4. Further report on relationships between cytoplasmic and genic male sterility.

Jones has earlier reported (MNL. 1954, p.20; Brookhaven Sym. in Biol. No. 9, 1956) the results of crosses which clearly indicated independence between restorer genes for cytoplasmic male sterility and the conventional ms genes. Dominant restorer genes did not act as dominant Ms_1 genes when crossed to ms_1/ms_1 male sterile plants. Jones also pointed out that Ms genes obviously do not act as restorer genes for sterile cytoplasm, since the former genes are present in all normal inbreds which have been converted to cytoplasmic male sterility. Further evidence on the independence of the cytoplasmic and genic male sterile systems comes from crosses which placed an ms_1/ms_1 genotype in plants carrying S type cytoplasm plus restorers for S cytoplasm.

Fertile plants of A158SF4-1A (S type cytoplasm, restored by Ky21 restorer, backcrossed four generations to A158, followed by one generation self) Y Ms_1/Y Ms_1 were pollinated by Y Ms_1/y ms_1 males in a WF9 genotype. All F_1 plants from this cross (ca. 15 plants) were fertile, indicating that the female parent was homozygous for the S-restorer, since the Y Ms_1/y ms_1 male parent was in a WF9 background and presumably carried no S restorers. The F_1 plants, then, possessed S cytoplasm and were heterozygous for the restorer genes. In addition, 50% of the F_1 plants were heterozygous Y Ms_1/y ms_1 (ignoring X-overs). The F_1 plants were selfed, and white (or light yellow) seeds from ears segregating yellow-white endosperm color were planted.

The white seeds should give rise to y ms_1/y ms_1 plants in S cytoplasm, except for X-overs (4-5%). Since the F_1 plants were heterozygous for the S restorer gene, 75% of the y ms_1/y ms_1 plants should have carried the restorer gene. Actually, according to Buchert's findings on the male transmission of S restorers in A158SF families (MNL 1958, p.15) all of the y ms_1/y ms_1 plants would possess the restorer gene, since only the restorer allele is transferred through the pollen. If the S restorer gene prevented the ms_1 gene from expressing itself, or if ms_1 were not capable of acting in S cytoplasm, at least 75%, and probably 100%, of the y ms_1/y ms_1 plants would be expected to be fertile. In fact, out of a total of 46 plants in two progenies, 43 plants were completely sterile and only 3 normal fertile (6.5% fertile). The proportion of fertile plants is about that expected as a result of X-overs between the y and ms_1 loci plus hetero-fertilization and mistakes due to misclassification of light yellow endosperm. It is concluded, therefore, that ms_1/ms_1 plants with S cytoplasm and S restorer genes are sterile; the ms_1 gene is not inhibited by S restorers, by S cytoplasm, or by a combination of both.

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5. Inheritance of a chlorophyll defect in a male fertile WF9S stock.

Previously reported (Jones, MNL 28, p.19; MNL 29, p.14) was a case involving a change from cytoplasmic male sterile to male fertile in a WF9 line carrying S cytoplasm. The evidence indicated that the loss of sterility was not due to a mutation to either a dominant or recessive pollen restorer gene. It was suggested that the alteration which brought about normal pollen fertility occurred in the S cytoplasm. Also pointed out was the fact that associated with the fertile WF9S plants was a rather severe yellow and pale green streaking, more pronounced than in normal WF9. The first record of this chlorophyll abnormality appears in both of the first generation selfed progenies from two fertile WF9S plants which had previously been backcrossed 6 generations by normal WF9. It was present every year throughout 4 subsequent generations of selfing. The character is variable in expression, ranging from a degree of yellow streaking similar to that found in some normal WF9 stocks to a very severe streaking and reduction in vigor. The estimations of the degree of streaking that have been made are subjective ones, and in some instances may be open to question. A green plant is one judged to be no more streaked than normal WF9, i.e. to be "normal WF9 green".

In the fifth generation selfed material grown in 1956 it was noted that all 17 plants in one family appeared to be normal WF9 green, while in a second family 9 plants were clearly streaked and 8 were green. An attempt was begun to follow the inheritance of the chlorophyll abnormality and to determine what bearing, if any, it might have on pollen fertility. Specifically the breeding behavior of green and streaked plants was compared in selfs and in reciprocal crosses with normal WF9.

To date, it has not been possible to isolate a line that breeds true for green. Two selfed progenies were grown in 1957 from the family mentioned above where all 17 plants were judged to be green. One progeny was again all green, but on selfing (1 plant) yielded 20 streaked plants and none green in 1958. The other progeny gave 4 green and 3 streaked plants, and a self of one of the four green plants gave all streaked plants (16). The behavior on selfing of two of the eight green plants in the second family grown in 1956 (which had 9 streaked and 8 green plants) was similar. These produced in 1957 progenies of green and streaked plants - 14 green, 2 streaked in one; 8 green, 8 streaked in the other. A further self of a green plant in each case gave all streaked plants in 1958.

Selfs made on the yellow streaked plants have given rise to progenies consisting exclusively of streaked plants - 11 plants in 1957, 14 plants in 1958. Based on only 2 generations and a small number of plants the difference in the breeding behavior of green and streaked plants on selfing appears to be that green plants can yield green as well as streaked plants whereas streaked plants give only streaked progeny. If this is true, then the green plants that were originally observed in the two families grown in 1956 have been lost, since by 1958 their descendants were all streaked. The essential correctness of the initial judgement made in 1956 that one family consisted of all green plants is indicated by a planting of remnant seed of this family in 1958, where again all 10 plants were about normal WF9 green. Thus in 2 years of selfing these plants have become streaked. However, the progenies descended from the green plants on the whole probably are less severely streaked than the progenies from the streaked plants.

Pollen fertility seemed to be about normal for WF9 in all of the above families, so that it was not possible to establish any connection between the chlorophyll abnormality and the change to pollen fertility that occurred in this material. One difficulty in estimating pollen fertility is the general reduction in vigor encountered in the most severely streaked plants. Such plants tend to produce reduced amounts of pollen.

Green and streaked plants have also been crossed reciprocally with normal WF9. Normal WF9 crossed as female parent by either green or streaked plants has given only green offspring, and the plants have remained green in a first backcross by green and streaked respectively. In contrast, the reciprocal cross green x WF9 gave green and streaked plants. Green plants from this cross were again pollinated by WF9, giving all streaked plants. These results in crosses and backcrosses by WF9 parallel those of the green plants on selfing. Streaked plants crossed and backcrossed by normal WF9 pollinators have produced only streaked plants, just as the selfs on streaked plants. Again, all plants from crosses with WF9 were judged to be normal fertile for this inbred.

These differences in reciprocal crosses with normal WF9 indicate that the chlorophyll abnormality is apparently transmitted only through the female parent. This suggests that some cytoplasmically inherited factor or factors, perhaps the chloroplasts themselves, are responsible for the alteration in chlorophyll phenotype. The role that nuclear genes play is unknown, since only a WF9 genotype has thus far been involved.

The behavior of what appear to be green plants both on selfing and backcrossing by WF9 is somewhat puzzling. The failure of green plants to breed true may mean the chlorophyll abnormality is easily modified by environment and in some plants fails to show in somatic tissue, but the altered cytoplasmic constituent is nevertheless present in some egg cells and hence is transmitted. Or plants may appear green because of the presence of only a relatively few altered plastids, or other cytoplasmic elements, which fail to manifest themselves visibly in somatic tissue, but which are present in sufficient numbers in certain egg cells to give rise to streaked offspring. It is also possible that the alteration which brings about the streaking is recurring in green plants; but if this is the case the change must be more or less restricted to germinal tissue, or be taking place so late in development that it fails to show somatically. There does appear to be a real difference in the breeding behavior of green and streaked plants in the proportion of streaked plants they give in selfs and in crosses, as maternal parents, with WF9. Evidently in streaked plants all, or nearly all, egg cells receive large enough numbers of altered cytoplasmic elements to produce recognizable streaked offspring. The variability in the degree of expression could be a consequence of the relative numbers of "good" or "bad" cytoplasmic elements in the zygote, which could be distributed randomly during somatic development.

The result reported here of apparent cytoplasmically inherited constituents which affect chlorophyll and vigor are generally similar to the examples cited by Brown and Duvick (MNL 32: 120). The relationship between the chlorophyll aberration and the change from male sterility to fertility remains obscure. The two in fact may not be causally related.

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6. Male gametophytic selection as the mechanism for non-segregation in the restoration of cytoplasmic male sterility.

In the 1958 issue of Maize News Letter a non-segregation of restorer genes for cytoplasmic male sterility was reported. A further investigation has revealed the mechanism of this phenomenon. For brevity only a summary of part of the data will be presented here.

The following symbols will be used:

S = a male-sterile plant with the "S" type cytoplasmic factor

SF(Het) = a fertile plant with S type cytoplasm and heterozygous for the restorer from Ky21.

SF(Hom) = same as above but homozygous for the restorer.

Type of cross	No. of crosses made	Residual genotype	No. of plts. per progeny	Results
SxSF(Het)	15	A158	10 - 48	all fertile
SF(Het) selfed	4	"	20 - 80	" "
SF(Het)xSF(Het)	3	"	19 - 47	" "
SF(Het)x Inbred	23	"	41 - 80	1 fertile:1 sterile

Thus, in the above data, whenever an SF(Het) plant was used as a male no segregation occurred; while, when one of these was not used as a male, segregation always resulted.

Microscopic observation of the pollen from SF(Het) plants revealed that about one half of the pollen in each anther was aborted. Since there is a correlation between the percentage of pollen grains carrying the restoring gene and the percentage of apparently viable pollen, and since all the pollen grains effecting fertilization have the restorer, the inheritance pattern can be explained by assuming that only the pollen grains with the restorer live, while those with the alternate allele abort.

This hypothesis has been tested in the following manner: (1) If an SF(Het) plant were self-pollinated half the progeny would be expected to have about 90% normal pollen (normal for the A158 inbred) and half the plants to have slightly more than half of the pollen aborted. Pollen from