature with the deep-planting adaptation. The strain of Hopi used in this cross was particularly vigorous, with plants fully as tall as those of the Boone variety.

The first generation was a complete surprise and was practically worthless. The plants were tall but differed from all the other first-generation hybrids of which brachytic was one parent in that they were weak and soon lodged. The ears were small and the yield poor.

TABLE IV.—*Distribution of plants with respect to the staminate spike characters in the brachytic × Boone and brachytic × Hopi hybrids of maize, including plants of the first and second generations.*

Progeny designation.	Normal stature.		Brachytic stature.		Total.	Percentage.		Coefficient of association.[1]
	Normal ears.	Ears with ♂ spikes.	Normal ears.	Ears with ♂ spikes.		Brachytic.	Staminate spikes.	
Brachytic × Boone:								
Dh 436 W2 L19, F_2	39	21	16	7	83	27.7	33.8	0.10±0.20
Dh 435 W1 L19, F_2	51	20	27	5	103	31.0	24.3	.45±0.17
Dh 436 W1 L19, F_2	48	18	18	0	84	21.4	21.4	1.0 ±0
Total	138	59	61	12	270	27.0	26.3	.37±0.112
Dh 436 F_1	63	17	......	......	80	......	21.3	......
Brachytic × Hopi:								
Dh 438 W1 L19, F_2	71	3	11	10	95	23.2	13.7	.91±0.04
Dh 438 F_1	20	2	......	......	22	......	9.1	......

[1] The correlations are between normal stature and staminate spikes with the exception of the last one, which is a correlation between brachytic stature and staminate spikes.

The second generation was little better, and no good plants were found. The brachytic plants especially were poor, one-half of the plants having ears which terminated in the staminate spikes found in the brachytic-Boone hybrids and described on pages 20–22. In the Hopi hybrid, however, the staminate spikes were much longer in proportion to the length of the pistillate part. The magnitude of this difference between the pistillate and staminate parts is shown in Table V. In the other hybrids the staminate spikes on the ears of brachytic plants were no longer than those borne on sister plants of normal stature. The ears with staminate spikes in the Hopi hybrid contrasted sharply with the normal ears, and no gradations were found. In this respect they differed from the Boone hybrids, where the appearance of the staminate spike was variable and not well differentiated from normal ears.

TABLE V.—*Measurements of the first and second generation plants of a hybrid between brachytic and Hopi.*

Character.	Dh 438F₁.	Dh 438F₂.		
		Normal.	Brachytic.	Difference.
Height of plant .... decimeters..	25.9±0.28	23.1 ±0.28	10.2 ±0.23	12.9 ±0.36
Length of longest tassel branch .... centimeters..	28.8±0.62	12.2 ±0.14	5.1 ±0.25	7.1 ±0.29
Length of branching space .... do....	14.7±0.33	12.5 ±0.27	10.4 ±0.35	2.1 ±0.44
Length of central spike .... do....	32.6±0.60	29.1 ±0.35	31.3 ±0.87	2.2 ±0.94
Number of leaves:				
Above the upper ear	4.1±0.07	23.0 ±0.40	22.7 ±0.56	0.3 ±0.69
Total	19.4±0.17	28.9 ±0.70	22.1 ±1.10	6.8 ±1.30
Longest leaf:				
Length .... centimeters..	90.5±1.15	94.6 ±0.72	91.5 ±0.87	3.1 ±1.14
Width .... do....	8.7±0.14	8.6 ±0.09	8.7 ±0.16	0.1 ±0.18
Number of tassel branches	29.8±0.98	3.79±0.05	1.50±0.31	2.29±0.31
Ear length:				
Upper ear .... centimeters..	19.9±0.47	16.9 ±0.31	10.1 ±0.67	6.8 ±0.74
Total [a] .... do....	21.9±0.78	20.0 ±0.53	21.7 ±1.2	1.7 ±0.56
Number of rows on upper ear	18.8±0.22	16.6 ±0.20	15.2 ±0.39	1.4 ±0.44
Length of staminate spike .... centimeters..	....	[b] 2.3	12.3 ±1.5	10.0

[a] The total ear length includes only the length of the pistillate portion on those ears which developed staminate spikes.
[b] Only three plants.

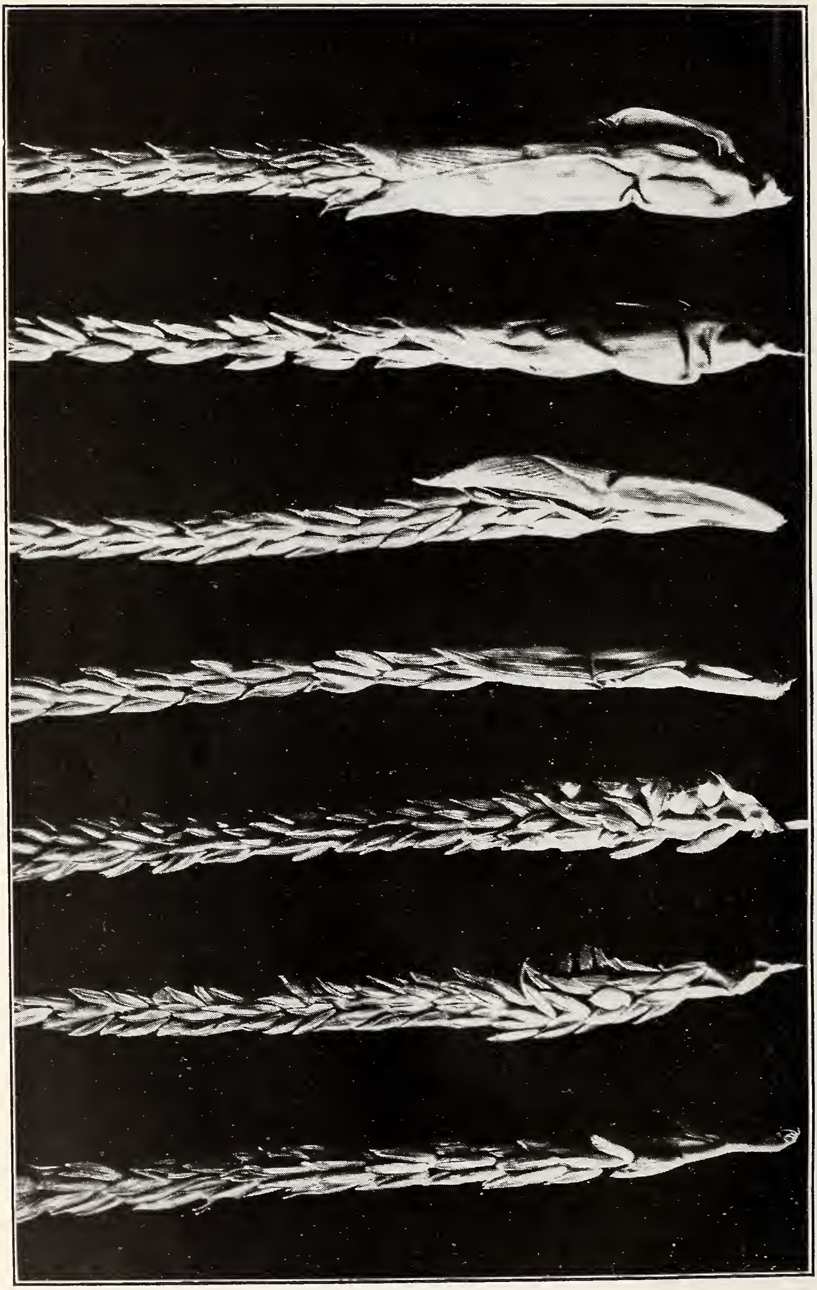
The brachytic plants of the Hopi hybrid also differed from the brachytic segregates of other hybrids in that the ears were borne in the axils of the uppermost leaves, or in extreme cases appeared as the lowest branches of the terminal inflorescences. This tendency to have ears at the base of the tassel is one which has been observed often in plants of the Chinese waxy variety and also in hybrids involving this type. (Pl. XVII.) Its appearance, therefore, in the brachytic-Hopi hybrid is not to be attributed to the same genetic change which caused the reduction in length of internode on the culm, although its expression in this hybrid was confined to brachytic plants.

Like most variations in maize, this tendency is inherited. Seven plants were grown from a self-pollinated ear of a Chinese plant which had produced ears at the base of the tassel. All seven of these plants showed evidence of this trait. On three of these plants the only symptom was a cluster of bracts at the base of the tassel; one plant, in addition to these bracts, had scattered pistillate spikelets on the lower tassel branches; another plant similar to the parent developed an ear at the base of the tassel; while the two remaining plants both had ears borne in the normal position, but terminating in staminate spikes.

The character is expressed in a variety of forms, sometimes appearing simply as a group of pistillate spikelets at the base of an otherwise normal staminate branch, and at other times well-formed ears with regular rows and not much smaller than those borne in the

BASAL SECTION OF A TASSEL OF CHINESE WAXY MAIZE, SHOWING CLUSTER OF EARS.

(Natural size.)



BRANCHES FROM THE TASSEL OF CHINESE MAIZE SHOWN IN PLATE XVII.

These branches show the transition from staminate to pistillate spikelets, the more advanced stages of which are shown in Plate XIX. (Natural size.)

EARS FROM THE TASSEL OF CHINESE MAIZE SHOWN IN PLATE XVII.

The bracts have been removed to show the gradations from pistillate to staminate branches. (Natural size.)

usual position are found. The intermediate stages between these well-formed ears and branches which have only a few pistillate flowers at the base closely resemble the ears that terminate in staminate spikes.

The pistillate branches, or ears, are clustered around the base of the tassel, the internodes being so short as to be indistinguishable from one another. (See Pl. XVII.) The transformation from male branches to ears is accomplished by a shortening of the rachis which is first noticeable at the base of the branch. In the advanced stages this shortening results in a crowding of the spikelets, which frequently is augmented further by a zigzagging of the rachis. In these cases there often is evidence of twisting. The spikelets in the early stages of the transformation of the branches are little altered, but with the added shortening of the rachis the glumes become reduced in length and gradually assume the characteristics of glumes on normal ears (Pls. XVIII and XIX).

While the tendency to have ears clustered at the base of the tassel is found on plants with normal internodes as well as on brachytic plants, the nature of the transformation from staminate to pistillate branches strongly suggests brachysm. Thus, there is an abrupt shortening of the main axis at the point where the branching occurs and also a marked shortening of the rachis of the branches, accompanied by a development of pistillate flowers. These changes are essentially those which took place in the development of the normal ear and are similar to those indicated in the brachytic plants of the Chinese-Algeria hybrid.

Taken in connection with the fact that half the brachytic plants of the Hopi-brachytic hybrid produced ears terminating in staminate spikes and that the brachytic plants had but few nodes above the ears, the close resemblance of tassel ears to ears in the normal position with staminate spikes suggests a possible origin of these staminate spikes.

Viewed in this light, the ear of maize may have developed not from a central spike of the terminal inflorescence of a lateral branch but from the transformation of the lower staminate branch of the terminal panicle into a pistillate branch. If this hypothesis is adopted, the sterile nodes which intervene between the pistillate and staminate inflorescences are not so difficult to explain and become with the ear a part of the terminal inflorescence.

The lower branches of the tassel occasionally develop into replicas of normal plants and even more frequently are subtended by bracts. These lower branches are relatively unstable, being the first to develop pistillate flowers, and the number of rows of spikelets often exceeds four. This increase in the number of rows may arise through the reduction of secondary branches or perhaps from a zigzagging of the rachis and subsequent twisting of the saddlebacks, as suggested by Collins (2).

The occurrence of ears at the base of the tassel and their restriction to brachytic plants suggests a relationship between these plants and the tassel-ear variation (6). Although the resemblance is not marked, the variation is in much the same direction, and seems to emphasize the association of brachysm with the development of pistillate flowers. Economically the combination of brachytic with Hopi has been a complete failure, and demonstrates the impracticability of predicting the value of a hybrid from the characteristics of the parents.

CONCLUSIONS.

Heritable variations occur frequently in maize. Few of these variations are of economic value and most of them are undesirable. One of the most frequent variations is a marked reduction in stature. A reduction in stature which affects only the length of the internodes while the other organs remain unaltered in size or number is known as brachysm. Such variations have appeared not only in maize but also in cotton, beans, peas, squashes, oats, wheat, and tomatoes, where some of them have been utilized by breeders to establish "bush" strains.

While brachytic maize plants are not of value directly for "bush" qualities, the reduction in stature produces a plant which seems admirably adapted to dry-land and irrigation culture.

The shortening of the internodes places more nodes in contact with the ground and thereby increases the number of primary roots. The plants in consequence of the short stature and highly developed root system are exceptionally sturdy, while the leaves are brought close together, thus effecting a partial shade.

The yield of the brachytic variation as compared with the varieties of the corn belt is low, but the reduced stature, sturdy erectness, and increased root development offer advantages for extreme conditions which may outweigh consideration of yield. Hybrids have been made with high-yielding strains in an effort to improve the yield of the brachytic plants, and a successful combination seems assured. Brachytic stature apparently reappears uncontaminated in the perjugate generations of hybrids with varieties of normal stature. This fact makes it possible to obtain rapidly the desired combination of yield and stature by repeatedly "back crossing" the high-yielding brachytic plants on high-yielding normal plants.

Only two teratological forms have appeared in the hybrids between brachytic and normal plants. One of these variations has not been observed previously, while the other is relatively common in many nonbrachytic strains.

The new variation appeared in the perjugate generation of the brachytic-Boone hybrid. This variation has been designated "adherence." It seems to be completely associated with normal stature and therefore offers no obstacle to securing the combination of high yield and short stature.

The other variation has appeared in several hybrids with brachytic. In this variation the ears terminate in staminate spikes. These spikes, to a certain extent, develop at the expense of the pistillate portion and therefore are undesirable. This variation also appears to be associated with stature, indicating that the genes for these characters are located in the same chromosome. The amount of crossing over, however, is relatively large, so that no difficulties are expected in obtaining brachytic plants of high yield free from this defect.

The close relation of ears terminating in staminate spikes to ears borne as basal branches of the terminal inflorescence is indicated in a hybrid between brachytic and Hopi. The evidence from this hybrid suggests that the ear of maize may have developed from the basal branches of the terminal panicle rather than from the central spike of the terminal inflorescence of a lateral branch of the main culm.

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