The biology of a male sterile mutant in wheat (Triticum aestivum L.)
by Duane Everett Falk

Abstract:
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Meiosis was normal in the microspores, but the pollen of male sterile plants degenerated before the mitotic divisions occurred. Aneuploidy was not associated with the male sterility. The cytoplasm did not influence the expression of the male sterility.

Heterozygous plants were completely male fertile and exhibited no detrimental effects from the male sterile alleles.

Four times as much crossed seed was produced per unit of time on male sterile plants as compared to emasculated fertile plants.

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THE BIOLOGY OF A MALE STERILE MUTANT
IN WHEAT (Triticum aestivum L.)

by

DUANE EVERETT FALK

A thesis submitted in partial fulfillment
of the requirements for the degree

of

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in

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Chairman, Examining Committee

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ABSTRACT

A spontaneous male sterile mutant in the F_3 generation of a 'Cheyenne' winter wheat (<u>Triticum</u> <u>aestivum</u> L.) backcross population was controlled by two coupled, duplicate, recessive genes.

The anthers of the male sterile plants were reduced in size and produced no viable pollen. Ovule fertility was normal.

Meiosis was normal in the microspores, but the pollen of male sterile plants degenerated before the mitotic divisions occurred. Aneuploidy was not associated with the male sterility. The cytoplasm did not influence the expression of the male sterility.

Heterozygous plants were completely male fertile and exhibited no detrimental effects from the male sterile alleles.

Four times as much crossed seed was produced per unit of time on male sterile plants as compared to emasculated fertile plants.

INTRODUCTION

The normal mode of reproduction in hermaphroditic, self-polli-

nated plant species leads to the evolution of heterogeneous, homozygous

populations. The amount of genetic variation within such populations

is finite. The 50% decrease in heterozygosity and the rapid approach

to homozygosity limit the recombination potential and decrease the

chance of superior genotypes emerging.

Genetic diversity is introduced into self-pollinated species by

spontaneous mutation and by natural outcrossing. Both of these occur-

rences are relatively infrequent and do not provide sufficient genetic

variation for efficient, continued cultivar improvement.

Artificially induced outcrossing has been used extensively to

combine potentially useful genetic variations in such numbers that

selection within segregating generations is practical. Artificially

created hybrids form the basis for most plant breeding programs in self-

pollinated crops.

Hand emasculation, the oldest and most widely utilized procedure

of producing crossed seeds, is laborious and time-consuming. Alter-

native methods such as chilling, chemical gametocides, and cytoplasmic

and genetic male sterilities have been employed to facilitate artifi-

cial crossing.

Genetic male sterility appears to offer the best combination of

efficiency, reliability, and ease of management to facilitate crossing

in wheat. It also has the added benefit of maintaining heterozygosity in segregating populations. Upon removal of the allele for male sterility, populations return to their normal self-pollinating, inbreeding status.

The discovery of a male sterile plant in a winter wheat population led to the initiation of this thesis research. A preliminary investigation indicated that the male sterility was genetic in nature. The objectives of this investigation were to: 1) examine the morphological characteristics; 2) study the cytological nature; and 3) determine the inheritance of the male sterile mutant involved.

LITERATURE REVIEW

Occurrence of Genetic Male Sterility

History

Male sterility as a result of a genetically controlled disruption.

of microsporogenesis occurs in many plant species (18,23). As early as

1915, Crane (8) described tomatoes (Lycopersicon esculentum L.) which

failed to set fruit normally but upon hand pollination produced fruits

with an abundance of seed. This male sterility was later found to be

due to a single recessive gene (29). Similar phenomena in which plants

failed to produce viable pollen but did set seed when cross-pollinated

were first observed in corn (Zea mays L.) in 1921 (13), in barley

(Hordeum vulgare L.) in 1940 (45), and in hexaploid wheat (Triticum

aestivum L.) in 1959 (32).

Gene Frequency and Numbers

Rick (37) found genetic male sterile mutants to occur spontane-

ously in 0.005% of the 'San Marzano' tomato plants he examined. Hockett

and Eslick (22) determined the frequency of naturally occurring genetic

male sterility in barley to be 0.0025%.

In separate studies, Rick (36,37) found 5% and 8%, respectively,

of the "unfruitful" tomato plants examined to be genetic male steriles.

Hockett and Eslick (22) found that 10% of the barley plants identified

as "highly sterile" in the field were genetic male steriles. This

figure was later corroborated by Foster (16).

While the majority of the male sterile genes described have occurred spontaneously, some have also been induced by mutagens. Fossati and Ingold (14) reported that one of three hundred M_2 rows of the winter wheat variety 'Probus' treated with X-rays segregated for genetic male sterility. Franckowiak et al. (17) induced ten genetic male sterile mutants with ethyl methane-sulfonate (EMS) in a population of 45,000 wheat plants. The ms_3 gene in barley was induced by acetone treatment (21). Foster (16) found that 17% of the "sterile" plants isolated from the M_3 of a barley population treated with diethylsulfate (DES) were genetic male steriles.

Yamashita (59) isolated more than 250 genetic male sterile mutant barleys from 12,240 M_1 plants treated with gamma rays and the chemical mutagens—EMS, ethyleneimine (EI), and nitrosomethylurea (NMU). Approximately two-thirds of these mutants were completely male sterile, and all except one of them were controlled by a single recessive gene.

Since 1915, eighteen different male sterile genes have been identified in tomatoes (38); forty-four in corn (56); and twenty-six in barley (20). Eight reports of genetic male sterility have been made in wheat (3,15,17,24,27,30,32,43). Two of these mutants are allelic (10).

Rick (37), Hockett and Eslick (22) and Foster (16) maintain that spontaneous genetic male sterile mutants can be obtained in any culti-var of the crops they studied, providing that sufficiently large popu-

lations are examined. Gottschalk and Kaul (18) concluded that male sterile genes are probably present in the genomes of all flowering plants, regardless of the taxa. Genetic male sterility has been decribed in more than forty-eight plant species in twelve families. Gottschalk and Kaul (18) cite evidence that some of these genes are homologous and represent similar anomolies in different species.

Morphology of Genetic Male Sterile Plants

General Morphology

Genetic male sterile plants are usually indistinguishable from their fertile siblings and normal fertile cultivars until the time of flowering (18,27). Male sterility is easily recognizable at maturity in self-pollinated plants by a reduced seed set (27,32,45) or fruit production (8,28,37) resulting from the failure of the plants to produce viable pollen.

The first indication of male sterility that Crane (8) noticed in tomatoes was that two F_2 plants had failed to set fruit. The anthers of these plants appeared to be "reflexed and somewhat aborted" and devoid of pollen. Lesley and Lesley (28) noted that male sterile tomato plants were often conspicuous by their excessive vegetative vigor and upright habit.

Eyster (13) reported that R. A. Emerson first detected genetic male sterility in corn by a failure of the anthers to extrude. The

sterile spikelets usually remained flattened against the rachis to give a characteristic tassel appearance. Such plants were easily detected at normal pollination time.

Suneson (45) identified male sterile barley plants by widely-opened glumes. This condition persisted for several days after flowering. The florets were observed to close upon pollination. Hockett and Eslick (21) reported that swelling of the unfertilized ovary caused barley flowers to remain open for seven to eight days after normal flowering. The lodicules open the flower briefly at anthesis but close soon after. The flowers close when the unfertilized ovary deteriorates. The spikes of male sterile plants also tended to remain more erect due to a reduction in seed set. Male sterile barley if often infected with ergot (Claviceps purpurea (Fr.) Tul.) under Montana conditions (12). Male sterile plants, in general, usually remain green and continue vegetative development longer than their fertile siblings (18).

Male sterile wheat, like barley, is characterized by opened florets at flowering and a reduced seed set (5,6,15,27,32). Male sterile durum wheat (Triticum durum Desf.) plants tended to head earlier than fertile plants (5). Suneson (49), however, observed the male sterile hexaploid wheat from A. T. Pugsley (32) to be up to two weeks later flowering than the fertile siblings at Davis, California. Some male sterile wheat plants tend to be shorter (27) and less vigorous (27,30, 49) than their fertile siblings. Male sterile 'Saratov 29' wheat

exhibited a greater anthocyanin content than fertile plants (27).
Ergot sclerotia have also been observed in the spikes of mature male
sterile wheat grown in Montana (14).

Anther and Pollen Morphology

The anthers of some of the male sterile mutants in barley appear
to be completely normal and produce stainable pollen while other mu-
tants are characterized by very small, shrunken anthers which fail to
dehisce (40). These rudimentary anthers usually contain little or no
pollen and the filaments often fail to elongate. Although the various
male sterile mutants in barley have very different appearances, the
expression of each individual gene is quite stable. More variation in
the anther morphology was noted in greenhouse environments than in
field-grown populations.

Male sterile wheat plants often possess anthers which are re-
duced in size (5,45) and may fail to extrude (27). The anthers con-
tain empty pollen grains which are sometimes agglutinated (5,6,27).
Some male sterile wheats exhibit a low level of pollen fertility which
appears to be affected by unknown environmental factors and modifying
genes (3,24,49). One male sterile mutant exhibits varying degrees of
anther transformation to nonfunctional ovaries (pistilloidy) (24).

Cytology of Genetic Male Steriles

Chromosome Numbers

Rich (36) reported that much of the unfruitfulness observed in tomatoes was the result of cytogenetic problems arising from aneuploidy. The majority of the sixty-six unfruitful plants isolated from approximately 55,000 plants of three commercial cultivars were aneuploids. Two plants were haploids, two were trisomics, forty-four were triploids, and three were tetraploids. Another fourteen were diploids, of which only four proved to be genetic male steriles. In a later study, Rich (37) found 108 of 150 unfruitful plants to be aneuploids.

Waninge and Zeven (54) and Zeven, Kampmeijer and Enink (60) examined the chromosome numbers of Pugsley's (32) male sterile wheat. They found the 2n chromosome number to vary from 40 to 44 for various plants. Some mixoploids were also observed. Male sterility in this cultivar was not due to aneuploidy.

Microsporogenesis

In an extensive review of genetic male sterility in higher plants, Gottschalk and Kaul (18) concluded that most of the male sterile (ms) genes influence the final stages of microsporogenesis between interphase II and pollen formation. A much smaller group of ms genes affects the very early stages of meiotic prophase and halts the development of microspores at that point. Very few of the known ms

genes function between diakinesis and anaphase II.

In most instances of genetically controlled male sterility, the stage at which the microspore degeneration occurs is highly specific and precise for each ms gene (18,36,37). The behavior of the chromosomes in meiosis is completely normal until the degeneration occurs.

In cytological examinations of meiosis in twelve male sterile corn lines, Beadle (4) found that eight of them went through meiosis normally but did not develop beyond the free microspore stage. Another failed during early prophase the three degenerated over a range of meiotic stages rather than at a specific stage.

Rick (28) found four male steriles in tomato which degenerated in the quartet stage and four more which failed to develop beyond free microspores. In five mutants the microspores collapsed during prophase I while in one other the sporogenous cells aborted before meiosis commenced. In three mutants the breakdown occurred from mid-prophase I to the early microspore stages. Rich (37) also reported an association between the time of breakdown in microsporogenesis and the amount of deformation of the tomato anthers. Genes which cause early microspore abortion are characterized by greatly reduced and degenerated anthers.

Roath and Hockett (42) showed that the degeneration of microspores in the ms mutant in barley occurs during the quartet stage of meiosis. The free microspores of ms_8 failed to undergo mitotic divisions and aborted. A completely normal microsporogenesis and pollen

maturation was observed for ms_6 mutants. The pollen of this barley mutant lacks a pore and therefore cannot germinate on the stigma (1).

Four cytologically examined genetic male sterile wheat mutants completed meiosis normally but failed to develop beyond the free microspore stage (3,5,6,30).

The stage in which the breakdown occurs does not seem to affect the final result--a failure to produce functional pollen (4,18,36,37, 41).

Megasporogenesis

Most male sterile (ms) genes do not alter the process of meiosis and therefore have little or no influence on megasporogenesis (4,18,21, 36,37). Male sterile plants readily set seed upon being pollinated with viable pollen, indicating normal female fertility (4,5,8,21,27,30, 37). An exception was noted in tomatoes for ms_8 which causes about 25% of the ovules to abort (37).

Inheritance of Genetic Male Sterility

Gene Action and Number

The majority of the male sterile genes reviewed by Jain (23) and and Gottschalk and Kaul (18) involved single, recessive factors. The heterozygotes were completely male fertile.

All nineteen of the male sterile genes in barley evaluated by

Hockett and Eslick (21) were monofactorial recessives. Rick (38) lists eighteen single, recessive genes for male sterility in tomato and Beadle (3) gives sixteen in corn. Five of the mutants isolated in wheat are single recessive genes (5,6,15,27,30).

There are exceptions to the recessive single gene male steriles, however. Lesley and Lesley (28) reported male sterility in tomatoes controlled by two complementary recessive genes. Beadle (4) mentions two cases in corn which are suggestive of duplicate recessive genes and others that may be more complex than single gene systems. Athwal et al. (3) and Jan (24) postulate that three additive genes control the expression of male sterility in the wheat stocks they investigated. Weaver and Ashley (55) described a dominant gene, MS_7, in cotton (Gossypium hirsutum L.) which causes male sterility. Another dominant male sterile mutant has been reported in wheat (17).

Gametic Transmission

Most of the male sterile genes act only in the sporophytic (2n) generation and therefore have little or no effect on the gametophytes (23). Lupton and Bingham (30), however, reported a male sterile in which the transmission of the mutant allele is normal through the ovule but is greatly reduced in the pollen of heterozygotes.

Briggle (6) indicated that preferential transmission of the domi-

mant fertile allele may occur in 'Chancellor' wheat. Rick (37) also
noted a deficiency of male steriles in segregating F_2 tomato popula-
tions.

Cytoplasmic Influences

Gottschalk and Kaul (18) reported that the cytoplasm of certain
strains of onion (Allium cepa L.) and carrots (Daucus carota L.) influ-
enced the expression of male sterile genes. When the male sterile
genotype was in the fertility restoring cytoplasm, the plant appeared
to be completely male fertile. Thus, the male sterile genes were
unable to express themselves in certain cytoplasms. Hermsen (19) and
Franckowiak et al. (17) have suggested that such a fertile cytoplasm
may be found for the male sterile genes in wheat and barley. Krupnov
(27) transferred the male sterile gene which he isolated from the wheat
cultivar Saratov 29 into the cytoplasm of the cultivar 'Sarrubra,'
where it segregated normally to show that the male sterility was ex-
pressed in another cytoplasm.

Utilization of Genetic Male Sterility

Crossing Efficiency

Shortly after Suneson (45) found a genetic male sterile mutant
in barley, he began using the male sterile plants as female parents to
facilitate routine crossing in his breeding program. Riddle and

Suneson (39) found that the stigmas of male sterile plants remained receptive up to ten days after first flowering. Seed set in hand pollinations was increased by clipping the florets back, but seed size was decreased. Open-pollinated seed set ranged from 10.6% with alternate rows of pollen parents and male sterile plants (fertiles were rogued) to 44.9% for male sterile plants in heterozygous backcross and F_2 populations.

Using Pugsley's male sterile wheat, Suneson (49) found that four times as much crossed seed could be produced per unit of time compared to normal varieties which required hand emasculation.

Composite Crosses

Suneson (46) developed Composite Crosses XIV and XV in barley using genetic male steriles as a mechanism which would allow for continued outcrossing and recombination. With such a system, self-pollinated crops can be manipulated like cross-pollinated species with appropriate techniques.

Suneson and Wiebe (50) created barley Composite Cross XXI by crossing 6200 lines from the USDA World Collection of barley onto genetic male sterile plants. This population provides an excellent source of material to be exploited through Suneson's "evolutionary" breeding method (47).

Using Pugsley's male sterile, Suneson et al. (49) combined 235 wheat lines in wheat Composite Cross I. This wheat composite has not

been exploited as widely as the barley composites with male sterile genes in them (48).

Hybrids

In 1960, Wiebe (57) proposed using a recessive male sterile gene (ms) closely linked to a recessive phytocide resistance gene (ddt) for the production of hybrid barley. By spraying a segregating population containing these coupled genes with the phytocide, DDT, all plants not homozygous for the recessive resistance would be eliminated. Because those plants homozygous for the ddt gene would also be homozygous for the coupled ms gene, the entire population remaining would contain only male sterile plants. This male sterile populations would then be pollinated by the desired male parents grown in adjacent blocks to produce hybrid seed.

In 1965, Ramage (34) proposed the balanced tertiary trisomic (BTT) system for producing hybrid barley. The balanced tertiary trisomic plants used by Ramage produced about 70% male sterile progeny because of the reduced transmission of the trisomic chromosome carrying the fertile allele through the pollen. A phytocide resistance gene was proposed to eliminate the 30% of trisomics from the female populations. Another phytocide resistance gene would then be used to eliminate the male steriles from the increase populations.

Wiebe and Ramage (58) added a built-in rogueing mechanism to the

BTT system by using an albino gene coupled to the male sterile gene.
Later, Ramage (35) proposed a more complex system using an albino gene,
a haplo-viable gene and a megaspore competition gene to streamline the
BTT.

Eslick (11) has proposed the use of balanced male sterile and
dominant preflowering genes for the selection of an all-female line to
be used in hybrid seed production. The dominant genes allow the rogue-
ing of fertile plants before pollination takes place.

In 1972, Driscoll (9) developed his X-Y-Z system for hybrid seed
production in wheat. The system employs an added alien chromosome
carrying the fertile allele which is not transmitted through the pollen.
With the proper manipulations, this system produces an all-male sterile
population to be used as the female plot for hybrid seed production.

Taylor et al. (51) and Johnson et al. (25) have proposed the use
of a telosomic line in the production of an all-female line for the
seed parent of a hybrid. This system, known as the telosomic catalyst,
is based upon a reduced transmission of a telocentric chromosome
through the pollen. Only alleles, such as ms, on the normal chromosome
are passed through the pollen. Crossing the telosomic catalyst onto a
male sterile gives all male sterile progeny for hybrid seed production.

The telosomic catalyst, the X-Y-Z system, and the BTT, all take
advantage of a discrimination against aneuploidy in the male gameto-
phyte to achieve the preferential transmission of the desired allele on

a normal chromosome.

Hermsen (19) and Franckowiak et al. (17) suggested that a cytoplasm may exist in wheat and barley which may cause a plant homozygous for a ms gene to be phenotypically fertile. This would allow the maintenance of a line homozygous for male sterility. When crossed onto a male sterile plant with a different cytoplasm, all male sterile progeny would be produced. These could then be used in a hybrid program.

Thompson's (52) work with barley in Arizona indicates that hybrid seed production using a genetic male sterile system is economically feasible in self-pollinated cereal crops.

MATERIALS AND METHODS

General Procedures

Greenhouse-grown materials were planted in benches containing pasteurized greenhouse potting soil (1 sand:1 clay:1 peat, by volume), approximately 15 cm in depth. Plants were grown in rows 15 cm apart with 7.5 cm between plants within the rows. A complete nutrient solution was used for watering and supplemental fluorescent lighting of 14-16 hours was provided to simulate long-day conditions.

Spring and fall field plantings were made in 3 m rows 30 cm apart with 10-15 cm between seeds within the row. Planting depth was about 5 cm. The field location was the Plant and Soil Science Field Research Laboratory at Bozeman, Montana. The soil type at this site is the Amsterdam silt loam, a Typic Cryoborall.

Statistical Methods

Comparison of Means

Because of the biological nature of the materials investigated, population sizes and the variances of the populations studied were often unequal. Snedecor and Cochran's (44) weighted t (t') test for independent samples with unequal variances and sample sizes was used to compare the means of the samples being tested. The calculated value of t was found in the usual manner using the following equation:

$$t = (\overline{X}_1 - \overline{X}_2)/ (s_1^2/n_1 + s_2^2/n_2) \qquad (\text{Note: } s_x^2/n = s_{\overline{x}}^2)$$

the tabulated t value was modified to compensate for unequal variances

in populations to give a weighted t (t'). The equation used for calcu-

lation of the tabular t' value was

$$t' = [(t_1 \times s_1{}^2/n_1) +)t_2 \times s_2{}^2/n_2)]/(s_1{}^2/n + s_2{}^2/n).$$

Snedecor and Cochran (44) recommend the assumption that $\sigma_1 = \sigma_2$

be avoided if there is any doubt, thus the modified tabular t (t') was

used in preference to the regulat t-test equation. Tests of the equal-

ity of variances between populations showed them to be significantly

different. A comparison of the calculated t to the tabular t' was used

to test the difference of the means at the chosen level of significance.

H_0 was rejected if the value of the t calculated was greater than t'

tabular.

Paired Comparisons

Snedecor and Cochran's (44) equation for paired comparisons was

used to determine the probability that differences were significant.

The equation used was:

$$t = \frac{\bar{D}}{s_{\bar{D}}}$$

The symbol $\bar{D}$ is used to designate the mean of the difference.

H_0 was rejected if the probability was less than .05.

Population Size

Mather's (31) equation to determine the population size required

to obtain a certain class at a given probability level was used to calculate the minimum population necessary in the genetics experiments. The equation is:

$$(1\text{-proportion of the desired type})^N = \frac{1}{(1\text{-probability of desired type})}$$

where N = the minimum population required at the chosen probability level to obtain one of the desired type.

Source Materials

The source of the male sterility studied in this investigation was a single plant in a 1974 field-grown F_3 head row of 'Yogo' Short Straw 4462/4*'Cheyenne.' This plant contained ergot sclerotia and set only seven seeds on five spikes. Cheyenne (CI 8885) is a widely-adapted hard red winter wheat. Yogo Short Straw 4662 ('Norin' 10/-'Brevor'//3*Yogo,4-6-6-2) is a semi-dwarf, backcross-derived selection utilized as a source of shatter resistance in a backcrossing program with Cheyenne at Montana State University.

The F_3 head row in which the male sterile plant occurred was uniform for height and maturity, but segregated for brown and white chaff. All of the lines derived from the original cross were homozygous for awns and winter growth habit.

The seven seeds on the original male sterile plant were sown in the greenhouse during the winter of 1974-75. Five of the F_1 plants produced were fertile and closely resembled the parental phenotype.

They were designated as Cheyenne male sterile (Cnn ms)-1,-2,-4,-5 and -6 (Figure 1, p. 21).

A sixth plant (Cnn ms-3) was also fertile but exhibited a spring growth habit and was awnletted. Cnn ms-3 probably resulted from an outcross of the original male sterile plant to a nearby awnless spring wheat. An F_2 population from this plant was grown in a preliminary investigation at Bozeman as a field observation plot (Figures 1, p. 21, and 2, p. 22) in 1975. Segregation ratios for awns, stem solidness, growth habit and male sterility were recorded.

The seventh plant (Cnn ms-7) was similar to the parental line in appearance, except that it was male sterile (Figure 1, p. 21).

Derived Materials

Spring Wheats

All of the spring-type wheats studied were descendants of the single F_1 plant Cnn ms-3 (Figures 1, p. 21, and 2, p. 22). Fertile plants in the preliminary F_2 population of 151 plants grown in 1975 provided eighty-two F_3 families in 1976 (Figure 2, p. 22). Crosses were made to the seventeen male sterile plants in the Cnn ms-3 F_2 population using normal cultivars and fertile siblings as male parents. Seed was also produced by open-pollination.

One hundred and forty of the F_1 seeds from the male sterile plants were grown in the greenhouse in the winter of 1975-76. The re-