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## A Cytoplasmically Inherited Abnormality in Maize

WILLIAM L. BROWN<sup>1</sup>

*Abstract.* Defective plants, ranging in degree from lethal to chlorophyll streaking of the leaves, are shown to be due to a factor or factors in the cytoplasm of the popcorn inbred P2. Five distinct genomes were found to be "incompatible" in P2 cytoplasm although the degree of abnormality varies between genomes, indicating a nuclear-cytoplasmic interaction in this material. One of the most distinctive characteristics of the defective P2 cytoplasm is the extreme phenotypic variability found in F<sub>1</sub> hybrids involving P2 females. The substitution of WF9 for P2 chromosomes in P2 cytoplasm is equally as abnormal as the original F<sub>1</sub> hybrid.

There is now ample evidence in maize of transmissible characters whose control resides essentially outside the nucleus or whose expression is governed by the interaction of nuclear and cytoplasmic factors. To date, such characters have been limited to two general categories, namely, chlorophyll variegation and pollen sterility. These were first demonstrated by Anderson (1923) and by Rhoades (1933). More recently, several students of maize have reported additional instances of cytoplasmically controlled pollen sterility and of the interaction of nuclear and cytoplasmic factors, (Jones, 1960; Rogers and Edwardson, 1952; Duvick, 1956). As a practical consequence of these investigations, cytoplasmic pollen sterility is now being utilized as a substitute for hand emasculation in the large scale production of F<sub>1</sub> hybrid seed for commercial use.

A further example of cytoplasmic inheritance in maize is reported here, the phenotypic expression of which varies from slight reduction in plant vigor to lethality of the F<sub>1</sub> hybrids when a particular strain is used as a maternal parent. In its most extreme expression the effect is more pronounced than that of any previously described cytoplasmic factor in maize known to the author.

### MATERIALS AND OBSERVATIONS

In a routine breeding experiment in which all possible crosses of eight inbred lines of popcorn were being tested for performance, it was observed that certain of the F<sub>1</sub> crosses were even more lacking in vigor than the inbred parents from which they were derived. All of the extremely weak hybrids had one parent in common, suggesting the aberrant performance might in some way be attributable to a single inbred, designated P2. In the original set of crosses no record was kept of which lines were

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used as male and female parents in each of the  $F_1$  combinations, so from the original data it was impossible to determine whether cytoplasmic effects were present. The following year the line P2 was crossed reciprocally with four unrelated dent corn inbreds, C25-13, WF9, CF23, K4-138, and one popcorn line, RS1.

When the resulting  $F_1$  hybrids were grown, it was immediately apparent that all crosses in which P2 was used as a female were strikingly different from their reciprocals. A certain percentage of the P2 female crosses always died as seedlings. As an average of three years' results the percentage of lethals amounted to 11.5% of the total number of plants grown. Among those plants which survived there was usually a small percentage which approached normality in phenotype. The remainder were characterized by marked reduction in plant height and ear size, reduction in number of leaves, chlorophyll streaking of the leaves, and varying degrees of pollen abortion. In the cross P2 x C25-13, the range of plant heights was from 58 cm to 209 cm, and the mean was 119.8 cm. The numbers of leaves ranged from 10 to 14 and the mean was 12.02.

The reciprocal crosses, in which P2 was used as a pollen parent, were in all cases normal in phenotype and uniform; they exhibited pronounced hybrid vigor characteristic of crosses of unrelated inbreds (Figures 1 and 2). The plant heights ranged from 216 cm to 258 cm, and the mean was 233.4. Leaf numbers were from 12 to 16, and the mean was 15.1. It would seem, therefore, that the marked contrast between reciprocal crosses in this material is ample evidence for assuming that the hereditary determinants of the differences observed are to be found primarily in the cell cytoplasm rather than in the nucleus. This assumption, of course, has its basis in the knowledge that in the process of sexual fusion most, if not all, of the cytoplasm is contributed by the female germ cell.

One of the most impressive features of this material is the wide range of variability occurring within any given  $F_1$  hybrid progeny. In contrast to the striking uniformity of normal  $F_1$  hybrids between homozygous inbred lines, the crosses in which P2 was used as a seed parent were highly variable. It is suggested that at least a part of this variability is due to an acute sensitivity of cytoplasmically controlled characters to environmental influence. Some support for this suggestion comes from a study of the behavior of genotypically identical P2 crosses grown in two or more years. P2 x C25-13 and its reciprocal have been grown for three successive years in south central Iowa. In 1958 approximately 15% of the plants of the cross P2 x C25-13 differed from the normal reciprocals only in exhibiting varying degrees of pale green streaking in their leaves. In the years 1959 and 1960,

on the other hand, not more than 3% of the plants of P2 x C25-13 approached plants of the reciprocal cross in vigor and phenotype, and in both years the cultures included a higher percentage of extremely weak individuals than were present in 1958.

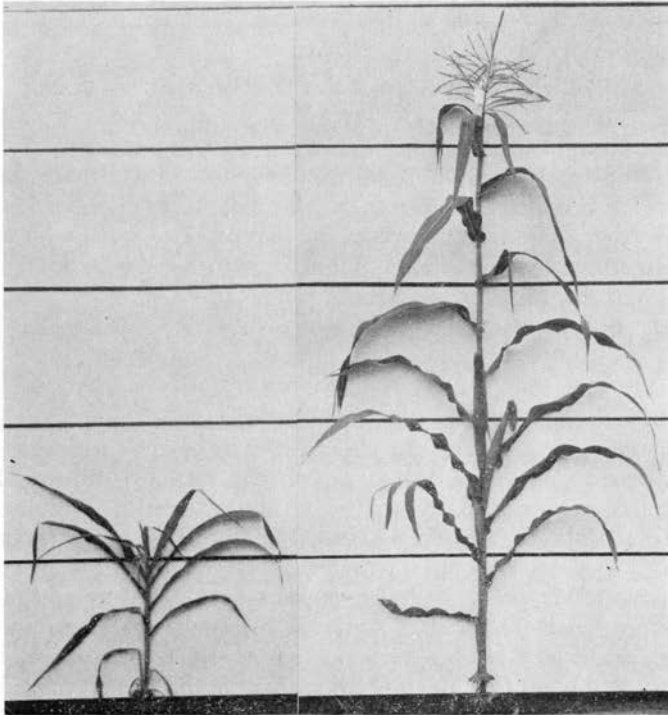


Figure 1. Reciprocal differences in plants of P2 x C25-13 (left) and C25-13 x P2 (right).

*Results from Backcrossing.* The line P2 has been backcrossed as a female for four successive generations to the normal line WF9. In this way the original chromosome complement of P2 has been largely replaced by the chromosomes of WF9. If it is assumed that in the fertilization process no cytoplasm is transmitted along with the male gamete, it can be further assumed that the original P2 cytoplasm has been retained throughout the backcrossing process. This then makes possible a comparison of a substituted genotype in P2 cytoplasm with the original F<sub>1</sub> hybrids involving P2 females. Individuals of the third backcross generation (the last to be observed) exhibit all the abnormalities of the original F<sub>1</sub>'s and aside from reduction in vigor due to inbreeding are very similar to the P2 x WF9. It is clear, therefore, that the substitution of WF9 for P2 chromosomes in P2 cytoplasm has little if any influence on the abnormality as expressed in the original crosses. Furthermore, the absence of any apparent

change in P2 cytoplasm following four backcrosses to WF9 is further support for the belief that cytoplasm is not transmitted through the male germ cell.

In addition to the backcrosses to WF9, two other lines, C25-13 and CF23, were included initially in the backcrossing pro-

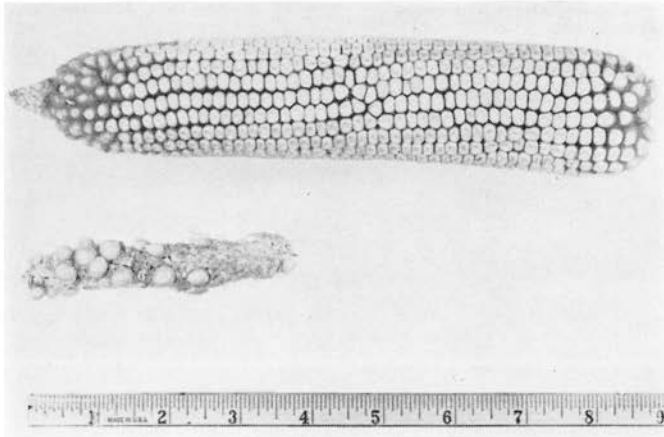


Figure 2. Typical ear of C25-13 x P2 (top) and P2 x C25-13 (bottom).

gram. Plants of both these cultures were so defective that practically no seed was obtained and for this reason it was impossible to continue the backcrossing beyond the first BC generation.

#### DISCUSSION

During the course of these studies five distinct maize genomes have been tested in P2 cytoplasm. In each of these five crosses the hybrids with P2 used as a female are strikingly different from their reciprocals. This suggests strongly that the differences observed are dependent in their expression upon something present in P2 cytoplasm and absent in the cytoplasm of the other five lines. This does not imply, however, that the abnormalities characterizing these crosses are independent of genic influence. On the contrary there is evidence to indicate the presence of an important nuclear-cytoplasmic interaction in this material. Among the hybrid combinations studied there are differences between crosses in the degree of abnormality of the  $F_1$ . The line CF23 in particular, when used as a pollen parent in crosses with P2 females results in an  $F_1$  in which nearly 25% of the plants are classified as near normals. These plants exhibit some leaf streaking but their vigor is only slightly less than that of an average of the reciprocal cross. This number represents a significantly higher percentage of near normals than has been observed in

any of the other crosses studied. On the basis of these differences one might conclude, therefore, that although P2 cytoplasm is required for reciprocal differences, the degree of difference may definitely be influenced by the genotype of the pollen parent.

Cytoplasm of the line P2 seems to be "incompatible" not only with each of the five unrelated genomes with which it has been tested but also to a lesser degree with its own genome. Small cultures of the line have been maintained by selfing for five generations. The first year in which it was grown it appeared to be quite normal in all ways. In succeeding generations, however, some of the abnormal phenotypic characteristics which typify its hybrids have appeared in the line itself. These vary considerably in their degree of expression from year to year and in any one generation one can always find some plants which are normal except for light chlorophyll streaking of the leaves.

The streaks of light green color which characterize the leaves of P2 and crosses involving P2 females are very similar in appearance to that found in viral infected Gramineae. This raises the question as to whether cytoplasmic effects of the type described here may in fact be due to viruses which are normally transmitted through the egg cell. Repeated attempts have been made with this material to transmit the effect from abnormal to normal plants by infection with ground tissue. The results of all such attempts, however, have been negative. This does not, of course, rule out completely the virus theory since, as Caspari (1948) has pointed out, virus particles, if present, may be unable to leave the living cell and may therefore only be transmitted by multiplying cells.

Like most other cases of known cytoplasmic inheritance, the basic underlying causes of the abnormality characterizing P2 crosses are as yet unknown. Nonetheless, the results described herein represent yet another example of a set of characteristics which are transmissible, are expressed in similar fashion in the presence of several distinct genomes, and require the presence of non-chromosomal material for expression.

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