1920

Heritable Characters of Maize II.-Pistillate Flowered Maize Plants

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Journal of Heredity 11 (1920), pp 65-76.

HERITABLE CHARACTERS OF MAIZE

II.—PISTILLATE FLOWERED MAIZE PLANTS[1]

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IN THE "freak" class at the Annual Corn Show held at Lincoln, Nebraska, in the winter of 1913-14, there was exhibited a corn tassel with a heavy setting of seeds. A few seeds are not infrequently found in the staminate inflorescence of maize, particularly in pod corn, and tillers of various corn varieties often end in ears instead of in tassels or have tassels, the central spikes of which are ear like. The freak exhibited at the corn show, however, was a large, much branched affair, wholly tassel-like in form except for the fact that it bore a heavy crop of seed like a well-filled head of broom corn or sorghum. It retained no indication of having had any staminate flowers. It was apparently a wholly pistillate inflorescence, though tassel-like in form.

This freak specimen came into possession of the writer, and seeds were planted at the Nebraska Experiment Station in the spring of 1914. All the resulting plants had normal tassels with no pistillate flowers and normal ears wholly pistillate, and were typical representatives of a large, rather late white dent variety commonly seen in the Middle West. The fact that no abnormal plants appeared was not unexpected, for the parent plant, being pistillate flowered, must have been pollinated throughout by other plants, presumably normal ones. If the abnormality in question were recessive, it would not appear in the first generation from crosses with normal plants.

One of the normal plants was self-pollinated. The progeny of this plant, grown at Ithaca, N. Y., in 1915 and later seasons, consisted of both normal plants and plants with pistillate flowered tassels like the original tassel found at the corn show. Evidently the abnormal tassel is inherited as a recessive to normal. On account of the tassel-like form of this pistillate inflorescence and of its position at the top of the stalk, the abnormality is known as "tassel seed" and is designated by the genetic symbol *ts*, its dominant normal allelomorph being *Ts*.

Wholly pistillate flowered plants appeared also in an unrelated lot of maize grown in 1915. The parent plant was grown in 1914 along with others of the variety known as Pride of the North. All these plants were normal, were rather small and very early, and had red-cobbed yellow dent ears typical of the variety. The seed was from a bulk sample obtained from the Agronomy Department of the Nebraska Experiment Station, the original stock having come from Mitchell, S. D. Several of the 1914 plants were self-pollinated, but only one showed abnormalities in the 1915 progenies. The progeny of this one plant consisted of normal plants and plants that had wholly pistillate flowered tassels. Evidently this abnormality also is inherited as a recessive. At first it was assumed to be identical with the one first described, but this is now known not to be the case. To distinguish it from the tassel-seed type, and because of the more nearly ear-like form of the tassel, it is called "tassel ear" and designated by

[1]This is the second in a series of papers on the heritable characters of maize, the first by G. N. Collins and J. H. Kempton, on "Lineate Leaves," having appeared in the January number of the Journal. The next will be a brief discussion of "Brachytic Culms."—Editor.

NORMAL AND "TASSEL EAR" TYPES OF MAIZE

A pistillate flowered maize plant, called "tassel seed" is shown on the right. That on the left is a normal plant from the same pedigree culture. The silks of tassel seed push out of the upper sheaths at about the same time that tassels appear on normal plants. (Fig. 9.)

A LATER STAGE OF THE TWO TYPES SHOWN IN FIG. 9

A normal plant on the left and a tassel-seed plant on the right. The silks of the terminal inflorescence of the tassel seed had been pollinated some days before and are withered, while the silks of the true ears are still fresh. (Fig. 10.)

the genetic symbol *te*, the dominant normal allelomorph of which is *Te*.

DESCRIPTION OF TASSEL-SEED AND TASSEL-EAR TYPES

The peculiarities of tassel seed and tassel ear are best appreciated by an examination of the illustrations accompaying this account. In Fig. 9 are shown two nearly entire plants of the same pedigree culture at the time the terminal inflorescence is pushing out of the upper sheaths. At this stage, ear shoots have not appeared above the sheaths in either the normal or the tassel-seed plant. A latter stage in the growth of such plants is seen in Fig. 10. The tassels, both staminate (normal) and pistillate (tassel seed), appear at about the same time, before the plants have completed their height growth and before ear shoots have appeared from the sheaths. By the time the plants have reached their full height and when the pollen has been largely shed from normal plants (Fig. 10), the silks of the terminal inflorescence of the tassel-seed plants are usually withering on account of having been pollinated. True ear shoots have by this time appeared in the usual position, not only on the normal but also on the tassel-seed plants. Since the terminal silks of tassel-seed plants appear and are receptive before pollen is shed from normal plants of the same stage of development, they are pollinated at once from earlier maturing plants, in which case they soon wither, or if no early normal plants are near, the silks remain fresh and continue to grow until pollen is shed by the normal plants of their own stage of growth. The terminal silks of such plants are usually pollinated before the silks of the true ears of the same plants have appeared. The latter are ultimately pollinated, however, and soon wither, and seeds begin to develop. Whether or not the true ears continue to develop seems to depend upon how fully the tassel silks have been pollinated. When the tassels set a full crop of seed the true ears usually fail to develop far and ripen no seed, but when, from one cause or another, little or no seed forms in the tassels, the true ears develop normally.

Full-grown tassel-seed plants are nearly as tall as normal plants of the same cultures (Fig. 10) and have about the same number of leaves. Tassel-ear plants, on the contrary, are much shorter than their normal sibs. As seen in Fig. 11, tassel-ear plants have nearly as many leaves as normai plants, but have considerably shorter internodes. The terminal silks of tassel-ear plants appear at about the same stage of plant growth as do those of tassel-seed plants. True ears also appear in many cases, but much less frequently than with tassel-seed plants. If the tassel silks are removed at an early stage, true ears usually develop normally, except that they are often tardy in appearing. On the whole, tassel-ear plants are considerably weaker than tassel-seed plants.

The differences between tassel seed and tassel ear with respect to the form of the terminal pistillate inflorescence are well shown in Figs. 12 to 16. In tassel seed the inflorescence is loose like that of most tassels, the individual spikelets being more or less separated. The tassels of normal plants of different strains differ much in the density of their spikes. It is not surprising, therefore, to find variations in the density of tassel-seed inflorescence in somewhat unrelated cultures, such as the second and later generations from crosses with diverse sorts of normal plants. Just such diversities are seen in Figs. 12 and 15. In some cases the tassel-seed inflorescence is fairly dense (Fig. 15), though even here there is little resemblance to an ordinary ear. Some are very loose (Fig. 12), and others intermediate. In rare cases (Fig 12) staminate flowers develop with the pistillate ones throughout the greater part of the tassel. Whether or not these staminate flowers are functional has not been determined. The glumes and palae of such flowers are long, narrow,

NORMAL AND "TASSEL SEED" TYPES OF MAIZE

A second type of pistillate flowered maize, called "tassel ear," is shown on the right, with a normal plant on the left. Tassel-ear plants are much smaller and weaker than tassel-seed plants. They have about as many leaves as normal plants of the same families but their internodes are shorter. (Fig. 11.)

and pointed as in normal tassels, while, in case of the pistillate flowers, these parts are shorter, broader, and more rounded.

The terminal inflorescence in tassel ear, on the other hand, is always compact and distinctly ear-like (Fig. 16). The glumes and palae are short, broad, rounded, and in all respects much like those of true ears. This can be seen not only in immature tassel ears (Fig. 14), but in mature ones as well, particularly when poorly pollinated (Fig. 16).

The terminal inflorescences of both tassel seed and tassel ear are very subject to attacks of smut, much more so than normal tassels. When attempts are made to guard these pistillate flowered tassels against foreign pollen in artificial pollination experiments, the smut fungus develops under the paper bags used in such work even more than when the inflorescences are exposed. Moreover, since the silks protrude from the sheaths while the upper leaves are still closely crowded together owing to the short upper internodes at this stage (Figs. 9 and 11), it is very difficult to protect the silks against accidental pollination. Either the upper leaves must be removed or enclosed with the silks in large paper bags. Again, the weight of the tassels when the seed has begun to develop often causes the tassels to break off in storms. But, fortunately, it is not necessary to make use of the terminal inflorescence in artificial pollinations. If the tassels are removed as soon as the silks appear, the true ears develop with little delay and can be pollinated just as in case of normal maize.

INHERITANCE OF TASSEL SEED AND TASSEL EAR

Mention has been made above of the fact that these abnormalities are recessive in inheritance. The original open-pollinated tassel-seed specimen produced 28 normal plants. Several tassel-seed plants occurring as segregates in later generations were crossed with normals, resulting in 64 normal plants. Various F_2 progenies were grown and gave a total of 238 normal to 67 tassel seed. This is a deviation of only 9.3 $\pm$ 5.1 seeds from the 3 : 1 relation expected when parents differ in a single pair of factors. When F_1 plants of some of these same crosses were back-crossed with the recessive tassel seed, there resulted 368 normals and 381 tassel seed, a deviation of only 6.5 $\pm$ 9.2 seeds from the expected equality. Four self-pollinated F_2 normals bred true in F_3, giving a total of 128 normal plants, while 10 other F_2 normals broke up again, throwing both normal and tassel seed in F_3. Evidently, tassel seed is differentiated from normal by the single factor pair *Ts ts*. It is assumed that the recessive tassel-seed plants would breed true if it were possible to test them. But, owing to the lack of staminate flowers, they can neither be self-pollinated nor crossed with other plants of the same type.

Tassel-ear plants crossed with normals gave 24 normal plants in F_1 and total F_2 progenies of 260 normal to 36 tassel ear. This is too great a deviation from a 3 : 1 relation to be due to chance. The expected numbers on a 3 : 1 basis with a total of 296 are 222 and 74, and the deviation is a 38 $\pm$ 5 plants. Such a deviation could not be expected to occur by chance even once in some millions of trials. The possibility is at once suggested that normal and tassel ear differ by two factor pairs, and that the F_2 progenies approach a 15 : 1 instead of 3 : 1 ratio. But the numbers calculated on this expectation are 277.5 and 18.5, a deviation of 17.5 $\pm$ 2.8. Even such a deviation as this would not occur by chance more than once in perhaps one hundred thousand trials. It is, of course, possible that in some crosses the parents differ by one factor pair and in others by two pairs. But no F_2 family with large numbers approached closely either a 3 : 1 or a 15 : 1 ratio.

If two factor pairs are concerned, about half of the normal F_2 plants, taken at random, should breed true normal, while, in case a single factor pair

MATURE INFLORESCENCE OF TASSEL SEED

A loose type like this sometimes has staminate flowers and even a few wholly staminate spikelets, particularly at the end of the branches. (Fig. 12.)

TERMINAL INFLORESCENCE OF TASSEL-SEED TYPE

In the terminal inflorescence of tassel seed, the "tassel" is a loose panicle like that of normal plants, but is almost wholly pistillate flowered. The branches are usually slender and the spikelets fairly well separated. (Fig. 13.)

TERMINAL INFLORESCENCE OF TASSEL-EAR TYPE

In the terminal inflorescence of tassel ear, the "tassel" is compact, with the spikelets crowded close together. Both the central spike and the branches are decidedly earlike (Fig. 14.)

is involved, only one-third should do so. Of 17 F_2 normals tested, 5 bred true and 12 broke up. This is certainly nearer the expectation for a single factor pair than for two pairs, but the numbers are too small to allow a definite decision. The F_3 lots not breeding true consisted of 745 normal and 78 tassel-seed plants. This is a deviation from a 3 : 1 ratio of 127.8 ± 8.4 and from a 15 : 1 ratio of 27.5 ± 4.7. While the observed numbers fit a 15 : 1 ratio much more closely than a 3 : 1 ratio, the fit is too poor to be due to chance alone. Moreover, if the F_2 relation were really 15 : 1, in F_3 some 3 : 1 as well as 15 : 1 ratios should have appeared, but none of these F_3 ratios were smaller than 6 : 1, and only 3 of the 17 were smaller than 10 : 1.

A bit of evidence favoring the assumption of two factor pairs differentiating tassel ear from normal is afforded by back crosses of F_1's with the recessive tassel seed. Four such back crosses gave 121 normal and 49 tassel ear. A 3 : 1 relation is expected from such crosses if two factor pairs are involved. The deviation from the 3 : 1 ratio is 6.5 ± 3.8, not a very bad fit. Another back cross, in which the F_1 plant was not closely related to those concerned in the back crosses noted above, gave 53 normal and 43 tassel ear, a deviation from equality of 5 ± 3.3. On the basis of the two-factor hypothesis, some normal plants are expected to have one of the two recessive pairs. Such normals when crossed to tassel ear should, of course, give a 3 : 1 ratio in F_2 and a 1 : 1 ratio from a back cross.

While the facts given above are favorable in part to the idea that tassel ear is differentiated from some normal types by two factor pairs, itself being a double recessive, the evidence is far from convincing. The writer is much inclined to think that there is another way of accounting for the deficiency of tassel-ear plants below the 25% expected on the basis of a single factor pair. Tassel ear is at best a small, weak type. In this respect it is not greatly different from "dwarf," a form described by the writer some years ago. Under ordinary field conditions, dwarf plants almost never appear in numbers approaching those theoretically expected. It has been possible, however, by germinating F_2 and back cross seeds in seed pans in the greenhouse, to show that dwarf is a simple Mendelian recessive. Carefully germinated seeds grown in large numbers have given almost exactly the expected percentage of dwarfs. Dwarfs are apparently often unable to germinate under field conditions or die soon after germination. This is so well known that progenies expected to contain dwarfs are almost always started in the greenhouse and later transplanted to the field.

It is not known as yet whether tassel ear behaves in this respect like dwarf, but, since the plants are small and weak, it seems probable that the deficiency seen in the field may be due to a failure of tassel-ear plants to survive. In this connection it is important to note that most of the records presented above were made from progenies grown under unusually adverse conditions. The soil in which they were grown is a heavy clay. Even the normal plants of the same families showed by no means a perfect stand. Previous inbreeding, in case of the F_3's particularly, had greatly weakened the whole stock. A number of F_4 progenies, grown from these weak F_3 normal plants, were even less vigorous than the F_3's. Out of 15 such F_4 lots, involving 486 plants, in only three lots did any tassel-ear plants appear, and here they numbered only 6 as against 80 normals. In two F_3 families, coming from a cross of tassel ear with a strong and quite unrelated normal stock, there appeared 44 normal and 13 tassel-ear plants, very nearly a 3 : 1 relation. Now the field notes show that these lots were the most vigorous of all those grown that season. It seems likely, therefore, that observed deficiencies of tassel ear are to be explained just as similar deficiencies of dwarf are, but this cannot

be determined until seed-pan germination is tried out.

TASSEL SEED AND TASSEL EAR AS GENETICALLY DISTINCT TYPES

It was stated early in this account that tassel seed and tassel ear were at first supposed to be identical, but that they are now known to be distinct types. The only evidence so far given in support of this statement, however, is the fact that the terminal inflorescence of tassel seed is a loose panicle, while that of tassel ear is more compact, both the central spike and the branches being ear-like in appearance. It remains to be shown that these two abnormalities are genetically distinct.

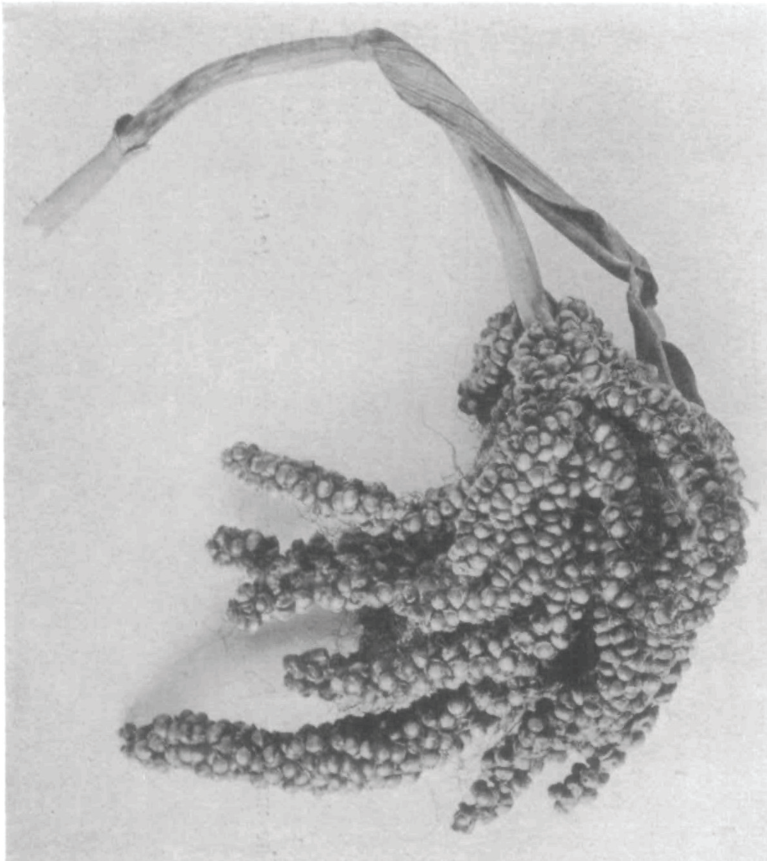
Crosses of Tassel Seed with Tassel Ear.—If tassel seed and tassel ear were fundamentally identical, differing only in density of the inflorescence, vigor of growth, and the like, somewhat as strains of normal corn differ, crosses between the two should give pistillate flowered plants. Of course it is impossible to cross two wholly pistillate flowered types directly, but no mere fact of this kind need bother us long. Conclusive evidence can be obtained from crosses of normal plants, the one heterozygous for tassel seed and the other for tassel ear. Or, better still, a plant heterozygous for one recessive type may be crossed with the other recessive.

If the two recessive types were the same, the cross of two heterozygotes should give 25% of pistillate flowered plants in the progeny. Or, on the same assumption, if an F_1 plant heterozygous for tassel seed is crossed on to a tassel ear and a plant heterozygous for tassel ear is crossed on to a tassel seed, 50% of the progeny should be pistillate flowered. All these crosses have been made and progenies grown. The cross of the two heterozygotes yielded 69 normal plants. A normal plant heterozygous for tassel seed crossed on to a tassel ear gave 40 normals, and a normal plant heterozygous for tassel ear crossed on to a tassel seed resulted in 33 normals. Not a single pistillate flowered plant appeared among the 142 normals. This is regarded as conclusive evidence establishing the genetic distinctness of the two pistillate flowered types. What the double recessive will be like cannot be told until another generation is grown.

Distinct Linkage Relations of Tassel Seed and Tassel Ear.—The story of the linkage relations of tassel seed and tassel ear is only partly known, but sufficient information is at hand to prove that the two abnormalities show distinctly different linkage relations with certain other factors of the maize plant.

A back cross involving tassel seed, *Ts ts*, and a factor pair for pericarp color, *P p*, gave 81 normal plants all with red pericarp and 77 tassel-seed plants all with colorless pericarp. The pair *Ts ts* is, therefore, very closely linked with *P p* or the two pairs are identical. In a similar back cross involving *P p* and tassel ear, *Te te*, there appeared normals with red and with colorless pericarp and tassel ears with red and with colorless pericarp. There were 50 plants of the parental combinations and 56 of the other two combinations of the two characters in question. This is a "crossover" percentage of 52.8, or a deviation from 50 of 2.8 ± 3.3. Apparently, therefore, tassel ear is not linked with pericarp color. Certainly it does not show the same linkage as tassel seed.

It has long been known that a recessive leaf abnormality called liguleless *Lg, lg*, is linked with a dominant plant color called sun red, in which the factor pair *B b* is involved. The crossover percentage commonly observed is about 30. A back cross involving *B b*. *Lg lg*, and tassel ear, *Te te*, produced 96 plants with all but one of the eight possible combinations of these three factor pairs. The crossover percentage for *B b* and *Lg lg* was 29.2, for *B b* and *Te te* 20.8, and for *Lg lg* and *Te te* 45.8. The crossover percentage for liguleless tassel ear is so near 50, deviation 4.2 ± 3.4, that, standing alone, it affords no satisfactory evidence of linkage. There can be little doubt, on the other hand, that *B b* and *Te te* are



A VERY COMPACT FORM OF TASSEL SEED

Even in this extreme form the spikes are hardly ear-like. (Fig. 15.)

TWO MATURE TASSEL EARS

The central spike and the branches are very like small ears. This is seen particularly well in the poorly pollinated specimen (left), and fairly well in the other one, from which birds have removed many seeds. (Fig. 16.)

linked, the deviation from 50% (independent inheritance) of 29.2 ± 3.4 being of such a magnitude that it would not be expected to occur by chance more than once in millions of trials. Moreover, there was in this back cross no great deficiency of tassel ear to mask the results, since the normals were to the tassel ears as 53 to 43. Again, the numbers of all the several classes were very close to expectation on the basis of the crossover percentages noted. Of the 96 plants, 50 were non-crossovers, 44 single crossovers, and 2 double crossovers.

Unfortunately there are no data available at present with respect to the possible relations of *Ts ts* with *B b* and *Lg lg*. There are, however, back cross data including no less than 3,700 plants involving *P p* and *Lg lg*, and 2,600 involving *P p* and *B b*, all without any indication of linkage. It follows, therefore, that tassel seed and tassel ear are not only distinct genetically as well as morphologically, but that they belong to distinct linkage groups.

Identifying the Double Recessive, Tassel Seed Tassel Ear.—It is not known what sort of plant the double recessive, tassel seed tassel ear, will be. There is available abundant material, in some of which *ts ts te te* should appear next season. If it should prove to be like one of the types described in this paper, tassel ear for instance, a 9 3 : 4 relation should be found to exist between the three phenotypes. Ordinarily, in such a case as this, it is necessary to conduct further breeding tests in order to distinguish the phenotypically alike, but genetically different single and double recessives. But such tests might here encounter serious difficulties. The most likely procedure, in case the double recessive is not distinguishable from one or other of the single recessives, is to cross random samples of the recessive plants with *both* heterozygous tassel seed and heterozygous tassel ear. This would involve considerable difficulty unless two true ears or one ear and the terminal inflorescence develop on each plant, a thing hardly to be expected in plants so weak as tassel ear. Of course it would doubtless be possible to make up the two classes of heterozygotes so that they differ from each other and from the recessives by dominant aleurone or endosperm characters. A single ear of each recessive could then be pollinated by both heterozygotes and the resulting seed separated into two lots corresponding to the two heterozygous parents. But all this would require much time and no little effort.

Fortunately, no such tests should be necessary in the particular case under consideration. The known linkage relations of tassel seed and tassel ear with other characters should make the solution of the problem much less difficult. To emphasize the aid that some knowledge of linkage affords in such a problem as this is the only excuse that the writer can plead for this attempt to cross an apparently difficult bridge before he is sure that such exists. It will not be difficult to introduce both *P p* and *B b* into the cross of tassel seed and tassel ear. Any resulting pistillate flowered plant with colorless pericarp is almost certain to be *ts ts*, and there are about four chances in five that any pistillate flowered plant having the factor of the pair *B b* present in the tassel-ear parent of the tassel-seed tassel-ear cross will also be *te te*.