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Analysis of a Completely Male-Sterile Character in American Upland Cotton[1]

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SCIENTISTS at the Texas Agricultural Experiment Station have conducted extensive studies leading to the discovery of cytoplasmic-genetic male sterility in corn (8) and sorghum (9, 10) and the development of methods and materials for using this type of sterility in commercial hybrid-seed programs. Researchers in cotton also have been interested in male sterility and have observed and analyzed a number of male-sterile stocks, none of which have proved to be of the cytoplasmic-genetic type.

In 1940 Beasley (1, 2) observed that synthesized tetraploids of *Gossypium arboreum*×*G. thurberi* were female fertile but usually male sterile. The early records, both published and unpublished, fail to establish which species contributed the cytoplasm. However, the synthesized amphidiploid used extensively at the Texas Agricultural Experiment Station originated from a cross in which *G. arboreum* var. *neglectum* was used as the female. Subsequent observations of the progeny of this tetraploid in backcrosses and outcrosses to *G. hirsutum* have revealed varying degrees of pollen development ranging from almost complete sterility to full fertility. These results were obtained when *G. hirsutum* contributed the cytoplasm as well as when it was contributed by *G. arboreum.* Beasley and Brown (3) analyzed the sterility found in the F_2 of crosses of certain varieties of *G. hirsutum* and *G. barbadense.* Sterility was found to be due to asynapsis which was conditioned by recessive genes at two loci, one from the *G. hirsutum* parent and the other from the *G. barbadense* parent. Asynapsis under monogenic control was shown by Newman[3] to be responsible for the sterility of several aberrant stocks of American Upland cotton, *G. hirsutum,* found in

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[3] Newman, J. S. A cytogenetic analysis of a sterile type in American Upland cotton. Unpub. M.S. thesis, Texas A. and M. College, College Station, Texas. 1958.

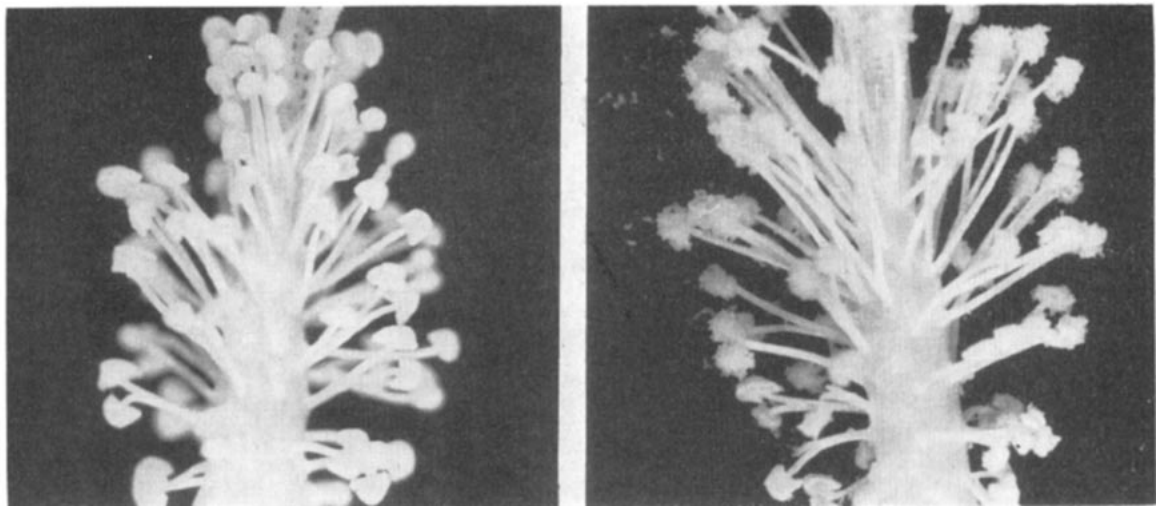

Figure 1—Indehiscent anthers of a male-sterile (MS 1-2-9) cotton plant (left) and dehiscent anthers of a normal plant.

the breeding plots of the Agricultural Experiment Station at Lubbock, Texas.

By 1956 the writers were convinced that the desultory methods being used in the search for male sterility among the cultivated American Upland cottons were unlikely to produce the desired results. Also Jones (5) and others had shown that pollen production was one of the characters in plants "most frequently affected by cytoplasmic factors" and that these factors had contributed importantly to speciation. The concept that the wider the cross the greater the probability of finding the cytoplasmic type of male sterility in the progeny of the hybrid gained general acceptance. An experiment in cotton embodying this concept was initiated during the winter of 1956–57. We wished to avoid as many as possible of the difficulties associated with breeding in interspecific hybrids, and at the same time to work with distantly related stocks. Therefore, 16 representatives of 7 of the races of *G. hirsutum,* as described by Hutchinson (4), were chosen as parental stocks to be used in a systematic search for cytoplasmic male sterility.

The purpose of this paper is to report the discovery of a male-sterile character and to give the results of genetic, cytoplasmic, and environmental analyses of it.

PROCEDURE AND RESULTS

Discovery of a Male-Sterile Plant

In order to maintain the race cytoplasm, each race-stock was crossed as female to a day-neutral, inbred line, D&PL-14, which has been used at this station for several years as a representative of cultivated American Upland cotton. Since all but one of the race-stocks were "short-day" in flowering response at College Station (i.e., would not initiate or set fruit in the long photoperiod of summer) it was necessary to make the crosses during the winter in the greenhouse. F_1 plants of each cross were grown in the greenhouse during the winter of 1957–58 and F_2 populations, each of approximately 1,000 plants, were grown in the field the following summer. The total experiment consisted of some 16,000 plants. All of the populations but the one with the day-neutral race parent segregated for response to length of day. On those plants which developed fruit forms, the flowers that persisted to anthesis were examined for abnormal or low pollen production. By the end of the growing season five plants had been tagged as being suspect. These five plants were cut back and transplanted to the greenhouse. Reciprocal crosses were attempted between each of these plants and D&PL-14. In four cases reciprocal crosses were made with equal facility and bolls were set in approximately

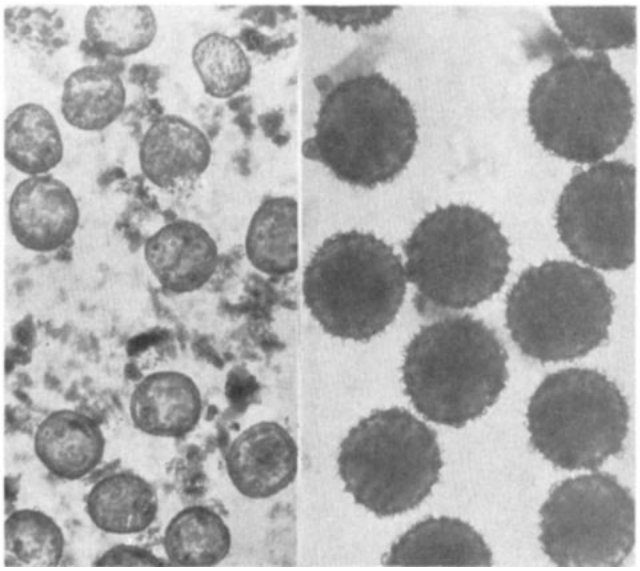

Figure 2—Abnormal pollen grains of a male-sterile (MS 1-2-9) cotton plant (left) and pollen grains from a normal plant.

equal numbers regardless of the direction of the cross. However, one plant, designated as 1-2-9 from the F_2 of the cross of Texas 86 (PI-153974), a stock of *G. hirsutum,* race *latifolium,* and D&PL-14, was male sterile; bolls were set only when 1-2-9 was the female parent. Since this experiment was designed to search for cytoplasmic-genetic male sterility in cytoplasms of the *G. hirsutum* races, the discovery of a male-sterile plant, hereafter referred to as MS 1-2-9, was of special significance.

Morphology and Cytology

The individual anthers of MS 1-2-9 are indehiscent and have shortened filaments. The characteristic compacted aspect of the androecia of flowers on MS 1-2-9 plants, as compared with the bristled appearance of those of normal plants in the same population, is shown clearly in Figure 1. Male-sterile plants are readily identified and flowers of MS 1-2-9 plants are consistent in the expression of the mutant character. Classification of segregating populations could be based on observation of only one flower per plant except that normally male-fertile plants occasionally have been observed to "go sterile" for short periods of time in the greenhouse at College Station. Therefore, to guard against possible misclassification of a normally male-fertile plant, rather than to be sure of the classification of MS 1-2-9 plants, we followed the procedure of observing at least 3 flowers per plant.

Table 1—Segregation in the F_2 generation of MS 1-2-9 × D&PL-14.

Family	Number of plants			χ^2	P*
	Male fertile	Male sterile	Total		
1	54	21	75	0.36	.70-.50
2	54	14	68	0.70	.50-.30
3	46	16	62	0.02	.90-.80
4	55	11	66	2.47	.20-.10
5	48	9	57	2.58	.20-.10
6	54	19	73	0.04	.90-.80
7	41	14	55	0.01	.95-.90
8	51	18	69	0.04	.90-.80
9	55	14	69	0.82	.80-.70
10	60	17	77	0.35	.70-.50
Pooled	518	153	671	1.73	.20-.10
Heterogeneity				5.66	.80-.70

* Assuming a 3:1 segregation

Table 2—Segregation in the backcross (BC^1_1) of F_1 (MS 1-2-9 × D&PL-14) to MS 1-2-9.

BC_1^1 family	Number of plants			χ^2	P*
	Male fertile	Male sterile	Total		
1	14	6	20	3.20	.1-.05
2	6	14	20	3.20	.1-.05
3	8	10	18	0.22	.7-.50
4	10	9	19	0.05	.9-.80
5	9	11	20	0.20	.7-.50
6	6	11	17	1.47	.3-.20
7	9	10	19	0.05	.9-.80
8	7	11	18	0.89	.5-.30
9	8	9	17	0.05	.9-.80
10	11	9	20	0.20	.7-.50
Pooled	88	100	188	0.76	.5-.30
Heterogeneity				8.77	.5-.30

* Assuming a 1:1 segregation.

On the day of anthesis, pollen of MS 1-2-9 flowers is even more strikingly aberrant than are the anthers. As shown in the photomicrographs, Figure 2, MS 1-2-9 pollen grains are smaller than those of normal self-fertile flowers and the characteristic spiney exine of normal cotton pollen grains appears to be missing. Also the light-staining, vacuole-like appearance of the contents of aberrant pollen grains suggests a greatly reduced amount of protoplasm.

Cytological analyses of 55 pollen mother cells in buds from MS 1-2-9 plants showed that the full complement of 26 pairs of chromosomes, characteristics of *G. hirsutum,* was present, and that pairing and disjunction were regular except in one bud. Some 4,000 sporads examined were normal and regular except in the case of one bud. Exactly what causes the pollen of MS 1-2-9 plants to be nonfunctional is not known but obviously the complete male sterility observed cannot be attributed to the low degree of chromosomal irregularity found.

Genetic Analysis

Early in the winter of 1958–59 MS 1-2-9 was crossed with D&PL-14. Being male-sterile, MS 1-2-9 had to be used as the female. The F_1 seeds produced were planted in the greenhouse in the spring. Ten F_1 plants were grown to maturity. Several selfed bolls were produced on each plant and male sterility was observed. The F_1 plants also were backcrossed to the MS 1-2-9 parental stock. The F_2, F_3, and backcross families, reported below, trace back to these F_1 plants.

Since the 1959 summer growing season was well advanced by the time the F_2 seeds were mature they were planted in the greenhouse instead of the field nursery. A population of 671 F_2 plants, representing 10 families, was produced. Every plant flowered and the androecia of a minimum of three flowers on each plant were examined. Two distinct phenotypes were observed: *(1)* one with androecia in which all or most of the anthers dehisced normally and produced normal quantities of fully developed pollen, as in normal stocks of Upland cotton; *(2)* the other with androecia in which the anthers were indehiscent and contained aberrant pollen, as in MS 1-2-9. The first phenotype was classified as male-fertile and the second as male-sterile. As shown in Table 1, 518 plants were classified male-fertile and 153 male-sterile, a ratio which does not deviate significantly from the 3:1 ratio expected for a character determined by a single pair of recessive genes. The data in Table 1 also show that the individual families segregated similarly and could be considered members of the same segregating population. Male-sterile F_2 plants were maintained for more than two months after bolls on the male-fertile siblings had matured and, though they continued to flower, they set no bolls.

The backcrosses of F_1 (MS 1-2-9 × D&PL-14) to MS 1-2-9 were grown in the greenhouse during the winter of 1960; the backcross was designated BC^1_1. Segregation for male fertility and male sterility in these backcrosses, representing 10 families and constituting 188 plants, did not deviate significantly from a 1:1 ratio (Table 2). Furthermore, as evidenced by the probabilities calculated for the individual family χ^2 values and the heterogeneity χ^2, the families segregated in the same manner; therefore they were pooled and goodness-of-fit to a 1:1 ratio was calculated for the total population. These findings confirmed the interpretation given to the results obtained from the analysis of the F_2, i.e., that inheritance of the MS 1-2-9 character is monogenetic.

During classification of the F_2 population an occasional indehiscent anther was observed in flowers of certain plants. Although the pollen extracted from such anthers appeared to be normal, a few indehiscent anthers occurred with such a degree of regularity in flowers of certain plants (and over such a period of time) as to suggest that this expression might be associated with the heterozygous state of the gene which presumably conditions the MS 1-2-9 expression. To test this assumption, 10 plants representing the occasional-indehiscent-anther condition and 5 plants representing the completely-dehiscent (normal) condition were chosen for progeny testing. F_3 progenies of 20 plants of each selected F_2 plant were grown in the field nursery during the summer of 1960. Each plant was examined periodically for dehiscence of anthers. Of the progenies from the 5 F_2 plants scored as completely dehiscent, 2 segregated for the MS 1-2-9 character and 3 did not, whereas 8 of the progenies from occasional-indehiscent-anther plants segregated and 2 did not. The slight indication of ability to identify the heterozygous genotype on the basis of phenotypic expression is not considered to be critical enough for use in the genetic analysis of the MS 1-2-9 character. Furthermore, the occasional-indehiscent-anther expression apparently occurs only under greenhouse conditions for it was not observed in the material grown in the field.

Those F_3 progenies which segregated for the MS 1-2-9 character did so in numbers that were not significantly different from the theoretical ratio of 3 male-fertile:1 male-sterile. Thus, essentially the same segregation occurs in F_3 progenies from heterozygous F_2 plants as occurs in F_2 populations from the F_1 of the MS 1-2-9× DPL-14 cross.

Cytoplasmic and Environmental Effects

Since race *latifolium* (Texas 86) contributed the cytoplasm to the first populations analyzed (those presented thus far), there was no opportunity in this material to study differential cytoplasmic effects that may be associated with the MS 1-2-9 character. Cytoplasmic effect can be tested critically by establishing the homozygous recessive condition of the gene which conditions the MS 1-2-9 character in a different or an unrelated cytoplasm. If all plants in the reconstituted populations prove to be male-fertile (normal), a cytoplasm-gene interaction will be demonstrated. On the other hand, recovery of male-sterile (MS 1-2-9 type) segregants in the reconstituted stocks will show that there is no interaction with the unrelated or new cytoplasm so far as the gene for MS 1-2-9 is concerned.

This test for cytoplasmic effect was conducted by using the inbred tester line, D&PL-14, as the contributor of unrelated cytoplasm. This stock was used because it was representative of one of the more widely grown varieties of cultivated American Upland cotton.

The same 10 F_1 (MS 1-2-9×D&PL-14) plants, which established the families reported on in the previous section, were reciprocally backcrossed to D&PL-14, i.e., D&PL-14 plants were used as females in one set of crosses (BC^2_1) and the F_1 plants were used as females in the reciprocal set (RBC^2_1). During the winter of 1959–60, 87 plants of BC^2_1, representing 9 families, and 50 plants of RBC^2_1, representing 5 families, were grown. Confirming expectations based on earlier assumptions regarding the inherit-

ance of the MS 1-2-9 character, all plants in both backcross populations were male-fertile, with one exception. The exceptional plant occurred in family 8 of the BC^2_1 population. Flowers on this plant appeared to be male-sterile and subsequent testing, by sibbing and outcrossing to the F_1 (MS 1-2-9×D&PL-14) stocks, proved that the gene which conditions the MS 1-2-9 character was involved; consequently, this anamalous plant was not used further in these experiments.

Theoretically, two genotypes were present in equal numbers in both the BC^2_1 and RBC^2_1 populations. Segregation for the MS 1-2-9 character was expected in the RBC^2_1 progenies since Texas 86 contributed their cytoplasm. However, segregation for the MS 1-2-9 character in the BC^2_1 progenies would have indicated that the D&PL-14 cytoplasm does not interact with the MS 1-2-9 genotype. To insure identification of the genotypes of the BC^2_1 population, regardless of the outcome of the progeny tests, as many as possible of the BC^2_1 plants were testcrossed to MS 1-2-9 stock, using the MS 1-2-9 stock as the female or cytoplasm-contributing parent. In actual practice MS 1-2-9 segregants from the F_2 of the MS 1-2-9×D&PL-14 cross were used as female parents in the testcrosses because the original MS 1-2-9 plant could not be expected to yield a sufficient quantity of seed for the testcrosses desired.

The recovery of one or more plants of the MS 1-2-9 type in selfed or testcrossed progeny of a BC^2_1 or RBC^2_1 plant would have been sufficient to demonstrate heterozygosity in the plant in question. To provide a high probability of obtaining such a plant all available seeds, up to 30 of the selfed progeny and 15 of the testcrosses, were planted in 6-ounce paper cups in the greenhouse in the spring of 1960. Approximately 3 weeks after emergence, 10 seedlings (less than 10 in 5) of each selfed progeny from plants in BC^2_1 and RBC^2_1 were transplanted to the field nursery and the remaining seedlings (averaging about 10) of each progeny were transplanted to 8-inch pots in the greenhouse. Similarly, about half the seedlings of each testcross were transplanted to the field and the other half to the greenhouse.

Flowers were scored for male sterility by the method described above. The test for cytoplasmic effect was of prime interest. Plants with the MS 1-2-9 (male-sterile) character appeared in progenies of BC^2_1 [D&PL-14 (female) × F_1 (MS 1-2-9 × D&PL-14)] demonstrating that there was no interaction between D&PL-14 cytoplasm and the MS 1-2-9 genotype.

A total of 72 BC^2_1 plants were progeny tested. Pooling the progeny segregation data from the greenhouse and the field, it was found that segregation for the MS 1-2-9 character occurred in 42 progenies while normal male fertility was found in 30 progenies ($P = .2–.1$ for goodness-of-fit, 1:1 ratio). Of the 74 testcross progenies which were grown from outcrosses of BC^2_1 plants to D&PL-14 (female), 30 segregated for the MS 1-2-9 character and 44 did not ($P = .2–.1$ for goodness-of-fit, 1:1 ratio). Segregations in the selfed and testcross progenies from each BC^2_1 plant were tabulated and analyzed according to the family to which the BC^2_1 plants belonged (see previous section). In all cases heterogeneity was insignificant, showing, as did the segregations reported in the previous section, that the families all may be considered members of one homogeneous population.

The data from the selfed progenies from RBC^2_1 [F_1 (MS 1-2-9×D&PL-14) (female) ×D&PL-14] plants serve only as further evidence of the monogenic nature of the inheritance of the MS 1-2-9 character. Segregation in RBC^2_1 was 18 male-fertile: 20 male-sterile, based on the scoring of plants in 38 selfed progenies.

Thus, while the data give abundant proof of monogenetic segregation in the backcrosses tested, they leave no doubt that there is no difference between race *latifolium* (Texas 86) and D&PL-14 with respect to the effect of their cytoplasm on the expression of the gene which conditions the MS 1-2-9 type.

All material tested previously had been grown in the greenhouse; so to supply critical data in the event of differential effect of the environment on the genotype ,each progeny was divided equally between the greenhouse and the field nursery. Whether the character was observed in the greenhouse or in the field, there was no difference in its appearance; furthermore, no significant differences in the segregation ratios were obtained under the two environmental conditions.

DISCUSSION

Because of the availability of additional data from the experiments designed to test for cytoplasmic effects, considerably more genetic data were accumulated than ordinarily would have been done in a study of the inheritance of a simple qualitative character. The results of the analyses of these extensive data leave no doubt that the male-sterile character, MS 1-2-9, investigated in these experiments is conditioned by a single pair of genes in the recessive condition. The gene in the heterozygous condition or in the homozygous dominant condition confers normal or regular fertility. This new gene, apparently the first to confer complete male sterility in cotton, is designated ms_2, the symbol *ms-1* having been assigned to a simply inherited gene which conditions partial male sterility, recently reported by Justus and Leinweber (6).

The D&PL-14 parent of the original cross in which the MS 1-2-9 character was discovered had been inbred at this station for more than 15 years and, though thousands of plants of this stock have been self-pollinated by hand, no such male-sterile character has been found. Therefore, it is assumed that ms_2 must have been carried in and contributed by the other parent of the cross, a stock known as Texas 86, a member of *G. hirsutum,* race *latifolium.* Being short-day in flowering habit, scarcely more than a dozen plants of Texas 86 have been observed in the flowering stage—these, of course, in the greenhouse. Considering the simple genetics of the character, one might expect to recover it from a small population. However, the character has not been expressed in the maintenance progeny of Texas 86 or in several testcrosses that have been made to the original MS 1-2-9 stock. Following this line of reasoning, it is also curious that only one completely male-sterile plant was found in the original F_2 population of more than 1,000. Photoperiodic response obviously was a factor but, based on reasonable probability, the number of plants that set fruit in this population was such that more than one plant of the MS 1-2-9 type should have been produced. A system of fertility-modifying genes operating in Texas 86 and segregating in the F_2 may well have been involved; however, until more information is obtained, it is equally reasonable to postulate a gene mutation as the origin and to assume that hybridity increases mutability at the ms_2

locus. The latter phenomenon would account for the anomalous male-sterile plant found in BC^2_1. This male-sterile, which proved to be of the ms_2 ms_2 genotype, was omitted from the analysis of the other 86 plants in the population, which were phenotypically male-fertile and, when progeny tested, proved to have been segregating Ms_2 Ms_2 and Ms_2 ms_2 in approximately equal numbers and in accordance with theoretical expectations. We are at a loss for any other biological explanation of the presence of a ms_2 ms_2 plant in this population.

In the discussion above it has been assumed that only one locus governs the MS 1-2-9 expression. As an alternative explanation, it could be postulated that duplicate loci are involved, i.e., Texas 86 could have carried a recessive gene for male sterility at one locus and D&PL-14 could have carried a similar gene at another locus. Then when these stocks were crossed the male-sterile plant (MS 1-2-9) recovered in F_2 could have been a recombinant homozygous at both loci. However, four sister plants were selfed and no male steriles were observed in their progeny. Progeny tests on such a small number of sister plants, however, do not furnish proof that duplicate factors were not present in MS 1-2-9. More conclusive evidence can be obtained by growing a similar F_2 population under short-day conditions where segregation for male sterility can be observed independent of photoperiodic response.

MS 1-2-9 should prove to be useful to cotton geneticists as a new character and a special "tool." Since the character is a completely male-sterile, it must be maintained by vegetative propagation of ms_2 ms_2 plants or by seed in the heterozygous condition. Being discrete and readily identifiable, the MS 1-2-9 character will be especially useful in the current linkage and chromosome-mapping programs here and at other stations.

The ms_2 gene has no apparent deleterious effects on other characters of the cotton plant. In segregating populations Ms_2 ms_2 plants are indistinguishable from Ms_2 Ms_2 plants in respect to plant type, boll size, and other agronomic characters, and when ms_2 ms_2 plants are adequately pollinated they are indistinguishable from their male-fertile siblings in these respects. In fact the MS 1-2-9 stock, when copiously pollinated with functional pollen, compares favorably in vigor and productivity with agricultural varieties of American Upland cotton grown in the same greenhouse or field nursery.

Important though the MS 1-2-9 character may be as a genetic stock, in its present form it cannot readily be used in a program for commercial production of the hybrid cottonseed. Possibly schemes, such as those proposed for sorghum by Stephens (9) and for barley by Wiebe (11), might be devised. Research along these lines should not be ignored or discouraged. However, as Richmond (7) pointed out some years ago, the main hope for successful hybrid cottonseed production on a commercial scale probably lies in the discovery and development of a functional system in which male-sterility genes interact differentially with different cytoplasms. (Reference here to hybrid seed is in terms of a controlled hybrid between definite parental lines in which the percentage of F_1 seed is 95% or higher.)

The attempt to discover a cytoplasmic interaction with ms_2 reported in this paper was unsuccessful. While the unrelated cytoplasm used was contributed by a stock developed from a well-known agricultural variety of Upland cotton there is no assurance that this stock represented the cytoplasm of all of the cultivated varieties. Furthermore, potential sources of new or untested cytoplasm are afforded by the races of *hirsutum,* various primitive Uplands, and the so-called foreign Uplands, as well as by the wild species of *Gossypium.* Additional experiments designed to test a wide range of cotton stocks for cytoplasmic-genetic interaction involving ms_2 are now in progress.

SUMMARY

A male-sterile plant was discovered in the F_2 generation of a cross of Texas 86 (a short-day stock of *Gossypium hirsutum,* race *latifolium*) and D&PL-14 (a day-neutral selfed line developed from a cultivated variety of American Upland cotton). This cross was one of several made between the races of *G. hirsutum* and D&PL-14 as part of a systematic search for cytoplasmic-genetic male sterility.

Genetic analysis of the male-sterile character, designated as MS 1-2-9, showed that the male-sterile expression is conditioned by homozygous recessive alleles at a single locus. This new gene has been assigned the symbol ms_2. Apparently this is the first published report of complete male sterility in cotton.

The cytoplasms of the two parents, Texas 86 and D&PL-14, were evaluated for possible interaction with the ms_2 gene. No interaction was found between the nuclear and the cytoplasmic systems of the two stocks.

Speculation on the origin and location of the ms_2 gene and the factors and processes leading to the production and discovery of the male-sterile character involved a discussion of *(1)* the confounding influence of photoperiodism on segregation, *(2)* mutation induced or accelerated by hybridity and, *(3)* the possibility of duplicate factor inheritance.

Because of the absence of a cytoplasmic interaction or effect, the practical value of the male-sterile character is believed to be limited.

REFERENCES CITED

1. BEASLEY, J. O. The production of polyploids in *Gossypium.* J. Hered. 31:39–48. 1940.
2. ————————. The origin of American tetraploid *Gossypium* species. Am. Nat. 74:285–286. 1940.
3. ————————, and BROWN, META S. Asynaptic *Gossypium* plants and their polyploids. J. Agr. Res. 65:421–427. 1942.
4. HUTCHINSON, J. B. Intraspecific differentiation in *Gossypium hirsutum.* Heredity 5:161–193. 1951.
5. JONES, D. F. The cytoplasmic separation of species. Natl. Acad. of Sci. 37:408–410. 1951.
6. JUSTUS, NORMAN, and LEINWEBER, C. L. A heritable partially male sterile character in cotton. J. Hered. 51:191–192. 1960.
7. RICHMOND, T. R. Procedures and methods of cotton breeding with special reference to American cultivated species. Advances in Gen. 4:213–245. Academic Press. 1951.
8. ROGERS, J. S., and EDWARDS, J. R. The utilization of cytoplasmic male-sterile inbreds in the production of corn hybrids. Agron. J. 44:8–13. 1952.
9. STEPHENS, J. C. Male sterility in sorghum: its possible utilization in the production of hybrid seed. J. Am. Soc. Agron. 29: 690–696. 1937.
10. ————————, and HOLLAND, R. F. Cytoplasmic male-sterility for hybrid sorghum seed production. Agron. J. 46:20–23. 1954.
11. WIEBE, G. A. A proposal for hybrid barley. Agron. J. 52: 181–182. 1960.