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Some Effects of Genes, Cytoplasm, and Environment on Male Sterility of Cotton (*Gossypium*)[1]

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ABSTRACT

Male sterility in Upland cotton (*Gossypium hirsutum* L.) has been produced by mutant genes, cytoplasm from other species, environmental stress, and chemical treatment. Genetic sterilities vary in expression from complete sterility due to a single dominant gene to partial sterility due to recessive genes. The cytoplasmic-genetic sterile strains with cytoplasm from either *G. anomalum* Wawra & Peyr. or *G. arboreum* L. vary in response to genes, cytoplasm, and the external environment. Daily maximum temperature 15 to 16 days before anthesis affects sterility more than any other aspect of the external environment. A-lines and B-lines have been produced for pure-breeding sterile strains, one set for *G. anomalum* cytoplasm, the other for *G. arboreum* cytoplasm. All of the commercial strains of *G. barbadense* L. tested with these two sterilities produced completely fertile F_1 hybrids. The commercial cotton crop is largely self-pollinated. The most critical problem for production of hybrid cotton appears to be finding some way to get the male-sterile flowers pollinated.

Additional index words: **Hybrids, Genetics, Pollination.**

FOR years plant breeders have tried to develop other commercially successful hybrid crop plants by the methods used for producing hybrid corn and hybrid sorghum. Growers of many horticultural crops can choose either standard varieties or hybrids. However, except for corn (*Zea mays* L.) and sorghum (*Sorghum bicolor* (L.) Moench), hybrids do not yet produce a high percentage of any field crop grown on a large scale.

During the past 20 years male-sterile cotton has been produced by several different techniques. At Stoneville we began to make progress with the male sterility studies after we realized that we were working with cotton, not corn or sorghum. A comprehensive report on these studies may be valuable to workers with other crops if it either presents useful information or emphasizes the fact that each crop species has its own biological system which determines its possibilities and limits.

Present knowledge of male sterility in cotton comes from experiments and observations carried out over many years, by many people, in cotton-growing areas throughout the world. At Stoneville the various aspects of the problem were studied by different experiments carried out in different years. Nevertheless, these different aspects fit together to form a clear picture.

GENETIC MALE STERILITY

Not all of the genes known to produce partial or complete male sterility in cotton have been reported in the literature. New mutants or combinations of genes capable of producing sterility will doubtless continue to occur in a crop so important and so widely grown as cotton.

The first published report which assigned a gene symbol to a genetic male sterility was by Justus and Leinweber (23) in 1960. A completely recessive gene (ms_1) produces partial or complete male sterility when it is homozygous in Upland cotton. The original plant was monosomic, but its ms_1ms_1 derivatives had a normal chromosome number. The monosomic condition probably permitted expression and discovery of the recessive gene.

A second sterility due to a single recessive gene (ms_2) was described in 1961 by Richmond and Kohel (53). Plants homozygous for the gene are completely male-sterile. The pollen grains lack the spiny exine of normal cotton pollen, and the vacuole-like contents suggest a greatly reduced amount of protoplasm (51).

Justus, Meyer, and Roux (24) reported a third male sterility of cotton due to a recessive gene (ms_3). Like ms_1ms_1, the homozygous ms_3ms_3 does not always produce complete male sterility in Upland cotton. The percentage of sterile anthers has been consistently higher at Stoneville for ms_3ms_3 plants than for ms_1ms_1 plants flowering in the same field on the same date.

The only dominant male sterility gene so far reported for cotton is Ms_4 (1). Upland cotton plants with the Ms_4 gene produce filaments with only very rudimentary anthers, or sometimes no anthers at all. The sterility is complete.

Male sterility isolated from derivatives of *G. armourianum* $\times$ *G. hirsutum* was found to be under the control of a single recessive gene, and was not affected by cytoplasm (54).

Loe and Sarvella (32) observed a single plant of Upland cotton in which both male and female sterility were complete. Apparently meiotic abnormalities were responsible. Since no test crosses could be made, the inheritance of this sterility could not be determined and no gene symbols were assigned.

Test crosses between ms_1, ms_2, *and* ms_3 stocks, using partially fertile ms_1 and ms_3 as male parents, produced F_1 progenies with no significant difference in fertility from M8, the fertile Upland cotton used as a check (Table 1). From testcrosses of both ms_1 and ms_3 with the dominant Ms_4 sterility, half the plants were completely sterile and the other half as fertile as M8. No testcross has been made between ms_2 and Ms_4; since both parents would have to be heterozygotes, no true F_1 population could be obtained, and relatively large segregating populations would have to be studied in order to obtain enough data for even preliminary conclusions. Obviously, ms_1 and ms_3 differ from each other and from ms_2 and Ms_4. Probably all four of the mutant genes have different positions and functions.

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Table 1. 1968 flower scores for testcrosses involving six different male-sterile strains of cotton: Justus (ms_1), Texas (ms_2), Roux (ms_3), Fisher (Ms_4), *G. arboreum* cytoplasm (A_2), and *G. anomalum* cytoplasm (B_1).

Genotype	Cytoplasm from Gossypium species	Mean flower score*
M8, Check	hirsutum	3.84 AB
A_2 male-sterile A-line	arboreum	0.60 F
A_2 male-fertile B-line	hirsutum	2.52 D
B_1 male-sterile A-line	anomalum	0.98 F
B_1 male-fertile B-line	hirsutum	3.19 C
$ms_1 ms_1$	hirsutum	1.53 E
A_2 ms_1	arboreum	3.39 ABC
ms_1 A_2	hirsutum	3.45 ABC
B_1 ms_1	anomalum	3.59 ABC
ms_1 B_1	hirsutum	3.55 ABC
Ms_2 ms_2	hirsutum	3.91 A
ms_2 ms_2	hirsutum	0 G
A_2 Ms_2 + A_2 ms_2	arboreum	3.49 ABC
ms_2 A_2	hirsutum	3.75 ABC
B_1 Ms_2 + B_1 ms_2	anomalum	3.65 ABC
ms_2 B_1	hirsutum	3.70 ABC
ms_3 ms_3	hirsutum	0.93 F
A_2 ms_3	arboreum	1.77 E
ms_3 A_2	hirsutum	3.66 ABC
B_1 ms_3	anomalum	1.70 E
Ms_3 B_1	hirsutum	3.51 ABC
ms_3 Ms_3	hirsutum	3.86 AB
ms_2 ms_1	hirsutum	3.66 ABC
ms_1 ms_3	hirsutum	3.58 ABC
ms_2 ms_3	hirsutum	3.38 BC
Ms_4 ms_4	hirsutum	0 G
ms_4 ms_4	hirsutum	3.82 AB
Ms_4 ms_1	hirsutum	0 G
ms_4 ms_1	hirsutum	3.60 ABC
Ms_4 ms_3	hirsutum	0 G
ms_4 ms_3	hirsutum	3.82 AB

* Based on flower scores 0 (no fertile anthers) to 4 (100% fertile anthers), calculated from totals for 6 weeks when all progeny rows had flowers and were scored. Each week was considered a replication in the analysis of variance. A_2 and B_1 are genome symbols, not gene notations. Mean scores followed by the same letter do not differ significantly at the .01 level of probability according to Duncan's multiple range test.

CYTOPLASMIC-GENETIC MALE STERILITY

Meyer and Meyer (37, 42) reported sterility in derivatives of cotton species hybrids which combine the cytoplasm of one species with genes and chromosomes of another. The first male sterility of cotton definitely known to be affected by cytoplasm was developed in the diploid Asiatic species *G. arboreum* L. When the *G. arboreum* genome is transferred into *G. anomalum* Wawra & Peyr. cytoplasm by repeated back-crossing, the staminal column bears petaloids instead of anthers. Petaloids are produced each generation if *G. arboreum* pollen is used (50), but *G. anomalum* pollen restores normal anther structure (J. Meyer, personal communication).

Two different pure-breeding male-sterile strains have been isolated from interspecific hybrids with Upland cotton (*G. hirsutum* L.), the species which produces nearly all of the commercial cotton crop. The history and gene-cytoplasm interactions of the strain with *G. anomalum* cytoplasm are described by Meyer and Meyer (42).

In the strain with *G. arboreum* cytoplasm the sterility appears to be due to two genes from diploid species, rather than to one gene, as in the material from *G. anomalum*. The number of genes has never been determined with certainty in the *G. arboreum* material, since all of the heterozygotes vary so much in response to environmental fluctuations that no clearcut distinction can be made between classes of plants in segregating populations. The two-gene estimate is based on the number of progeny rows from F_2 populations which produce only sterile plants, and on the number of highly sterile plants in segregating rows. It has never been feasible to grow enough F_3 progeny rows to prove that the *G. arboreum* sterility is actually due primarily to two genes interacting with *G. arboreum* cytoplasm. Nevertheless, pure-breeding male-sterile lines have been isolated from heterozygous material at several stages of the backcrossing program, a fertile B-line with the genes for sterility homozygous in *G. hirsutum* cytoplasm has been developed, and small-scale tests have shown it is easy to move the sterility into commercial varieties by backcrossing.

Although they differ in levels of sterility, the overall gene-cytoplasm-environment interactions are very similar in both the strains derived from (*G. anomalum* Wawra and Peyr $\times$ *G. thurberi* Todaro) $\times$ *G. hirsutum* L. and those from (*G. arboreum* L. $\times$ *G. thurberi* Todaro) $\times$ *G. hirsutum* L. In either case, a very high level of sterility results from cytoplasm from a diploid species, plus the proper genes for sterility, plus maximum daily temperature above 32C (90F). Fertility increases as we add the G. hirsutum alleles of the sterile genes, *G. hirsutum* cytoplasm, or unusually low field temperatures. All of the several *G. barbadense* L. varieties used in testcrosses produced F_1 populations completely male-fertile under all field temperatures which occurred during two growing seasons at Stoneville. Crosses with the *G. hirsutum* Ak Djura Red also produced fertile F_1 plants, but in subsequent generations all of the plants became partially sterile following hot, dry weather. Red plants from the Ak Djura hybrids backcrossed to homozygous sterile plants were significantly more fertile than green plants. Kammacher, Poisson, and Schwendiman (25) found linkage between ms_3 and R_1, a gene for red plant color.

Testcrosses grown in 1968 included combinations between the four available genetic sterilities and the two cytoplasmically controlled sterilities (Table 1). As noted earlier, ms_1, ms_2, ms_3 and Ms_4 appear to be independent of each other. When ms_1 and ms_2 were crossed with either of the cytoplasmic sterilities, progenies were highly fertile; they did not differ significantly in fertility from the M8 check. This occurred both with the two cytoplasms from diploid species and with cytoplasm from Upland cotton. Kohel and Richmond (28) found no difference in fertility of cytoplasms from 22 different stocks of Upland cotton, in crosses with Ms_2 ms_2.

The situation was quite different for the Roux sterility gene ms_3. The two F_1 populations with *G. hirsutum* cytoplasm were highly fertile. On the other hand, the F_1 populations with *G. arboreum* or *G. anomalum* cytoplasm were partially sterile, although significantly more fertile than either parent.

One "wild" allele of ms_1, ms_2, ms_3, or the genes present in the cytoplasmically controlled sterilities is sufficient for fertility if it acts in *G. hirsutum* cytoplasm at normal temperatures. One "wild" allele is also enough for fertility with ms_1 and ms_2 in the two diploid cytoplasms studied. However, the "wild" alleles of ms_3 and of the sterility genes from *G. arboreum* (A_2) and *G. anomalum* (B_1) are not fully effective as heterozygotes in cytoplasm from the A_2 and B_1 diploid species. Fertility is increased significantly ($P=0.01$) in the double heterozygotes of ms_3 with the two cytoplasmic steriles, but it is still low. The available data are a solid basis for concluding that cytoplasm affects the expression of the ms_3, A_2, and B_1 sterility genes.

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ENVIRONMENTAL EFFECTS ON MALE STERILITY

Almost any variety of cotton will produce occasional sterile anthers, or even entirely male-sterile flowers. Usually there are enough fertile anthers remaining so that the crop is not noticeably affected.

Crazy-top of cotton has sometimes been a serious disorder in Arizona. According to King and Loomis (27), it was first noticed in 1918. Cook described the disease in 1924 and named it acromania. The name comes from the distorted flowers, leaves, and branches; the yield damage comes from the indehiscent anthers of the affected plants, which also shed their flower buds and young bolls. It is most severe on soils where water penetration is difficult (58). The disease damages Upland more than Pima cotton (8). Affected plants sometimes recover under late-season conditions and set a fair crop of bolls in the tops of the plants.

Ever since work began with sterile cottons at Stoneville, the people working with the problem have commented on the way that all of the sterility plots in the area (some of them 2 or 3 miles apart) would "switch" at the same time. This was particularly noticeable one year when studies were being carried out with gametocides, genetic male sterilities, and a large assortment of interspecific hybrids, some of them the sources of the cytoplasmically controlled sterilities isolated later. Both the C-9 cytoplasmic-genetic male sterility (42) and the weaker male sterility associated with the External Ovule abnormality (40) increase sterility with higher daily maximum temperatures. In both cases correlation is significant at the 0.01 level between percent sterile anthers and maximum temperature 15-16 days before anthesis. ($r = 0.63$ for C-9 and 0.47 for EO). The "switch" is large enough and predictable enough so that crossing and selfing can be planned 2 weeks in advance for the most sensitive sterilities like ms_1, ms_3, and the heterozygotes in the cytoplasmic male sterile plots. In general, homozygous sterile plants produce nearly 100% sterile anthers if maximum temperatures go above 32C (90F) each day. Near 38C (100F) maximum temperature the heterozygotes also become completely sterile if they have cytoplasm from a diploid species. As maximum temperatures increase above 38C (100F), more and more sterile anthers appear on both the "fertile" plants with *G. arboreum* or *G. anomalum* cytoplasm and the B-lines for both cytoplasmic sterilities (genetically "sterile" plants with *G. hirsutum* cytoplasm). The time interval — 15 to 16 days — between temperature and its effect is the same for all of the strains studied at Stoneville.

Relative humidity has scarcely been studied in connection with male sterility of cotton. It appears to have more effect on whether anthers develop than on their fertility. Very high relative humidity about a month before anthesis prevents expression of the "multiple carpel" abnormality (41). For both normal *G. hirsutum* and the "external ovule" abnormality, anther number was significantly and positively correlated ($r=0.43^{**}$ for M8, 0.49^{**} for F_1 (EO $\times$ M8), 0.27^{*} for EO) with mean relative humidity 22-23 days before anthesis (40).

Sarvella (57) found that sterility in male sterile stocks of cotton showed negative correlations with wind velocity, pan evaporation, and heliometer in the period 2 to 3 weeks before anthesis, while maximum and minimum temperatures showed positive correlations. (The contradiction with Sarvella's paper is only apparent. Correlations based on sterility scores will be reversed from those based on percentage of sterile anthers.) Sarvella's correlations with high temperatures 17 to 20 days before flowering probably reflect the lower temperatures at State College, which would cause slower development than for plants at Stoneville where the interval is 15 to 16 days.

CHEMICAL OR PHYSICAL MODIFICATION OF ANTHER FERTILITY

In 1957 Eaton (9) reported that sodium α-dichloroisobutyrate (FW-450) could produce male sterility in cotton. During 1957 and 1958 extensive field trials with FW-450 were carried out across the cotton belt. Results of these tests constitute a large proportion of the papers presented at the XI Cotton Improvement Conference in 1958. Some of the workers have published their data in journals (47, 52, 69).

Male sterility which continues throughout the growing season requires repeated applications of FW-450 (10). Roux and Chirinian (55) found that sterility could be maintained by an initial spray of 1% FW-450, followed at 3-week intervals by sprays of 0.5% FW-450. Best results were obtained when the entire plant was wet with the spray.

A measurable amount of absorption of labeled FW-450 occurred within 15 min after application, and absorption was complete within 22 hours after treatment (36). The compound moved more readily into young leaves and flower buds than into mature leaves; also, it moved upward from the point of application more readily than downward. After it reached the flowers, FW-450 selectively accumulated in the anthers. Although the timing apparently varied somewhat in response to growth rate of the plants, the first male-sterile flowers appeared 2 to 3 weeks after treatment; the effect lasted 2 to 3 weeks, during which time a graph of percentage of sterile flowers would make a symmetrical peak.

Scott (58, 60) found that the FW-450 combines with co-enzyme A; it competes with pantoate for a site on the enzyme of pantothenate synthesis. Adding D-ribose or other precursors of coenzyme A reversed the effect of the gametocide. Coenzyme A also seems to be involved in the indehiscent anther of the "crazy-top" cotton discussed earlier. Choline chloride or urea applied to the plants reversed the crazy top symptoms more completely than did the other effective chemicals known to be involved in coenzyme A function — pantothenic acid, adenine, L-lysine, indole-3-acetic acid, napthalene acetic acid, fructose, and glucose. Conversion of nondehiscent anthers to anthers that release pollen occurs within 2 weeks after either chemical is applied (61).

Male sterility of cotton has also been produced by dalapon, a chemical closely related to FW-450, and by maleic hydrazide (38). The maleic hydrazide produced highly abnormal flowers at concentrations effective for male-sterility. Maleic hydrazide sprayed in combination with FW-450 reduced both the leaf burn and the male sterility below the level obtained by treatment with FW-450 alone (39).

A much increased percentage of outcrossing occurred with cotton plants grown from irradiated seed. Con-

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stantin (6) concluded that radiation treatment, which probably increased pollen sterility, was impractical. The severe decrease in seed-cotton yield and seedling survival more than offset any increase from outcrossing.

DISCUSSION

Production of fertile anthers must be both complex and sensitive. Mutant genes can cause development of flowers with anthers replaced by either petaloid (37, 50) or carpelloid (41) structures. A single Ms_4 gene in the genome allows filaments to develop, but not normal, fertile anthers. When ms_2 is homozygous, the anthers begin normally, but no functional pollen is produced. Other mutant genes produce partial to complete male sterility in cotton. Many of the genes produce variable effects in response to either environmental fluctuations or the different cytoplasms introduced by reciprocal crossing. Within Upland cotton, varieties differ in the ease by which sterility can be brought about by chemical treatment, by adverse environment, or by introduction of genes or cytoplasm from other species of cotton.

There is very great variability within and between the various treatments which can produce male sterility in cotton. Nevertheless, one particularly vulnerable stage of development stands out in nearly all of them. We must ignore the two genes which produce complete male sterility, ms_2 and Ms_4; their absolute effect makes it impossible to pinpoint their times or thresholds of action. The other agents of sterility studied at Stoneville — the genes ms_1 and ms_3, the cytoplasmically controlled sterilities, treatment with FW-450, high temperatures — all have sensitive periods a little more than 2 weeks before anthesis. Let us consider too Scott's findings that the same chemicals can reverse the effects of either FW-450 or the stress conditions which produce "crazy-top," and that the effective time to spray is approximately 2 weeks before flowering. Now let us add the lower susceptibility of *G. barbadense* Pima to "crazy-top" and the general ability of *G. barbadense* varieties to act as fertility restorers for cytoplasmically controlled sterility. The overall picture is of a process which occurs approximately 2 weeks before anthesis and which involves a labile substance. High temperatures or water stress deplete the substance below the critical level. Its destruction or depletion can be buffered or prevented by some cytoplasms, by some genes (particularly those from *G. barbadense*), by chemical substances associated with coenzyme A, or by cool, moist growing conditions.

For cotton we have a sensitive stage of anther development accessible to manipulation by physical means, chemicals, genes, or cytoplasm. Only a few treatments, compounds, genes, and foreign cytoplasms have been tested in experiments with Upland cotton. Nevertheless, we already know that male sterile cotton can be produced, or in some cases made fertile, by all of these means. Virtually all of the studies on male sterile cotton have been either terminated or greatly reduced. This is because their real objective is not just to produce male sterile cotton (which we can do in several ways), but rather to find a practical way to produce hybrid cotton.

We have considerable information on the amount of heterosis for yield from experimental cotton hybrids, either within Upland cotton or between species (2, 4, 5, 7, 11, 12, 13, 16, 17, 18, 20, 21, 22, 26, 31, 34, 43, 44, 46, 48, 63, 64, 67, 68, 70). Many of the reports agree on a maximum heterosis for yield of between 25 and 35%.

Pollination is the major unsolved problem which prevents the development of hybrid cotton on a commercial scale. Even though some outcrossing does occur, even though insects do pollinate some cotton flowers, most of the North American Upland cotton crop is self-pollinated as the flowers open. Pollination of even 50% of the flowers would probably be insufficient for economic seed production. Sappenfield (56) found 13.6% to be the average percent of natural crossing for a 6-year period in Missouri. Berninger (3) reported 28 to 44% natural crossing for Tikem. Simpson (62) has perhaps the most extensive published data on natural crossing of cotton; the range of percentages for individual plants is from 0 to 90% natural crossing. Most natural crossing occurs in areas where cotton is not a major crop, where small fields, woodlots, and hedgerows are common, and where spraying with insecticides is either infrequent or carefully timed to avoid killing the bee population. On the other hand, where fields are large, agriculture is intensive, and noxious insect control is nearly complete, percentage of outcrossing drops to a very low figure. It was below 1% for the 1967 plots where outcrossing was measured in the Mississippi Delta (W. R. Meredith, Jr., personal communication).

Thies (66) reported that bumblebees were responsible for most of the cross pollination of cotton at Stillwater, Okla. Green (14) found that honeybees generally limit their feeding to leaf nectaries. On the other hand, Peebles (49) and McGregor, Rhyne, Worley, and Todd (35) found honeybees to be effective pollinating agents for Pima cotton. Both the study by Stephens and Finkner (65) and that by Harvey and Weaver (19) emphasize the importance of maintaining an effective bee population in order to get high levels of natural crossing. Harvey and Weaver found that selection could increase a variety's susceptibility to natural crossing; they found selection for stigma length to be the most effective means for increasing natural crossing. In view of the importance of showy flowers for increasing natural crossing (15), the large yellow petals of some *G. barbadense* varieties might be an important characteristic for making cotton flowers attractive to bees. Perhaps some progress could be made by working with the bees. Some encouraging preliminary results have been obtained in pollinating alfalfa (*Medicago sativa* L.) in New York with leaf-cutting bees (*Megachile rotundata*) imported from Utah (30). Nye and Mackenson (33, 45) have been able to breed honeybees with an increased preference for alfalfa pollen. Lederhouse, Caron, and Morse (29) found that sugar concentration of the nectar usually determined the particular floral source exploited by honeybees. They found that male onion (*Allium cepa* L.) flowers produced a nectar with about 10% more sugar than infertile or female flowers; they recommended a planting regime with two-seed (female) rows alternate with one interrupted row of male plants.

Possibly the problem of cotton pollination could be solved by breeding cotton attractive to bees, by

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breeding bees attracted to cotton flowers, or by an overall crop management, which includes maintaining colonies of bees in the field and protecting them from insecticides. However, no comprehensive studies have been carried out to determine whether insects could handle the job of producing hybrid cotton on a commercial scale.

We now know several ways to produce male sterile cotton and to restore its fertility. If we are going to have hybrid cotton, the basic plant work has been done, but the bee breeders and their bees still have a lot of work to do.

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