Genetic characterizations of three male-steriles in wheat, Triticum aestivum L.
by Duane Lee Johnson

A thesis submitted in partial fulfillment of the requirements for the degree of DOCTOR OF PHILOSOPHY in Crop and Soil Science
Montana State University

Abstract:
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Chi square analyses of homogeneous F2, F3, F4, and F5 families were made for various expected ratios for the three male-sterile sources using spring and winter grown populations. Selections made from the 41 original sibcrossed families of the Siete Cerros mutants were evaluated as spring grown F3, F4 and F5 headrows. F2 and F3 plantrows of Chancellor male-sterile x various winter wheats were evaluated as winter wheats.

An abnormal 7:1 segregation predominated in most Siete Cerros families with an unexpected high number of nonsegregating headrows.

One family of the original 41 segregated for male-sterility as a single recessive allele.

The influence of background genotype on the Chancellor male sterility was attributed to a superior gene(s) in the parental cultivars.

Monosomic analyses of the three male sterile sources suggested complex inheritance. The male-sterile expression in Siete Cerros may be due to aneuploidy or gamete lethality. The major factor controlling male-sterility in Chancellor confirmed the results of Driscoll (10) as being associated with chromosome 4A. Five additional chromosomes may also be involved.

DEDICATION

This thesis is dedicated to the memory of C. A. Suneson, a pioneer of genetic male sterility in small grains.

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ABSTRACT

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INTRODUCTION

The goal of plant breeding for yield has not changed over time but knowledge and control of the environment have changed the methodology used to attain that goal. Many present day plant breeding programs emphasize developing high yielding cultivars adapted to a specific environment with high quality standards and insect and disease resistance that must be met. As a result of these requirements, the technology for determining these factors is improving but the breeder is still manipulating the same pollination systems used by his prehistoric ancestors.

Using genetics, modern man is learning to circumvent the limitations of natural pollination mechanisms. Corn (Zea mays), normally a cross-pollinated crop species, can now be treated as a self-pollinated species. Barley (Hordeum vulgare), a self-pollinated species, can likewise be manipulated as a cross-pollinated crop.

Genetic male-sterility in a self-pollinating species provides the plant breeder with a combination of factors which reduce the costs and increases the number of potential crosses substantially. The major advantage of genetic male-sterility in a self-pollinated crop, however, in the ability to shift from self-pollination to cross-pollination and back to self-pollination at the desire of the researcher.

The occurrence of two spontaneous male sterile mutants in the spring wheat (Tricitum aestivum L.) cultivar 'Siete Cerros' led to the initiation of this study. A winter wheat cultivar, 'Chancellor', which

contained a simply-inherited genetic male-sterile was included as a standard by which progress within the selection of Siete Cerros could be measured.

The objectives of this research were to:

1. Examine the inheritance of male-sterility within two spontaneous male sterile mutants of Siete Cerros spring wheat and a single gene male-sterile isolate of Chancellor winter wheat.

2. Locate as to chromosome the factor(s) causing male sterility.

LITERATURE REVIEW

Male Sterility

History

Wheat (Triticum aestivum, L.), a self-pollinated species, has very low levels of cross-pollination. Natural outcrossing in wheat varies between 0.16 and 8% (19,22,24,74) and can be affected by environmental conditions (3,26,27,66). The low, natural levels of cross-pollination are insufficient and too unreliable to be used effectively for genetic recombination in wheat.

The importance of controlled crossing has been recognized by wheat breeders since the latter part of the 18th century (46). The popularity of producing hybrid populations for selection in the production of new cultivars increased and spread from Great Britain to Europe and the United States. By the end of the 19th century, wheat breeders throughout the western world recognized the importance of obtaining new genetic recombinants for varietal improvement (46).

Since that time, breeders of self-pollinated crop species have attempted to accelerate their breeding programs through controlled genetic recombination. Most of these efforts have been involved with rendering the male gametes inviable in selected plants. This phenomenon, termed male-sterility, can be attained by emasculation (common in self-pollinated crops) or othrough genetically controlled manipulation of factors affecting fertility.

Genetically controlled male-sterility is particularly useful in wheat breeding. This phenomenon relieves the wheat worker of the tedious task of hand emasculation and allows opportunity for the manipulation of wheat as a cross-pollinated species. There are two common methods of creating male-sterility in wheat: (1) cytoplasmic male sterility (CMS), and (2) genetic male-sterility (GMS).

Cytoplasmic Male-Sterility

During the 1930's, CMS was discovered in corn (12). The use of CMS in the development of corn hybrids resulted in improved corn yields at a reduced cost and caused breeders to examine the potential of male sterility in other crops (13).

CMS in rye (Secale montanum Guss.)(41), barley (56) and wheat (32,49,82,83) involve the use of alien cytoplasms. In rye, only one of the parent cytoplasms was effective in evoking male-sterility (40).

Currently, wheat hybrids derive their cytoplasmic male sterility from Tricitum timopheevi, first reported by Wilson and Ross (84). In wheat, Aegilopis caudata cytoplasm commonly gave a high incidence of pistilloidy and consequently partial or complete female sterility (6, 49). Other cytoplasmic sources, such as Aegilops ovata, tended to produce late flowering female wheat lines with decreased seed set in crosses with hexaploid wheat pollen parents (49).

CMS has been developed in hexaploid wheat specifically for F_1 hybrid wheat production. CMS is therefore limited in its poential

uses. The problems of uneconomical yield increases (21), incomplete restoration and the necessity of multigenic restorers at northern latitudes (83) limit the use of cytoplasmic male-sterility in Montana.

Genetic Male-Sterility

GMS offers a flexibility unattainable in the CMS system (29,30). GMS-derived hybrids can potentially be used as commercial F_1 hybrids, in recurrent selection populations and for conventional varietal improvement (16,29,30,70,77). GMS also offers wheat breeders the ability to shift easily from a program of conventional breeding to recurrent selection to hybrids (30).

The first isolation of GMS in small grains was made by C. A. Suneson (73). In 1936, Suneson discovered a single male-sterile barley plant which phenotypically resembled some male-sterile wheat he had previously studied. In the earlier study, freezing temperatures had caused complete male-sterility in some wheat tillers (66). However, the male-sterility observed in the barley plots proved to be a simply-inherited single gene male-sterile (68)

In 1945, Suneson (67) suggested the use of a simply-inherited, recessive, male-sterile in composite cross populations of barley to allow continued recombination coincident with plant competition favoring the most vigorous plants. In 1951 (69), he suggested the use of GMS in a program of male-sterile facilitated synthetic hybrid barley. Suneson later termed this male-sterile accelerated recurrent

recombination (72). Eslick suggested a similar program termed male-sterile facilitated recurrent selection (14).

With the discovery of GMS in barley, an interest grew in the possibility of producing commercial F_1 hybrids. Several systems have been proposed involving chemically-induced lethals (80), aneuploidy (51,53), balanced genetic lethals and male-steriles (13,23), and others. Since the breeding systems of barley and wheat do not differ greatly, the potential exists for similar developments in wheat.

Since the identification of the first genetic male-sterile in barley in 1940 (67,68) twenty-seven additional genes for male sterility have been reported (22).

Genetic Male Sterility in Wheat

In 1922, Sax (55) reported an increased proportion of sterility in wheat in conjunction with an increased proportion of univalents from interspecific crosses. The observed male and female-sterility was attributed to aneuploidy.

In 1938, partially sterile F_2 plants were noted in the cross 'Pathology 4592' x 'Nebawa' (65). The partial male-sterility was attributed to chromosomal aberrations.

Pugsley and Oram (50) found what appeared to be a genetic male-sterile in an F_3 family of 'Kenya Farmer' x 'Javelin 48'. The inheritance of this male-sterility was unclear (50,71). This male-sterile was used in conjunction with induced male-sterile mutants in the first

wheat composite cross population (73,76). Suneson's investigations of the inheritance of this particular male-sterile were not conclusive. Suneson hypothesized the male-sterility, in this instance, could be due to a single recessive gene which was environmentally sensitive (71). Cytological studies by Wanige (79) and Zeven et al. (85) were also inconclusive concerning this male-sterile mutant. The chromosome number varied irregularly (79,82,85) and no apparent relationship between aneuploidy and the male-sterile character was noted.

From Pugsley and Oram's original male-sterile germplasm, Briggle (5), through backcrossing, isolated and transferred a single gene for male-sterility to the cultivar 'Chancellor'. The gene behaved irradically when placed in different parental combinations. Other genetic backgrounds differentially influenced the expression of male-sterility. Briggle (5) hypothesized that modifiers from other cultivars or a gamete competition might be responsible for this difference in reaction.

Types and Patterns of GMS in Wheat

Two types of GMS appear to exist in wheat. The first involves multiple genes which act in a cumulative fashion to express male-sterility (1,18,27).

The multigenic male-steriles have common characteristics. All are reported to involve three recessive genes having cumulative effects and exhibit partial sterility (1,19,28). An ability to set 5% selfed

seed has been advocated for the maintenance of male-sterile lines in hybrid wheat production (1,19,28).

The second type of GMS involves single gene inheritance such as the spontaneous male-sterile mutant found by Kruysnov (34) in 'Saratovskaya-29' in 1964. Fourteen of twenty-two F_3 families from the original mutant, segregated for the male-sterile character. Thirteen of the fourteen segregated for a single, recessive male-sterile gene. The fourteenth family segregated for a complimentary two-gene recessive ratio (34). Plants grown under field conditions deviated more from the monofactorial ratio than did greenhouse grown material. Krupnov (34) proposed that decreased viability of the male-sterile phenotypes affected the ratio of fertile to sterile plants.

Bozzini and Scarascia-Mugnossa (4) found a spontaneous mutant in the tetraploid wheat cross 'Yuma' x 'Capeits'. The mutant allele acted as a single recessive gene for male-sterility.

Bingham (2) reported a spontaneous male-sterile mutant in the hexaploid cultivar 'Maris Widgeon'. This single gene mutant was meiotically normal. Pollen transmission of the character was reduced while female transmission of the gamete appeared to be normal. This finding corroborated other studies involving monogenic male-steriles in wheat (11,17,34).

Monogenic male-steriles have also been induced. Fossanti and Ingold (16) induced a single gene male-sterile in the cultivar 'Probus'

using x-ray. Driscoll (11) induced a similar male-sterile in the cultivar 'Pitic-62' using gamma radiation.

The GMS isolated from the original material of Pugsley and Oram and transferred to 'Chancellor' (5) is allelic with the Probus mutant and located on chromosome 4A (10). The 'Cornerstone' mutant gene, isolated from 'Pitic-62' by Driscoll (11), is also on chromosome 4A. The Cornerstone source of male-sterility appears to involve a terminal deletion of the alpha arm of that chromosome (11).

Maan (41) found the alien substitution line involving the transfer of a single chromosome of Aegilops longissima (20" T. aestivum + 1" A. longissima) to be completely fertile. Telosomic and isosomic analyses showed the single A. longissima chromosome to be homologous to that of chromosome 4A in wheat. The substitution line is completely self-fertile. All male gametes carrying the A. longissima chromosome are fertile and functional. Thus, chromosome 4A in wheat appears to perform a vital function in fertility expression.

Monosomic Analysis

Aneuploidy - A Genetic and Plant Breeding Tool

Aneuploidy involves an imbalance of chromosome pairs or between chromosomal homologues. Initially, aneuploid types such as monosomics, nullisomics and trisomics were used only for the chromosomal location of specific characters. These characters have been summarized by Morris (43). More recently, nullisomics and monosomics have provided

wheat researchers with the opportunity to transfer specific chromosomes from cultivar to cultivar (54,64,78) and from species to species (39,41).

Monosomics involve the loss of one member of a homologous pair of chromosomes. Instead of the expected 21 pairs of chromosomes (21"), the monosomic has 20 chromosome bivalents and a single univalent (20" + 1') (33).

Monosomic plants, when self-pollinated, produce disomic (21"), monosomic (20" + 1') and nullisomic (20") progeny. The proportion of these progeny depend upon the frequency with which the 20-chromosome (n-1) gametes function in fertilization and upon the degree of viability of the nullisomic progeny (35).

Approximately 75 percent of the functional female gametes are n-1, regardless of the chromosome involved (35,61). Functional male gamates are generally of the 21 chromosome type since certation favors the 21-chromosome pollen (35). The percentage of functional 20-chromosome pollen varies from approximately 1 to 10 percent depending upon the chromosome concerned (61).

The failure to transmit specific male gametes may be effective in plant breeding research. Recently, in conjunction with genetic male-sterility, proposals have been made to use aneuploids for hybrid wheat and barley production (8,9,51,53).

Monosomics - Cytological Problems

Monosomics are meiotically unstable. The absence of one dose of chromosome, 1B, 4B, 2D or 4D can promote misdivision of the centromere (31) and other meiotic irregularities (47,57,58). Chromosomes 1B, 4B and 6B appear to control regular bipolar segregation of homologous chromosomes and, in the hemizygous state of the monosomic, can produce elevated numbers of double monosomics (31). In the monosomic series of 'Cheyenne' and 'Wichita' wheat, plants which lacked bivalents for 6A, 6B or 6D showed some necrosis in the seedling stage (44). Apparently, there was no suppression of leaf necrosis when one of these chromosomes was in the hemizygous state. Reduced pollen transmission of n-1 gametes is common. The failure to effect fertilization by n-1 gametes is remarkably consistent across observed polyploid species (20,36,45,61). The actual number of viable n-1 gametes varies between monosomic lines within a species (39,61). More information concerning the theoretical aneuploid ratios is available from Kuspira and Unrau (35).

Univalent shift is another potential problem with the use of monosomics. Person (47) found univalent shift occurred frequently. Univalent shift involves the mispairing of a chromosome with a univalent from one of its homologues. For example, a univalent of 4A could occasionally mispair with a univalent of 4B leaving the 4B homologue to become the new univalent. Since all wheat chromosomes

are essentially metacentric, it is difficult to discriminate when univalent shift has occurred (47). Person (41) also found partial asynapsis to occur. New aneuploid types such as double monosomics could result.

A final potential problem in using monosomics is non-expression of a character in the hemizygous state (61). As a result, evidence gathered from monosomic analyses may be inconclusive.

Study I

THE INHERITANCE OF GENETIC MALE-STERILITY IN Siete Cerros AND Chancellor

MATERIALS AND METHODS

Genetic Materials

Siete Cerros

Two spontaneous male-sterile mutants, found in the spring wheat cultivar 'Siete Cerros' (C.I. 14493) by University of Arizona Professor R. K. Thompson, were studied. Seeds from open-pollination with Siete Cerros were assigned the population-designation A and B for identification. These identifying letters were maintained throughout this study. Each seed was assigned an Arabic number as a family designation (A-1 through A-21 and B-1 through B-20).

Chancellor

A single recessive gene for male-sterility was transferred from the original male-sterile mutant population of Pugsley and Oram, commonly called Pugsley's male-sterile, to the soft, red, winter wheat cultivar, 'Chancellor' (C.I. 12333) by Dr. L. W. Briggle (5). Briggle found no logical segregation pattern in the F_2 of the original cross. Continued selection for a single, recessive male-sterile gene with four backcrosses to Chancellor was, however, successful. Partially sterile plants in the F_2 and early backcross generations were discarded by Briggle.

The Chancellor male-sterile (ms C) is cytologically normal (21") in both fertile and male-sterile phenotypes (5). Driscoll (10)

reported the male-sterile allele from ms C was on chromosome 4A and allelic to the 'Probus' male-sterile.

Cytologic and Genetic Procedures

Figure 1 provides an outline of generation procedures for greenhouse and field materials of Siete Cerros A and B populations. Pollen mother cells (PMC) from twenty A and twenty-one B F_1 plants, heterozygous for the male-sterile allele(s), were examined cytologically. PMC analysis followed the techniques of Zeven et al. (85).

Preliminary allelism tests were made between cytologically normal F_2 families of A and B during the summer of 1975. Allelism test evaluations were based upon primary tiller phenotype. Additional allelism test crosses were made among elite F_4 families of A, B and C furing the summer of 1977. Test cross offspring were evaluated for fertile to male-sterile segregations in 1978.

Crosses were made between male-sterile individuals from F_2 families of Siete Cerros A and B with various hard red winter wheats (HRWW) to examine the influence of genotypic background. These F_2 progeny were fall and spring planted for field observation in 1977.

Crosses were made between male-sterile individuals of Chancellor (ms C) and the HRWW cultivar 'Centurk' in the greenhouse during 1974-1975. The F_2 analysis of the cross was made during the summer of 1976. All field grown materials were evaluated for male-sterility at

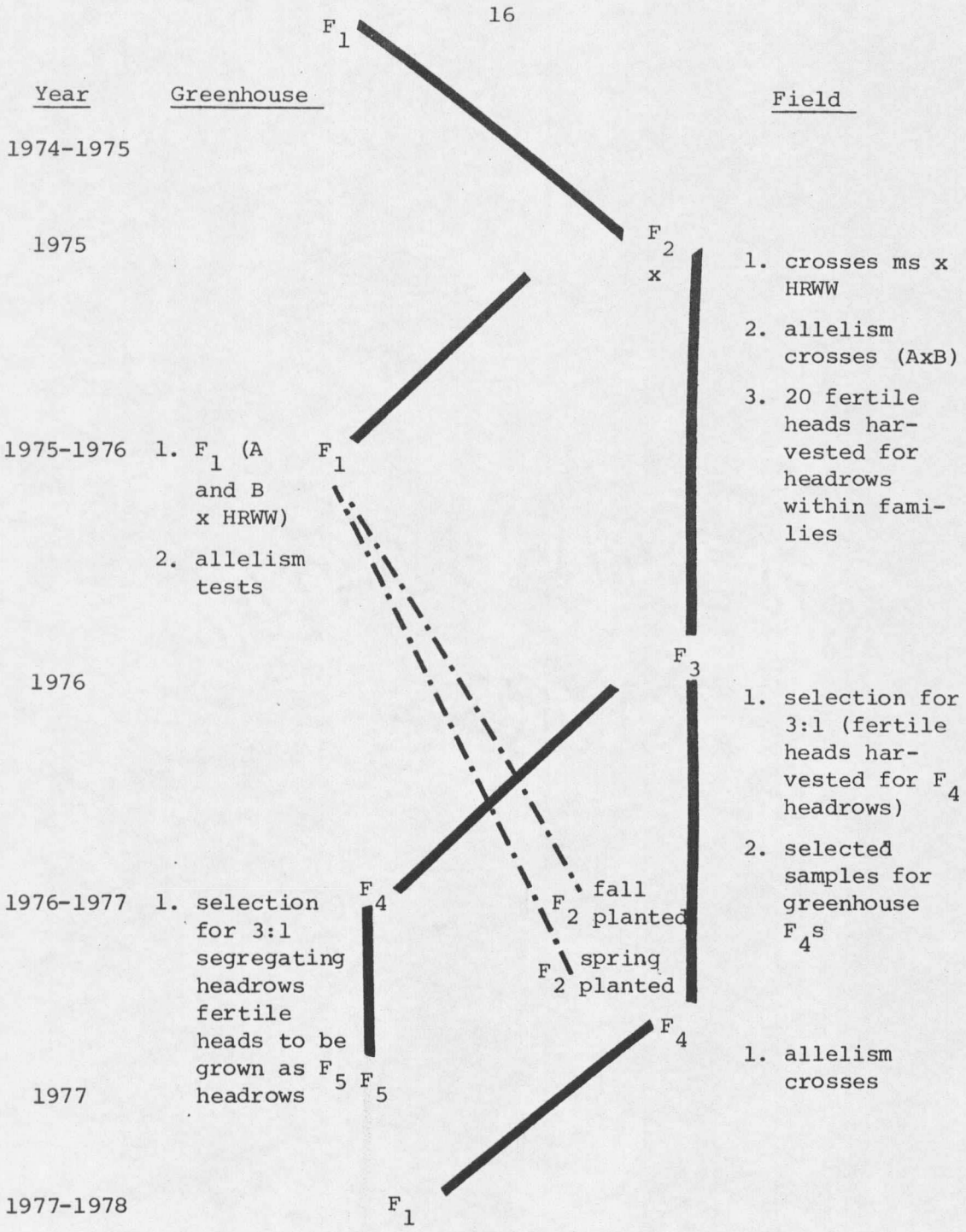

Figure 1. Generation procedures for Siete Cerros A and B.

the Plant and Soil Science Field Research Laboratory, Bozeman, Montana. Individual F_2 progeny (ms C x Centurk) were harvested and classified as to awnless, awnletted or awned plant types. F_3 C families from individual F_2 plants were planted in the fall of 1976 and classified for male-sterility in 1977.

Greenhouse Procedures

Materials derived from populations A and B and families of C were greenhouse grown in steam-pasteurized benches of a sandy-loam soil (2 parts sand:2 parts Amsterdam silt loam:1 part peat) and were irrigated with a complete nutrient solution. Greenhouse temperatures were maintained at 60-75°F for spring and 40-50°F for the winter wheat with a gradual increase to 60-75°F.

The original open-pollinated F_1 progeny of Siete Cerros populations A and B were greenhouse grown from December, 1974 to April, 1975. Progeny resulting from field sib-crossing within Chancellor (ms C x C) were also grown at this time.

F_4 and F_5 headrows were greenhouse grown during 1976 and 1977. Greenhouse grown selected fertile F_4 plants, segregating for single gene male-sterility, provided seed for F_5 headrows.

Field Procedures

The F_2 families obtained from selfing individual F_1 plants of populations A and B were field planted in April, 1975 to determine F_2 segregation ratios for male-sterility. Twenty random spikes, when available, from twenty fertile F_2 plants from each A and B F_2 family were harvested to provide seed for F_3 families.

Greenhouse sub-crossed material from Chancellor (ms C x C) and F_1 progeny of ms C x Centurk were field grown during the summer of 1975. Male-sterile plants from sib-crosses were crossed with various hard red winter wheats.

Determination of fertile and male-sterile individuals within segregating families of A, B and C was based upon the phenotypic expression of the primary tiller and 0% seed set from bagged heads of suspected male-steriles.

F_2 A and B family segregations were tested using chi square tests of goodness of fit to three Mendelian ratios. The tested ratios were:

1. 3:1, a single gene, recessive male-sterile;
2. 15:1, a two gene, recessive male-sterile;
3. 63:1, a three gene, recessive male sterile.

Sample sizes for determining genetic ratios ($p = .90$) were based on the formula of Mather (42). Samples sizes exceeding 146 observations were considered definitive for all ratios tested at the family level.

Chi square analyses were used to determine goodness of fit within Chancellor for the following ratios:

1. 3:1, a single gene, recessive male sterile with complete gamete transmission of the male-sterile allele;
2. 4:1, a single gene recessive male-sterile resulting from an assumed 10% reduction in pollen transmission of the male-sterile containing gamete;
3. 5:1, a single gene recessive male-sterile resulting from an assumed 15% reduction in pollen transmission of the male-sterile containing gamete;
4. 7:1, a single gene recessive male-sterile resulting from an assumed 18% reduction in pollen transmission of the male-sterile containing gamete;
5. 15:1, a two gene recessive male-sterile ratio with complete gamete transmission;
6. 13:3, an epistatic, two gene male-sterile ratio with complete gamete transmission.

In 1976, segregation ratios for male-sterility of mx C x Centurk F_2's and spring planted F_3 headrows of A and B were determined. F_3 and F_4 A and B family analyses included the ratios:

1. 7:1, an observed segregation ratio of unknown origin similar to one found by Falk (15);

2. 1:0, a nonsegregating (fertile:male-sterile) headrow ratio.

Homogeneity of F_2 and F_3 families of C and F_3 and F_4 families of A and B were tested using heterogeneity chi square (42). Headrows with within each A and B F_3 family were analyzed using chi square tests of goodness of fit to the expected ratios.

RESULTS AND DISCUSSION

The Siete Cerros Male-Steriles

Allelic factors producing male-sterility were not evident in crosses between heterozygous, cytologically normal (2n = 21") individuals within families of A and B (Table 1). Consequently, the two populations were maintained separately and considered two mutational events.

F_2 family analyses of A and B were essential to the determination of inheritance in the Siete Cerros mutants (Tables 2 and 3). Probability values provided information concerning the actual segregation ratio. Since random pollen parents were used in crosses to the original male-sterile mutants, individual families could segregate for different numbers of genes.

Table 1. Allelism tests between meiotically normal Siete Cerros A and B

Parentage	Frequency		X^2	Probability
	Fertile	Male-Sterile	(1:1 expected)	Value
ms A-1/B-8	15	0	15.0	<.001
ms A-5/B-8	3	0	3.0	.05-.10
ms A-8/B-8	7	0	7.0	<.01
ms A-11/B-8	3	0	3.0	.05-.10
ms A-6/B-6	17	0	17.0	<.001
ms B-8/A-15	5	0	5.0	<.01

PMC analysis showed chromosomal observations (telosomy and translocations) and provided a determination of meiotically normal and aberrant F_1 percents of Siete Cerros A and B (Tables 2 and 3).

Family A-19 (Table 2) does not fit any of the expected ratios. Family A-2 (Table 2) best fits a three gene model ($p = .50 - .70$). Other families of A best fit 3:1 or 15:1 fertile to male-sterile segregation.

Most F_2 B families best fit 3:1 segregation ratios (Table 3). Families B-7, B-17 and B-18 best fit a 15:1 ratio. Families B-5, B-6, B-16, B-19 and B-21 did not fit any of the tested ratios.

F_3 families (Tables 4 and 5) of Siete Cerros A and B did not fit segregation patterns consistent with observed segregations within F_2 families.

There was an unusual, high number of nonsegregating F_3 headrows in A and B (Tables 6 and 7). The reduced number of segregating classes may be due to a gametic failure, aneuploidy or a factor conditioning gametic lethality such as pollen killer, Ki (62).

F_4 families generally fit a 7:1 ratio of fertile:male-sterile (Tables 8 and 9). Falk (15) reported an 8:1 ratio which may be associated with gametic lethality. A-15 and B-20 were the only families which fit a desired 3:1 ratio.

F_3 and F_4 data are similar for a number of non-segregating headrows (Tables 10 and 11). Greenhouse F_4 and F_5 headrow

Table 2. Siete Cerros A F_2 family fertile and male-sterile segregation and associated probability values for three genetic ratios

Family	Frequency		Probability for tested ratios†		
	Fertile	Male-Sterile	3:1	15:1	63:1
A-1§	55	6	--‡	.20-.30	--
A-2	37	1	--	.30-.50	.50-.70
A-3	41	9	.20-.30	--	--
A-4	48	6	--	.10-.20	--
A-5§	28	4	.10-.20	.10-.20	--
A-6§	19	1	--	.80-.90	.20-.30
A-7	46	12	.30-.50	--	--
A-8§	16	2	.10-.20	.30-.50	--
A-9	14	2	.20-.30	.30-.50	--
A-11	29	11	.70-.80	--	--
A-12	44	15	>.99	--	--
A-13	9	2	.50-.70	.10-.20	--
A-14	20	7	.90-.95	--	--
A-15§	37	14	.50-.70	--	--
A-16	51	2	--	.30-.50	.10-.20
A-17	60	4	--	>.99	--
A-18	36	6	.10-.20	--	--
A-19	63	10	--	--	--
A-20	28	3	--	.30-.50	--

† Probability determined by chi square tests of goodness of fit
‡ $P < .05$ are not given
§ Meiotically normal F_1 plants