THE INHERITANCE OF CERTAIN "ABNORMALITIES" IN MAIZE^a

R. A. EMERSON

University of Nebraska

Some of the abnormalities considered in this paper seem to have no effect on the yield or quality of grain while others result in greatly decreased yields and some even cause the total destruction of the plants. Between these extremes there are many grades of injuriousness. None of the characters listed here as abnormalities are actually known to increase the yield or improve the quality of the crop, though some of them, liguleless leaf for instance, may possibly be found to lessen transpiration and in that way enable a variety possessing it to withstand drouth better than sorts with normal leaves.

A classification that separates characters into *normal* and *abnormal* is not entirely satisfactory. If we are to consider abnormal any character that is out of the ordinary, we are likely to find characters that in one type of corn are perfectly normal, but in another type decidedly abnormal. The tendency to produce numerous tillers, 7 or 8 per plant, or to produce 4 or 5 ears per stalk, characters common in some very small varieties of pop corn, would doubtless be considered abnormal by one unacquainted with such sorts, particularly if those tendencies should crop out in a field of some large dent corn. The characters listed here as abnormal are all doubtless the resultants of inherited tendencies on the one hand and environmental influences on the other, exactly as are so-called normal characters. It is scarcely conceivable that there is any fundamental difference between the two categories. Some characters of maize are, however, commonly spoken of as abnormalities. Several such are discussed here.

Dwarf hermaphrodites.—In 1910 there were found in 3 families of corn certain dwarf plants that differed from the normal tall plants of the same families not only in stature but also in having short and relatively broad leaves, thick, little branched tassel, and small ears which usually ended in a thick unbranched tassel and always had well developed stamens throughout (see figs. 1 and 2). Moreover, the anthers of the tassels did not shed pollen normally but sufficient

^a Some of the tests reported here were conducted at the Bussey Institution of Harvard University during 1911. I am indebted to that institution and to Dr. E. M. East particularly for placing at my disposal room in the greenhouses and gardens and for photographic and other facilities for laboratory and field work. The remainder of the work was done at the Nebraska Agricultural Experiment station with funds of that institution.

pollen was obtained for selfing a few ears by scraping it from individual anthers with the point of a knife. The three 1909 parent plants of these three 1910 families were normal with respect to all these characters, and the 1910 progenies contained slightly over 4 normal tall plants to 1 dwarf hermaphrodite—exactly 107 to 25. The counts were made after the plants had reached their full size. Some of the dwarfs may have perished while young.

The self-fertilized seed of the dwarf plants, though apparently well developed, germinated very poorly or else the plants died while very

FIG. 1. AN ENTIRE PLANT OF THE SMALLEST TYPE OF DWARF HERMAPHRODITIC CORN, AND AN EAR OF NORMAL SIZE.

The latter is a first-generation cross of a dwarf hermaphrodite of a somewhat larger type than the one shown here with a plant of normal size.

young, only 9 plants having matured in 1911 from 94 seeds planted. All of these 9 plants were dwarf hermaphrodites like those of the preceding year, suggesting that the type breeds true. The seeds of several ears that resulted from the application of pollen of various tall strains of corn, to the silks of the 1910 dwarfs germinated well and produced in every case perfectly normal plants with well developed ears—310 plants in all from seven such crosses—showing that the normal type is fully dominant. Three of the normal plants of

these 1910 families when selfed, yielded only normal plants in 1911 while three others yielded both normal and dwarf plants, the respective numbers in these progenies being 58 tall and 11 dwarf. (Again the records were not made until after the plants had completed their growth so that it cannot be known whether the numbers reported represent correctly the numbers of the two classes at the time of germination.) Finally, some of the first generation crosses of 1911—normal plants as noted above—were selfed and their progenies grown

FIG. 2. EARS OF DWARF HERMAPHRODITES SHOWING STAMENS THROUGHOUT (NATURAL SIZE).

in the greenhouse the present winter. These plants were grown thickly in shallow pans to the age of three or four weeks. While it was obviously impossible to tell from the seedlings whether they would later have abnormal ears and tassels, the segregation into tall plants with long comparatively narrow leaves and dwarf plants with short, broad leaves was so distinct that it could not be mistaken (see fig. 3). Every one of these progenies, 17 in all, contained both types of plants, the total number of individuals being 714, of which 528 were tall and 200 dwarf. This near approach to the simple Men-

delian ratio of 3 : 1 in case of the families germinated under the favorable conditions in-doors suggests that the deficiency of dwarfs found in field-grown hybrid families and the small number of plants in pure dwarf families (as indicated by counts after the plants had completed their growth) are due to poor germination or early death of dwarfs under field conditions rather than to departure from ordinary Mendelian behavior.

These results indicate that the abnormality in question is a recessive character, or group of correlated characters, and that therefore it may be transmitted through perfectly normal, productive plants which are hybrid for the abnormality. In fact, it must under ordinary field conditions be thus transmitted, if transmitted at all, since the dwarfs themselves, even if they live to mature, shed almost no pollen and produce such very inferior ears that they would under no circumstances be selected for seed and probably would never even be harvested. How general this defective type is cannot be said. It has been reported in 4 or 5 distinct strains of corn from three widely separated localities.^b The fact that such dwarf plants as these are not commonly noticed in fields does not prove the absence of the abnormality from the strain in question. Under ordinary field conditions they would almost always be overlooked.

Yellow leaves.—In a small plat of silage corn grown at the Nebraska Experiment Station in 1910 there were found twenty-four plants of a distinctly light yellowish-green color resembling somewhat the so-called "golden" varieties of various shrubs alleged to have value as ornamentals. As indicated by their color these plants doubtless possessed a considerable quantity of chlorophyll since they grew to maturity and were of normal height though rather slender. All of them produced pollen in abundance, apparently as much as normal plants. Only four of the twenty-four, however, showed any indication of silks and not one of the four produced an ear. They were therefore practically barren. Obviously no self-pollinated ears were obtained. A similar yellow plant found in a field of another variety of corn did, however, produce a fairly good ear by open pollination. Seed from this ear planted in 1911 resulted in a considerable percentage of yellow plants, most of which produced no ears or only very poor ones. Pollen from some of the barren yellow plants of 1910 was applied to silks of green plants of two other strains and the resulting cross-bred plants of 1911 were all of a fully green color and were

^b See East and Hayes, Bulletin 167, Conn. Agr. Exp. Sta., 1911; Montgomery, Pop. Sci. Mon., Oct., 1911; and Emerson 24th Ann. Rpt., Neb. Agr. Exp. Sta., 1911.

FIG. 3. NORMAL AND DWARF SEEDLINGS FROM A SELF-POLLINATED EAR OF A HETEROZYGOTIC NORMAL PLANT.

The tall seedlings were removed from one side of the flat and the dwarf ones from the other side shortly before the photograph was taken.

normal in productiveness. The total number of such plants was 137, a sufficient number to show the completely recessive nature of this abnormality. No second generation has been grown. The most interesting cross-bred plants of this yellow-leaved corn came from a small ear of the dwarf-hermaphrodite corn discussed above, pollinated from a barren yellow plant. Notwithstanding the fact that both parent plants were worthless from a corn producer's standpoint—one of them having produced no ear and the other only very inferior ones—their hybrid progeny was nevertheless one of the most productive lots grown in 1911, having yielded at the rate of nearly 40 bushels per acre from a poor stand in a year of unprecedented drouth (see fig. 4). The plants inherited normal size from the yellow-leaved parent and full green color from the dwarf parent.

This yellow-leaved type of corn is more likely to persist in a commercial strain than the dwarf type because of the abundant production of pollen from the pure yellow plants though they may produce no corn that would ever be selected for seed. It of course has the same chance as the dwarf type to persist in the hybrid condition in perfectly normal, productive plants.

White seedlings.—It is not uncommon to find numerous pure white seedlings in a field of corn. Such plants owing to their inability to make food for themselves, always die as soon as they exhaust the food stored in the seed (see fig. 5). Such a total loss of power to produce chlorophyll in a certain percentage of the seedlings is a characteristic of some stocks of corn. Five such stocks, all apparently unrelated, have been included in my cultures. The results obtained from a study of them are presented in detail in a paper to be published in the twenty-fifth annual report of the Nebraska Agricultural Experiment Station.

When all of my corn families that have shown white seedlings (a total of 42) are lumped together, they are found to have contained a total of 1903 plants, 1457 of which were green (including nine striped plants) and 446 of which were white. This is not far from the three-to-one ratio expected when dealing with a recessive Mendelian character. While the nature of this abnormality makes it impossible to produce a true-breeding white strain that can be crossed with pure green strains, there are, nevertheless ways of testing the method of its inheritance. If whiteness is a pure recessive, the green plants in any family in which white seedlings occur must be of two sorts, one homozygous green, producing nothing but green offspring, the other heterozygous green, yielding on self-pollination about 3 green

FIG. 4. FOUR TYPICAL FIRST-GENERATION EARS PRODUCED BY CROSSING A WORTHLESS DWARF HERMAPHRODITE.

They bear ears like the three shown at the left of the cut, with pollen from a tall yellow-leaved plant, a type which rarely produces anything better than the two "ears" shown at the right.

seedlings to 1 white one. There should, of course, be 1 pure green to 2 hybrid green plants. Of 43 plants tested from such families, 15 have been found to breed true to the green color and 28 have produced both green and white seedlings. Similarly of plants from all-green families resulting from a cross of pure green plants with hybrid green ones, half should breed true green and half produce both green and white seedlings. Of 17 plants tested from such fam-

FIG. 5. HETEROZYGOUS GREEN PLANTS.

If selfed or crossed among themselves, produce approximately three green seedlings to one white one. The latter die within two or three weeks because they cannot produce food for themselves.

ilies, 9 have produced green plants only, and 8 have yielded both greens and whites.

White seedlings are of not infrequent occurrence in corn fields. Whether this is a more common abnormality than dwarfness, yellow leaves, etc., or is merely more commonly seen on account of its conspicuousness, cannot be said. While it apparently always results in the death of the plants showing it, it is really not much worse from an economic standpoint than dwarfness or yellow leaves.

Erect leaves.—In another paper, to be published in the twenty-fifth annual report of the Nebraska Agricultural Experiment Station, I have described a very peculiar erect leaf habit due to the absence of the small, triangular, leathery connection between the leaf blade and leaf sheath, called the auricle. This, in my corn, is accompanied in almost all cases by the absence of the ligule, a membraneous projection of the sheath above the base of the blade. The peculiarity results in a lessening of the exposed leaf surface and should on that account lessen water loss from the plant. It may also impair the plant's ability to produce carbohydrate food. The enclosure of the tassel by the upper leaves of the plant causes the pollen to spoil in wet weather but may be found beneficial as a protection against too severe drying of the pollen in certain climates (see fig. 6). Erect leaves associated with a one-sided (monostichous) arrangement of the upper leaves, not uncommon in this and other types of corn (see Collins, Bulletin 161, Bureau of Plant Industry, U. S. Dept. Agr.) whereby the tassel is enclosed except on one side, is less likely to cause rotting of the pollen while still presumably affording considerable protection against drying. Stocks of corn not lacking the auricle may also have fairly erect or ascending leaves due to the size and stiffness of the mid-rib. This condition does not result in a lessened exposure of the leaves and their stiffness makes them more easily torn or broken by the wind. The non-auriculate leaf always has the lower part of its blade wrapped more or less closely about the stalk much as the sheath is, and the upper part of the blade free. The abnormality does not seem to lessen the production of grain and in this respect therefore is quite unlike the forms already discussed. This leaf type has not been reported before for corn so far as I am aware. Like many other abnormalities, however, it may have been in existence for a long time though unobserved, and may even now be more or less common.

In inheritance, this peculiarity is a simple Mendelian recessive as are the other abnormalities so far considered. Since it was first discovered in 1910, I have grown progenies of six self-pollinated non-auriculate leaved plants amounting to 175 individuals, all lacking the auricle. A total of 103 first generation plants from four crosses between abnormal and normal leaved types have all had normal leaves. In the second generation of such crosses 672 normal and 221 abnormal leaved individuals have appeared. My results also indicate that this peculiarity is not correlated with such other abnormalities as dwarfness, white seedlings, etc.

Irregular kernel rows.—It has been suggested by East and Hayes (Conn. Agr. Expt. Sta. Bulletin 167) that the irregular arrangement of kernels on the cob is a dominant Mendelian character, though perhaps not a simple one. What little evidence I have seems to indicate on the contrary that the arrangement of grains in regular rows is perhaps the dominant character. The only records I have bearing upon the inheritance of this character are from a hybrid between a dwarf pop corn with “zigzag” rice-pointed grains and a large dent corn with fairly straight rows. The arrangement of kernels on ears of the parent races and of first and second generation plants of the cross is shown below. All the plants from which these records were made were grown in adjoining rows at the Nebraska Experiment Station during the summer of 1911. One well developed ear, usually the upper one, was taken from each plant and from these ears alone the records were made. All ears in which the rows could be easily followed from one end to the other were classed as regular, those in which the rows could be followed readily for a considerable distance from one end of the ear, but in which no rows could be traced at the other end, were classed as intermediate, and finally those in which the grains had a zigzag arrangement throughout were classed as irregular. Since the number of plants representing the several generations differ widely, the records are here given in approximate percentages to facilitate comparison.

	Number of plants.	Per cent regular.	Per cent intermediate.	Per cent irregular.
Dent corn parent.....	29	90	10	
Pop corn parent.....	67		13	87
First hybrid generation.....	59	85	10	5
Second hybrid generation.....	344	63	20	17

If it were not for the 5 per cent irregular-rowed ears in the first hybrid generation, the results might well be interpreted as due to simple Mendelian dominance of the regular-rowed condition. The ears of intermediate type would then have to be regarded as non-inherited fluctuations as suggested by East and Hayes. It may be that even the fully irregular ears of the first hybrid generation are extreme cases of fluctuation. It is not worth while to prolong this discussion, however, because no detailed record as to regularity of rows was made in case of the earlier generations of the parent stocks and it cannot be shown, therefore, that the parent plants were fully

FIG. 6. ERECT LEAF HABIT DUE TO THE ABSENCE OF LEAF AURICLES.

Wet weather often spoils much of the pollen as is shown by the plant at the left of the cut, a leaf of which has been pulled away from the tassel.

homözygous for the character concerned, though they came from self-pollinated strains. The indications of these results, that irregularity in rows is a recessive character, accords with the experience of Halstead with crosses of Country Gentlemen sweet corn and various straight rowed sorts (see Rept. Bot. Dept., N. J. Agr. Expt. Sta., 1906).

Other recessive abnormalities.—In addition to the five abnormalities considered in detail above, all of which are recessive, I have very incomplete records of the behavior of a few others that are apparently recessive. In none of these cases are my records sufficient to make it worth while to present them in detail. I have two strains of corn that show a noticeable inability to stand erect in strong winds, probably due to poor rooting. First generation crosses between these and normal strains stand erect as well as any corn I have. In case of one small second generation a few of the plants blew over while the remainder stood up well.

Several of my families of pop corn, all more or less closely related, have a peculiar zigzag stalk above the upper ear accompanied by a shortening of the internodes at the same place. Such plants seem at first to have broad flat stems but this appearance is due to the spreading apart of the over-lapping leaf sheaths by the abrupt crooks in the stalk. Sometimes the sheaths are shoved aside so far that they no longer clasp the stalk and are therefore unable to give their customary mechanical support to the rapidly elongating and therefore not very rigid stalk and as a consequence of this the whole upper part of the stalk breaks off above the ear. Crosses of this type of corn with normal types have given only normal plants in the first generation.

Dominant abnormalities.—Fasciated, bifurcated, and branched ears are classed as Mendelian dominants by East and Hayes. The only one of these that I have had to do with is fasciated ears. The degree of fasciation varies much even between the different ears of a single plant, some ears being very broad at the tip while others are only slightly flattened. Notwithstanding the probability that this pronounced variation within a strain is mere fluctuation, I am of the opinion that different degrees of fasciation may be inherited. I have one stock in which nearly all the ears show an extreme type of fasciation not seen at all in other families. Of course this difference may not be due to the presence of distinct factors for fasciation in the different strains but merely to a different resultant from the

interaction between a single fasciation factor and other diverse characters of the different strains.

Fasciated ears from families that produce both fasciated and normal ears breed true fasciated or produce a large percentage of fasciated ears along with some normal ones, thus indicating that some plants with fasciated ears are homozygous and others heterozygous. From a 1910 family of pop corn that contained both types of ears, four fasciated ears were used as parents of 1911 families. Two of these produced 18 and 46 plants respectively, all with strongly fasciated ears. Of the other two families one had 12 plants with ears more or less fasciated and three with ears that were apparently perfectly normal. The fourth family, consisting of 28 plants, had some ears that were strongly fasciated, some that were apparently normal, and about all grades between these extremes, making definite classification almost impossible. A 1911 family of dent corn grown from a fasciated ear of the year before contained 32 plants with more or less fasciated ears and 35 plants with ears apparently normal, though some of the latter may have been slightly flattened. While these results suggest that fasciation is dominant, they also indicate that it is not a simple character.

No cross between a pure fasciated strain and a pure normal one has been studied. The heterozygous fasciated plant, which when selfed produced the dent corn family noted above, was crossed with a plant of a family of normal 8-rowed flint corn. The first generation consisted of 63 plants every ear of which was apparently perfectly normal. I do not remember ever to have seen a fasciated ear in any type of corn with so few as twelve rows. The apparent dominance of normal over fasciated ears in this cross may perhaps be due in some way to the fact that it was largely made up of 12-rowed ears. If the normal eared plant used in the cross had been of a family having a larger number of rows, the results might have been different. But all that can be said now is that this case must be given further study.

Some strains of pop corn often have staminate spikelets intermingled with the ordinary pistillate flowers of the ears. Sometimes the staminate flowers are clustered together at one side of the ear, or may extend entirely around the ear near the middle or between that and the tip end, thus separating the ear into two parts, the connection resembling the central spike of a tassel. Often the staminate spikelets are interspread with pistillate spikelets near the tip of the ear, which then tapers rapidly. Not uncommonly one flower of a spikelet

may be pistillate and the other staminate. Finally the ear may be normal except that it ends in a club-shaped tassel. This intermixture of staminate and pistillate flowers on the same ear is not to be confused with the hermaphrodite ears of the dwarf corn discussed earlier in this paper, for in the latter each grain has associated with it from three to six stamens and the glumes are of the roundish cob type, while in the case here considered the stamens are limited to the staminate flowers and are always associated with rather slender, pointed, tassel-type glumes.

FIG. 7. INTERRUPTED EARS.

Representatives of a first generation of a cross of a normal-eared strain of pop corn with a strain having interrupted ears.

The only indication I have of the dominant nature of this abnormality is derived from a single cross between a plant having it and a plant from a family all individuals of which were apparently normal. Every ear of the first generation was interrupted to a greater or less degree by staminate flowers (see fig. 7).

Various unclassified abnormalities.—There are several other abnormalities which are certainly inherited since they always occur in all or in a considerable number of the plants of certain families, while they are not seen in other families. As yet, however, not enough is known regarding the manner of their inheritance to say even whether

they are dominant or recessive characters. It will not be worth while to do more than mention them here.

In most varieties of corn the silks appear after the ear shoot has pushed well out of the sheath, and usually a day or two after the pollen has begun to shed. From two varieties of pop corn, Tom Thumb and White Rice, I now have strains in which the silks push up out of the sheath considerably in advance of the ear shoot and appear from one to four days before any pollen is shed. It seems probable that in corn protogynous habit and the appearance of the silks directly from the sheath are both the same thing—a precocious development of the silks.

In a single family of corn grown from a cross of sweet corn and pop corn made some years ago, the tassels of every plant were held in a position varying from horizontal to fully pendant. The peculiarity is due to the formation just beneath the tassel of one or more small ears, or sometimes of a small tassel enclosed in husks, which push the stalk out of its supporting leaf sheaths. These accessory ears appear several nodes above the upper one of the normal ears and at about the same time as the latter. The reason why they crowd the stalk to one side and even out of its leaf sheath, while the normal ears borne lower on the stalk do not, is doubtless due to the fact that the stalk is elongating rapidly and is therefore not so rigid just beneath the tassel as it is lower down at the time the ears develop.

A strain of Red Rice pop corn in my cultures of 1910 and 1911 had opposite instead of alternate leaves for a few nodes above the ear and whorled leaves just beneath the tassel, usually accompanied by considerable shortening of the upper internodes and even of the tassel itself. This results in a partial enclosure of the tassel in the clustered upper leaf sheaths and a consequent decay of much of the pollen.

Other abnormalities of considerable interest that have occurred in my cultures are forms of sterility in varying degrees. In some cases almost no pollen is produced though the tassels, anthers and the plant in general are otherwise normal. In other cases both ears and tassels are greatly reduced and in the final stages consist of mere stems absolutely bare of flowers.