ITERRELATIONS OF CYTOPLASMIC-GENIC MALE-STERILITY SYSTEMS IN SORGHUM

By

JIMMY MACK RITCHEY

Bachelor of Science
Texas Technological University
Lubbock, Texas
1968

Master of Science
Texas A & M University
College Station, Texas
1977

Submitted to the Faculty of the Graduate College
of the Oklahoma State University
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Thesis Approved:

Dale E. Weibel
Thesis Adviser

Charles M. Taliaferro

Billy B. Tucker

Charles E. Denman

Norman N. Durham
Dean of the Graduate College

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CHAPTER I

INTRODUCTION

Genetic diversity in a crop is very important. The epiphytotics of late blight caused by Phytophthora infestans (Mont.) De By of potatoes (Solani tuberosum L.) in the early 1840's and stem rust caused by (Puccinia graminis Pers. f. sp.tritici Eriks S.E. Henn) of wheat (Triticum aestivum L.) of 1916, 1935 and 1951 are examples of using germplasm with a narrow genetic base. More recently, the epiphytotic of southern corn leaf blight caused by [Helminthosporium maydis Nisik and Miyake (Cochliobolus heterostrophus Drechs.)] showed the danger of having a narrow germplasm base in the cytoplasm of corn (Zea mays L.). The disease affected corn hybrids made with germplasm containing "T" cytoplasm.

Only one cytoplasmic-genic male-sterility (CGMS) system is presently used in the commercial production of hybrid sorghum (Sorghum bicolor (L.) Moench) seed. If susceptibility to a particular disease should become associated with milo cytoplasm, hybrid production would be jeopardized and farmers would have to use cultivars instead of hybrids. The use of different sterility systems would broaden the genetic base in sorghum hybrids and lessen vulnerability to genetic and environmental hazards. New CGMS systems have been found in recent years that differ among themselves and from the conventional milo-kafir system, although the inheritance and genetic control of these traits are not known.

The objectives of this study were to:

1. Determine the inheritance of CGMS systems in sorghum and clarify their genetic control mechanisms.

2. Study the differences and similarities between the CGMS systems known as 9E and SC299 as to disease reactions, and starch content of pollen grains of testcrosses and paired progeny (A- and B-lines).

3. Measure the reaction of paired-progeny to common disease organisms including those causing downy mildew [Peronosclerospora sorghi (Weston and Uppal) C.G. Shaw] and head smut [Sporisorium reilana (Kuehn) Lang. and Fullerton].

CHAPTER II

REVIEW OF LITERATURE

Cytoplasmic-Genic Male-Sterility Systems

Bateson and Gairdner (3) were the first to describe and explain how a cytoplasmic-genic male sterility system worked in flax (Linum usitatissimum L.). Twenty-five percent of the offspring from corsses of selected parents were male sterile in the F_2 generation whereas no male sterilty was observed in the progeny from the reciprocal crosses. Male sterility was inherited only through the female although its expression was controlled by genes which could be contributed by either parent.

Jones and Clarke (13) described the results of crossing male-sterile onion (Allium cepa L.) plants with commercial varieties. One of three types of offspring was always observed: all flowers were male fertile, all flowers were male sterile, or flowers segregated for male fertile or male sterile. The segregating populations occurred sometimes in the F_1, where a one fertile to one sterile ratio occurred, sometimes in the F_2 generations, where a three fertile to one sterile ratio was observed, and sometimes in the first backcross generation, where a one fertile to one sterile ratio was observed. Jones and Clarke assumed a male sterile plant (A-line) contained sterile (S) cytoplasm and was homozygous recessive for maintainer nuclear genes msms. A maintainer line for male sterility (B-line) contained normal cytoplasm (N) and was homozygous recessive for maintainer genes msms. A restorer

line (R-line) could contain either sterile or fertile cytoplasm, but had to be homozygous dominant for restorer genes (MsMs) to give all fertile hybrid progeny.

Cytoplasmic male sterility in sugar beets (Beta vulgaris L.) was described by Owen (21). He assumed cytoplasmic male sterility to be controlled by two homozygous recessive gene pairs in sterile cytoplasm. He later proposed a procedure to produce hybrid sugar beets.

W.H. Davis is cited by Bradner and Childers (5) as discovering the first source of cytoplasmic male sterility in Alfalfa (Medicago sativa L.) in 1968. They assumed that clone Oms-5 probably possessed sterile cytoplasm and it was multiplex for restorer genes.

Burton (6) described male sterility in an inbred line of pearl millet [Pennisetum americanum (L.) K. Schum]. This line produced little pollen and set very few seeds when self-pollinated. When male-sterile plants from this line were crossed with fertile lines, all progenies were fertile. In the F_2 generation male-sterile plants were selected and crossed by an inbred line which maintained sterility. Continued backcrossing produced a male-sterile line "identical" to the maintainer line in phenotypic characteristics except fertile anthers. Burton and Athwal (7) worked with three other sources of cytoplasmic-genic male steriles and concluded that one to three independent recessive genes controlled male sterility in these lines. Environment and modifying genes apparently influenced the action of fertility-restoring genes.

Rhodes (27) first described cytoplasmic male sterility in corn in 1931. Duvick (9) described the use of cytoplasmic male-sterility in hybrid seed production and later (10) presented an excellent review of

cytoplasmic male sterility in corn. Rogers and Edwardson (28) isolated a male sterile plant in the open-pollinated variety Golden June at the Texas Experiment Station in 1944. This male-sterile cytoplasm from Texas later became the Texas or "T" cytoplasm which was the female used to make most hybrid corns until 1970. In 1970, southern corn leaf blight caused by [Helminthosporium maydis Nisik and Miyake (Cochliobolus heterostrophus Drechs.)] caused great losses due to corn hybrids containing "T" cytoplasm. Several other sources of cytoplasmic male sterility were known, but they had not been used because the "T" cytoplasm had always worked satisfactorily.

Beckett (4) classified 30 lines with male sterility that were backcrossed to a series of corn inbreds. The major groups were designated as T, S, and C. Today corn hybrids are being produced by detasseling, and by the use of sterility systems involving T, S, and C cytoplasm. Other reviews on cytoplasmic- genic male-sterility have been written (11, 22). Nearly every crop has at least one cytoplasmic male-sterility system.

Cytoplasmic-genic male-sterility (CGMS) in grain sorghum was discovered by Stephens and Holland (33). They observed male sterility resulting from the interaction of milo cytoplasm with the nuclear genes from kafir(Al-milo-kafir sterility system). Stephens and Holland used this sterility system to devise a procedure by which sorghum hybrids could be produced. To produce grain sorghum hybrids, a male sterile (A-line) is crossed by a restorer line (R-line). The seed from the male sterile plants is harvested and sold as a hybrid. To maintain and increase an A-line, the male sterile plants are backcrossed to a maintainer line (B-line). To increase the seed of the maintainer line

(B-line) or restorer line (R-line), these lines are selfed by growing in isolation from other sorghums. This system is used to produce most of the grain sorghum hybrids in the United States.

Mital, et al. (18) reported the occurrence of cytoplasmic-genic male-sterility in India. A sterile plant was observed in a tall forage type cultivar, 'IC2360'. It was pollinated with pollen from a fertile plant of the same cultivar. The progeny from the cross were completely male sterile. Progeny plants were crossed using pollen from fertile plants of the parent cultivar. All progenies from these crosses were also completely male-sterile.

During 1959 and 1960, Rao (25) observed male-sterile plants in the seed increase plots of nine different lines. Primary panicles of these nine lines which had been bagged for selfing, only set a few seed if any, while secondary heads set seed on open-pollination. Open-pollinated seed and the few seeds on the selfed heads were planted and fertility of the progenies was observed. Progenies from eight lines-W.E.1, Bilichigan, Burma Black, G.J. 103, B.D. 8, Red Jonna-1, Indore local-1, and Norghum-1 were sterile. Rao concluded that the origin of male sterility in these varieties could be traced to natural cross pollination.

Hussaini and Rao (12) observed spontaneous occurrences of male sterility in two different populations. Two plants from the cultivar 'PJ22K' and three plants from another cultivar were observed to be sterile.

Webster and Singh (36) reported a cytoplasmic-genic male sterile which came from a selection of cultivar '9E' from Ghana. When male steriles from cultivar 9E were crossed by a milo, kafir, durra,

broomcorn, or sorgo, the respective F_1 progeny were male sterile with nondehiscent anthers. The nondehiscent anthers had pointed tips, but were normal in size and color, and did not shed pollen.

Appathurai (2) reported a cytoplasmic-genic male sterile containing genes nonallelic to those of the Al sterility system. M.S.1601-A, a cytoplasmic-genic male sterile, maintained by Combine Kafir-60, and G 2-S maintained by G 1 were used for his test. The F_1 hybrid G 2-S by Combine kafir-60 was sterile and the hybrid M.S.1601-A by G 1 was fertile. Appathurari concluded that the cytoplasms inducing male sterility in M.S.1601-A and G 2-S were not identical, since the hybrids differed in their fertility reactions.

Ross (29) and Ross and Hackerott (30) conducted studies on the sterility response of several cytoplasms from diverse sources and found that each gave a sterility response like milo. Kafir was used to maintain these lines (KS34 to KS39). Although they contain cytoplasms other than milo, their sterility responses are similar to the milo-kafir system.

Rao (26) reviewed much of the work done in India on CGMS systems. Using a new cytoplasmic source he sterilized M-35-1 (an Indian winter sorghum) and IS3691 (a yellow endosperm hegari) which are restorers in the milo-kafir system. Fertility restoration was difficult to obtain on the new steriles of these two lines. Additional sources of cytoplasmic male sterility have been reported in durra (G2, VZM 1 and VZM 2). Another CGMS system may be in the line M-31-A, which is an induced mutation line. These CGMS lines are from a different source than milo.

Tatwawadi et al. (35) found sterile plants in an F_2 population from a cross of IS84 (feterita) by B Combine Kafir-60 (BCK-60 maintainer

line). They observed that the amount of sterility increased with the number of backcrosses to BCK-60. Since IS84 was used as a female parent, the F_1 and F_2 progenies were carrying feterita cytoplasm. They concluded that the feterita cytoplasm contained a sterility inducing system similar to milo.

Nagur (19) and Nagur and Menon (20) studied six different male-sterile stocks from diverse cultivated varieties. The male-sterile lines were ACK-60 (milo cytoplasm) AG1 (durra cytoplasm), AVZM1 (durra cytoplasm), AVZM2 (durra cytoplasm), AM-35-1 (dochna cytoplasm) and AM-31-2 (cernuum cytoplasm). These lines were crossed with BCK-60 and the F_1 hybrids were all male sterile. The maintainer line for each of the steriles was crossed on ACK-60 and all F_1 hybrids were fertile. These results indicated that the six maintainer lines differ from BCK-60 and the cytoplasms of the steriles probably differ from the milo cytoplasm of ACK-60.

Schertz and Ritchey (32) using lines of diverse types from widespread geographic locations from the conversion program (34) made intercrosses and backcrosses. Three male steriles were tested to determine their cytoplasmic diversity. Fertility of the F_1 hybrids from crosses of each sterile line with a series of tester lines was compared with fertility of hybrids from crosses of a milo-kafir sterile (ATx3197) with the same testers. Differences in fertility responses indicated that each of the three sterile cytoplasms probably differed from milo cytoplasm of ATx3197 and from each other. Sources of the three different cytoplasms were IS12662C, IS7920C and IS1116C.

Schertz (31) released the CGMS made from IS12662C x IS5322C as germplasm A2 Tx2753. The A2 CGMS system differs from the milo-kafir

system because in the A2 cytoplasm TAM428 acts as a maintainer line while in the milo-kafir system TAM428 acts as a restorer.

Pring et al. (24), using a biochemical procedure,analyzed different cytoplasms for differences in mitochondria DNA restriction fragments. From the seventeen cytoplasms studied nine were similar to the milo-kafir cytoplasm (Tx3197). Six cytoplasms were different from each other and from the milo-kafir cytoplasm. Two cytoplasms were similar but different from all other groups.

Inheritance of CGMS in Sorghum

Stephens and Holland (33) failed to obtain satisfactory data on inheritance of the CGMS system because of the poor environment of 1951 and 1952. They suggested that more than two pairs of genic factors in association with sterile cytoplasm were responsible for the lack of viable pollen production.

Maunder and Pickett (15) conducted inheritance studies on the milo-kafir sterility system and proposed that a single homozygous recessive gene pair $\underline{ms}_c\underline{ms}_c$ interacts with sterile cytoplasm to produce complete male sterility. The F_1 progeny of crosses between fertile ($\underline{MS}_c\underline{MS}_c$) x sterile ($\underline{ms}_c\underline{ms}_c$) lines segregated in a ratio of 3 fertiles to 1 sterile. However, the restored class of plants was not 100% fertile, but expressed a wide range of fertility. $\underline{MS}_c\underline{MS}_c$ plants are considered to be R-line plants or restorers while $\underline{ms}_c\underline{ms}_c$ plants are considered to be A-line plants or male-sterile plants.

Miller and Pickett (16) working with intercrosses of the inbred parents of RS610 and RS650 hypothesized that partial male fertility may be caused by two major genes, ($\underline{Pf}_1$ and $\underline{Pf}_2$). Inter- and intra-allelic

interactions in the genotypes caused fertility to vary from 5 to 100%.

In 1961, Pi and Wu (23) studied the F_2 generations from crosses of ACK-60 by nine restorer lines. They found three different ratios of segregation for male fertility and sterility. Their results showed that a single pair of recessive genes interacted with the sterile cytoplasm in five crosses, two independent recessive genes were effective in two crosses, and two crosses could not be explained with a simple hypothesis.

The BC_1 and F_2 generations from crosses between ACK-60 and 14 sudangrass cultivars were studied by Craigmiles (8). In the F_2 populations only fertile and partially male fertile plants were observed. When the F_1's were crossed back to ACK-60, certain progenies fit basic ratios. The cross ACK-60 x PI219759 gave a 1 fertile:1 sterile ratio indicating one gene for restoration. The crosses ACK-60 x PI214346, ACK-60 x 'Sweet Common', ACK-60 x 'Piper' and ACK-60 x 'Lahoma' agreed very closely with an expected 3 fertile:1 sterile ratio of two independent genes for restoration. The crosses ACK-60 x 'Samatra' and ACK-60 x 'Ga337' were in agreement with a 7 fertile:1 sterile ratio which indicated that restoration was controlled by three pairs of independent genes. The other seven combinations of ACK-60 x cultivar could not be explained by simple hypotheses.

Alam and Sandal (1) also studied the inheritance of cytoplasmic male sterility in sudangrass, using male-sterile 'Rhodesian' crossed to six sudangrass lines. The F_2 and BC_1 progenies of each cross were observed. The F_2 progenies of three crosses segregated into a ratio of 3 fertile:1 sterile and a BC_1 ratio of 1 fertile:1 sterile. Two crosses produced ratios in F_2 and BC_1 of 9 fertile:7 sterile and 1 fertile:1

sterile, respectively. The last cross produced an F_2 ratio of 54 fertile:10 sterile and BC_1 ratio of 3 fertile:1 sterile. They concluded that one, two, or three independent recessive gene pairs controlled male sterility in sudangrass.

Miller (17) reported in 1979 on the identification of a single independent recessive gene that controlled male sterility. The material used for his study was a cross between the lines BTx3197 (B-line) and SC170-6 selection (R-line). Selections from this cross in the F_6 generation were indentified as B-lines or R-lines. The B-lines crossed on ATx623 produced all sterile progeny. The R-lines crossed onto ATx623 produced all fertile progeny. Miller concluded that a single dominant gene without modifiers controlled male-sterility in this case.

CHAPTER III

MATERIALS AND METHODS

In the winter of 1978-79 hand emasculated crosses were made in the greenhouse at Oklahoma State University among six parental lines (Table I) to give the fifteen possible F_1 combinations (F_1 tester lines). All emasculations of a line were made on one sorghum panicle, using one to three branches for each cross and enclosing each cross in a separate parchment bag to exclude pollen. Basal branches of each panicle were bagged to provide selfed seed of the individual parent plant.

In 1979 the fifteen F_1 tester lines, the six parental lines, ten publicly released lines (Table II), and four different cytoplasmic-genic male-sterile lines (Table III) were grown on a Teller loam soil (a fine, loamy, mixed, thermic Udic Arguistolls) at the Perkins Agronomy Research Station, Perkins, Oklahoma. Based upon the soil test recommendations, urea (45-0-0) and muriate of potash (0-0-60) were applied broadcast preplant at a rate of 120 and 72.6 kg/ha, respectively. Water was applied by sprinkler irrigation as needed. Rows were 91 cm apart, 9.1 m long, and the within row plant spacing was 2 to 10 cm. Pollen for each of the four male-steriles came from one F_1 tester line. The four different male-sterile lines were bagged before anthesis so that crosses could be made. Three crosses were made with each parental line, one cross was made with each F_1 tester line, and one cross was made with each of the ten publicly released lines on each of the four

TABLE I

LINES WHICH WERE USED AS PARENTS

Parental lines	Alternate designation
Martin	Tx398
Wheatland	Tx399
Redlan	Tx378
Tx2536	Tx2536
TAM428	SC110
SC370	IS7435C

TABLE II

PUBLICLY RELEASED LINES USED AS POLLINATORS

Released lines	Released lines
Dwarf Redlan	OKY76
OKY8	OKY78
OKY10	OKY62
OKY15	Tx2567
OKY34	TX2568

TABLE III

PARENTAGE OF THE CYTOPLASMIC-GENIC MALE-STERILITY SYSTEMS

System	Origin or Source
A1Wheatland	Milo-kafir
A2TAM428	SC171 x TAM428
9E sterile	Ghana 9E maintained by Martin
SC299 sterile	SC299 x Tx2536

TABLE IV

PAIRED A- AND B-LINES FOR DISEASE REACTION

Lines	Lines
A&B KS56	A&B OKY54
A&B KS57	A&B OKY55
A&B KS65	A&B Redlan
A&B KS50	A&B Wheatland
A&B OK8	A&B Dwarf Redlan
A&B OK11	A&B Tx2754
A&B OK12	A&B Tx2755
A&B OK24	SC299 sterile
A&B WD4	9E sterile
A&B WDY18	A2TAM428

different cytoplasmic-genic male steriles.

All crosses and parents were threshed separately and packaged individually.

In March 1980, twenty paired progenies (A- and B-lines, Table IV) were planted in a disease nursery of Cargill Seed Company at Tivoli, Texas to be rated for naturally occurring head smut and downy mildew. The rows were 7.7 m long and the plants varied from 10 to 15 cm apart. The nursery was planted on a Victoria clay soil (fine montimorillonitic, hyperthermic typic Pellusterts) and rainfall was the only source of water. One preplant application of ammonium nitrate was applied at 90 kg/ha in December, 1979. The 9E sterile and SC299 sterile crossed by common pollinators were also planted in this nursery. Every tenth row was planted to a check cultivar or hybrid. The checks were 7169 A (a male-sterile sorgo used in the production of hybird sorghum-sudangrass), 'Piper' (a sudangrass restorer line), and R102 (a hybrid made with a feterita restorer line). The 7169 A and R102 were used to check the level of inoculum of Race 1 and Race 3 head smut, respectively. Piper was used to check the level of inoculum of downy mildew. Readings were taken in June on single rows as visual estimates of the percentage of diseased plants.

In early June 1980 all of the crosses made on the four cytoplasmic-genic male steriles by the six parental lines, the fifteen F_1 tester lines, and the ten publicly released lines along with the six parental lines were planted for fertility-sterility readings at Perkins, Oklahoma. The crosses of the male-steriles by the six parental lines were planted as crosses paired with pollinators. Ten panicles per row were bagged before anthesis on all crosses, and two panicles of the

pollinators were selfed. Every panicle of each plant of each row of the four male steriles by the fifteen F_1 tester lines was bagged.

In early October, plant counts and male fertility readings were taken. The hybrids of the male steriles crossed by the six parental lines and crossed by the ten publicly released lines were checked and the data were recorded for male fertility and male sterility by examining the ten bagged panicles. The total number of plants per row and the number of male-sterile and fertile panicles were recorded on the crosses of the male steriles by the fifteen F_1 tester lines.

A row of bagged panicles of the hybrids was classified as male-sterile, partial male-fertile, or fertile. Definitions of the three classifications used in describing the material are:

F = Male-fertile, all bagged panicles contained normal seed set (70-95%);

P = Partial male-fertile, bagged panicles had some seed set (1-70%), or one or more panicles were fertile, but not all were fertile;

S = Male-sterile, all bagged panicles contained no seed.

The open-pollinated panicles of all test crosses had normal seed set 70-95%), indicating that female sterility was not a factor in these materials.

Data from crosses with plants segregating for male-sterile and fertile panicles were compared with theoretical backcross ratios by the chi-square test for goodness of fit.

The backcross ratios that should be observed if sterility is a recessive trait conditioned by one, two, three, or four gene pair would be a 1:1, 3:1, 7:1, or 15:1 fertiles to steriles, respectively.

To determine the differences between the two non-dehiscent anther

steriles 9E and SC299 the crosses of these two steriles by the six parental lines, by the fifteen F_1 tester lines, and by the ten publicly released lines were evaluated for sterility and fertility. Head smut and downy mildew were recorded as described before for the two nondehiscent anther steriles crossed with the six parental lines and by three of the ten publicly released lines. Before anthesis a panicle branch was taken from one progeny plant of each individual cross of the two nondehiscent anther steriles by the six parental lines and ten publicly released lines. The panicle branches were stored in a solution of alcohol and glacial aectic acid in individual bottles from each of the lines and crosses until fall when the pollen was stained with a I_2KI solution. Pollen counts from anthers of each cross were checked for starch fill of pollen cells. Usually 100 to 150 pollen cells were checked per panicle.

The lines and crosses with sufficient seed were planted in 1984 on the Cargill Research Farm near Aiken, Texas on a Pullman clay loam (a fine clay loam, mixed, thermic, Forrestic Paleustolls). Based upon soil test recommendation, a fertilizer was applied at the rate of 34 kg/ha of nitrogen and 17 kg/ha of P_2O_5. Water was applied by flood irrigation as needed. Rows were 101.6 cm apart, 7.6 m long, and the within row plant spacing was 6 to 10 cm. A mid-August spraying of Malathion was used to reduce greenbug Schizaphis graminum (Rondani) populations. Ten panicles of the hybrid row of each cross were bagged. One panicle from every plant in each row of the four male-steriles crossed by the F_1 tester lines was bagged. Floret samples were also collected and preserved for the iodine test for starch content of the pollen cells as was done in 1980.

In October 1984, the fertility readings were taken from the bagged panicles of the four CGMS systems crossed by the parental lines, by the F_1 tester lines, and by the ten publicly released lines. The iodine test for starch fill of the pollen cells was done in the laboratory.

CHAPTER IV

EXPERIMENTAL RESULTS

Inheritance Studies

Male fertility readings for all hybrids of the four cytoplasmic-genic male-steriles (CMGS) crossed by the six parental lines and by the fifteen F_1 tester lines in 1980 are shown in Tables V and VI, respectively. Similar types of data gathered from Aiken, Texas in 1984 are shown in Tables VII and VIII. Fertility appeared to be increased in 1980 by temperatures of 6.4°F above the mean during July and August at Perkins, Oklahoma (14).

To determine backcross genetic ratios for male-sterility for a given sterility system, there must be a sterile producing ($\underline{ms_c}\,\underline{ms_c}$) and a fertility restoring ($\underline{MS_c}\,\underline{MS_c}$) parental line crossed to produce the F_1 tester ($\underline{Ms_c}\,\underline{ms_c}$) which is crossed onto one of the four cytoplasmic-genic male-steriles ($\underline{MS_c}\,\underline{ms_c}$ x $\underline{ms_c}\,\underline{ms_c}$). Only the milo-kafir system gave both sterile (when crossed with Redlan and Wheatland) and fertile (when crossed with Tx2536 and TAM428) progeny from the parental lines in both years. The other three sterility systems gave either partially fertile and sterile readings or all partially fertile readings.

The inheritance of the A1 milo-kafir CGMS was determined by examining the segregation ratios of the six parental lines crossed on the milo-kafir (A1 Wheatland) sterility system (Table V). In 1980 the Martin, Redlan, and Wheatland crosses were male-sterile and the Tx2536,

TABLE V

FERTILITY READINGS OF THE HYBRIDS OF THE FOUR CYTOPLASMIC-GENIC MALE-STERILITY SYSTEMS CROSSED BY SIX PARENTAL LINES IN 1980

Parental lines used as males	Cytoplasmic-genic male-sterility systems			
	A1Wheatland[1]	A2TAM428	9E Sterile	SC299 Sterile
Wheatland	S	P	S	S
Martin	S	P	S	S
Redlan	S	P	S	S
Tx2536	F	P	S	S
TAM428	F	P	S	S
SC370	F	P	P	P

[1]A1Wheatland is representative of the milo-kafir system

TABLE VI

FERTILITY READINGS OF THE HYBRIDS OF THE FOUR CYTOPLASMIC-GENIC MALE-STERILITY SYSTEMS CROSSED BY THE F_1 TESTER LINES MADE FROM THE SIX PARENTAL LINES IN 1980

F_1 Tester lines used as males	Cytoplasmic-genic male-sterility system			
	AlWheatland[1]	A2TAM428	9E Sterile	SC299 Sterile
Tx2536*TAM428	F	P	-	S
Tx2536*Wheatland	-[2]	P	S	S
Tx2536*Redlan	P	P	S	S
Tx2536*SC370	F	P	S	S
Martin*Tx2536	P	P	S	S
Martin*TAM428	P	P	S	S
Martin*SC370	P	P	P	S
Martin*Wheatland	S	P	S	S
Martin*Redlan	S	P	S	S
Wheatland*SC370	P	P	S	S
TAM428*SC370	-	-	-	-
Wheatland*TAM428	P	P	-	S
Redlan*TAM428	P	P	-	S
Redlan*SC370	P	P	P	P
Wheatland*Redlan	-	-	S	S

[1]AlWheatland is representative of the milo-kafir system.

[2]Not observed.

TABLE VII

FERTILITY READINGS OF THE HYBRIDS OF THE FOUR CYTOPLASMIC-GENIC MALE-STERILITY SYSTEMS CROSSED BY SIX PARENTAL LINES IN 1984

Parental lines used as males	Cytoplasmic-genic male-sterility systems			
	A1Wheatland[1]	A2TAM428	9E Sterile	SC299 Sterile
Wheatland	S	S	S	-
Martin	-[2]	S	S	-
Redlan	S	S	P	P
Tx2536	F	P	S	S
TAM428	F	P	S	S
SC370	-	P	P	P

[1]A1Wheatland is representative of the milo-kafir system.

[2]Not observed.

TABLE VIII

FERTILITY READINGS OF THE HYBRIDS OF THE FOUR CYTOPLASMIC-GENIC MALE-STERILITY SYSTEMS CROSSED BY F_1 TESTERS MADE FROM PARENTAL LINES IN 1984

F_1 Tester Lines used as males	Cytoplasmic-genic male-sterility systems			
	A1Wheatland[1]	A2TAM428	9E Sterile	SC299 Sterile
Tx2536*TAM428	-[2]	P	-	-
Tx2536*Wheatland	-	P	-	-
Tx2536*Redlan	P	P	P	P
Tx2536*SC370	P	P	S	S
Martin*Tx2536	P	P	S	S
Martin*TAM428	P	S	S	S
Martin*SC370	P	P	-	P
Martin*Wheatland	S	S	S	S
Martin*Redlan	S	S	P	S
Wheatland*SC370	P	P	-	S
TAM428*SC370	-	-	-	-
Wheatland*TAM428	P	-	-	S
Redlan*TAM428	P	-	-	P
Redlan*SC370	P	-	-	-
Wheatland*Redlan	-	P	S	S

[1]A1Wheatland is representative of the milo-kafir system.

[2]Not observed.

TAM428, and SC370 crosses were fertile. The male-sterility reactions of the F_1 tester lines on the milo-kafir (Al Wheatland) sterility system (Table VI) were as follows: two crosses were male sterile, two crosses were male fertile, eight crosses were partially male fertile, and seeds were not available for three crosses. These reactions were expected since the two male-sterile crosses came from B-line crossed by B-line testers, the two fertile crosses came from R-line crossed by R-line testers, and the eight partial male-fertile crosses came from B-line crossed by R-line testers.

In 1984, as shown in Table VII, seeds were available for crosses with only four of the six parental lines. The readings available agreed with those from 1980. The male-sterility reactions of the F_1 testers on the milo-kafir male-sterility systems as shown in Table VIII were in close agreement with 1980 and were as follows: two crosses were male sterile (same as in 1980), no crosses were fertile, nine crosses were partially male-fertile (same as in 1980 plus one more), and seed were not available for four crosses. These results were expected except that Tx2536*SC370 crossed onto Al Wheatland was expected to be fertile rather than partially fertile.

Since the milo-kafir male-sterility system was the only system which gave different sterility and fertility readings for the parental lines used in 1980 and 1984, the milo-kafir male-sterility system was the only one in which the inheritance could be determined. When one considers the genes for fertility-sterility reactions, the crosses of the F_1 tester lines ($\underline{MS}_c\underline{MS}_c$, $\underline{MS}_c\underline{ms}_c$, $\underline{ms}_c\underline{ms}_c$) onto the Al Wheatland CGMS ($\underline{ms}_c\underline{ms}_c$) can be treated as backcrosses. Therefore, Chi-Squares for backcross data for the milo-kafir (Al Wheatland) male sterility system

were calculated and are presented in Tables IX and X.

The ratios observed in 1980 were somewhat different from those observed in 1984. In 1980 the three tester lines, Tx2536*SC370, Martin*SC370, and TAM428*Redlan, when crossed on the Al male-sterility (Al Wheatland) system gave 15:1 backcross ratios of fertiles to steriles indicating four independent recessive genes. The three tester lines, Tx2536*SC370, TAM428*Martin, and TAM 428*Redlan, when crossed on the Al sterility system gave 7:1 backcross ratios of fertiles to steriles indicating three independent recessive genes. The hybrids from the Al milo-kafir male-sterility system by the two tester lines Tx2536*SC370 and TAM428*Redlan, fit two different genic ratios for fertility to sterility. Five other crosses of Al male-steriles by the tester lines Tx2536*Redlan, Tx2536*Martin, Wheatland*SC370, TAM428*Wheatland, and Redlan*SC370, fit a three fertile to one male-sterile backcross ratio, indicating two independent recessive genes for sterility.

In 1984, two ratios were observed for the Al milo-kafir male-sterile system by the F_1 tester lines. Four hybrids fit a 1:1 backcross ratio, indicating one independent recessive gene for sterility. They were Tx2536*Redlan, TAM428*Martin, Wheatland*SC370, and TAM428*Redlan. The other five crosses from the F_1 tester lines on the Al male-sterile fit a 3:1 backcross ratio indicating two independent recessive genes for male-sterility. Six of the nine crosses tested showed more male-sterility in 1984 than 1980, while three of the nine crosses produced the same genetic ratio for male-sterility.

The readings of the crosses of the Al milo-kafir male-sterility system by eight of the ten publicly released lines gave fertile readings both years (Table XI and XII). The publicly released lines OKY76 and

TABLE IX

CLASSIFICATION OF BACKCROSS POPULATIONS OF CROSSES OF A1WHEATLAND BY F_1 TESTER LINES WITH CHI-SQUARE AND PROPABILITY VALUES IN 1980

Cross	Observed number of plants in classes			Expected ratio	Values	
	Fertile	Sterile	Total		X^2	P
Tx*2536*Redlan	60	25	85	3:1	0.882	.50-.30
Tx2536*SC370	59	5	64	15:1	0.267	.70-.50
	59	5	64	7:1	1.286	.30-.20
Tx2536*Martin	61	19	80	3:1	0.067	.90-.70
TAM428*Martin	71	12	83	7:1	0.291	.70-.50
Martin*SC370	81	4	85	15:1	0.346	.70-.50
Wheatland*SC370	51	20	71	3:1	0.380	.70-.50
TAM428*Wheatland	55	15	70	3:1	0.476	.50-.30
TAM428*Redlan	47	4	51	15:1	0.221	.70-.50
	47	4	51	7:1	1.011	.50-.30
Redlan*SC370	50	17	67	3:1	0.005	.95-.90

TABLE X

CLASSIFICATION OF BACKCROSS POPULATIONS OF CROSSES OF A1WHEATLAND BY F_1 TESTER LINES WITH CHI-SQUARE AND PROPABILITY VALUES IN 1984

Crops	Observed number of plants in class			Expected Ratio	Values	
	Fertile	Sterile	Total		X^2	P
Tx2536*Redlan	20	16	36	1:1	0.440	.70-.50
Tx2536*SC370	27	10	37	3:1	0.080	.90-.70
Tx2536*Martin	43	10	53	3:1	1.062	.50-.30
TAM428*Martin	22	20	42	1:1	0.095	.90-.70
Martin*SC370	36	8	44	3:1	1.091	.30-.20
Wheatland*SC370	7	14	21	1:1	2.333	.20-.10
TAM428*Wheatland	32	13	45	3:1	0.362	.70-.50
TAM428*Redlan	17	11	28	1:1	1.286	.30-.20
Redlan*SC370	23	12	35	3:1	1.609	.30-.20

Dwarf Redlan were not crossed onto the A1 milo-kafir sterility system.

The reaction of A2TAM428 crossed by the six parental lines was studied in 1980 (Table V) and 1984 (Table VII). In 1980 all of the progenies were partially-fertile. In 1984, three of the six crosses (Wheatland, Martin, and Redlan) were male-sterile while the other three crosses were partially-fertile. A2TAM428 crossed by B2TAM428 should have been sterile both years, but some outcrossing, partial fertility genes, or modifiers resulted in some fertility occurring.

In 1980 all of the crosses of A2 sterile by the F_1 tester lines were partially-fertile (Table VI), but in 1984 the readings from the crosses of A2 sterile by the F_1 tester lines Martin*TAM428, Martin*Wheatland and Martin*Redlan were sterile (Table VIII). All of these crosses involve Martin.

The A2TAM428 by Wheatland*Redlan was partially fertile, but it was expected to be sterile because both parental lines were sterile on A2TAM428 sterility system. Probably some restorer genes or modifiers to the A2 sterility system can be found in the Redlan parent.

In 1980, the crosses from the A2TAM428 sterile by the ten public lines were fertile (Table XI). In 1984 (Table XII), the crosses from the A2TAM428 sterile by the public lines OKY8, OKY10, OKY34, and OKY78 were fertile, while the crosses with OKY15, OKY62, Tx2567, and Tx2568 were partially fertile with 1-2% fertility per panicle per cross. The fertility reaction of the cross of A2TAM428 sterile by Dwarf Redlan was sterile in 1984, whereas in 1980 the reaction had been fertile. Publicly released lines OKY15, OKY62, Tx2567, and Tx2568 could probably be made into maintainer lines for the A2TAM428 CGMS system. Male sterility in the A2TAM428 cytoplasm tends to increase as the temperature

TABLE XI

FERTILITY READINGS OF THE HYBRIDS OF THE FOUR CYTOPLASMIC-GENIC MALE-STERILITY SYSTEMS CROSSED BY TEN PUBLICLY RELEASED LINES IN 1980

Public lines used as males	Cytoplasmic-genic male-sterility systems			
	A1Wheatland[1]	A2TAM428	9E Sterile	SC299 Sterile
OKY8	F	F	S	S
OKY10	F	F	S	S
OKY15	F	F	S	S
OKY34	F	F	S	S
OKY62	F	F	S	S
OKY76	-[2]	F	S	-
OKY78	F	F	S	S
Tx2567	F	F	S	S
Tx2568	F	F	-	S
Dwarf Redlan	-	F	S	S

[1]Wheatland is representative of the milo-kafir system.

[2]Not observed.

TABLE XII

FERTILITY READINGS OF THE HYBRIDS OF THE FOUR CYTOPLASMIC-GENIC MALE-STERILITY SYSTEMS CROSSED BY THE TEN PUBLICLY RELEASED LINES IN 1984

Public lines used as males	Cytoplasmic-genic male-sterility systems			
	A1Wheatland[1]	A2TAM428	9E Sterile	SC299 Sterile
OKY8	F	F	S	P
OKY10	F	F	P	F
OKY15	F	P	S	S
OKY34	F	F	P	-
OKY62	F	P	P	P
OKY76	-[2]	-	S	-
OKY78	F	F	F	-
Tx2567	F	P	S	-
Tx2568	F	P	-	S
Dwarf Redlan	-	S	P	P

[1]Wheatland is representative of the milo-kafir system.

[2]Not observed.

moderates.

Comparison of 9E and SC299 Sterility Systems

Fertility and Sterility Studies

To determine the differences between 9E and SC299 male-sterility systems, the fertility reactions of crosses of these steriles by six parental lines (Table V and VII) and ten F_1 tester lines (Table VI and VIII) were compared in 1980 and 1984.

In 1980 the crosses of the six parental lines onto 9E sterile and SC299 sterile gave sterile progeny when crossed by Wheatland, Redlan, Martin, Tx2536, and TAM428. The crosses using SC370 were partially fertile. The male-sterility readings in 1980 of the crosses from the 9E sterility system by the F_1 tester lines indicated the following: nine crosses were male-sterile, two crosses were partially male-fertile. Four crosses were not observed. The male-sterility readings of the crosses from the SC299 male-sterility system by the F_1 tester lines in 1980 indicated the following: thirteen crosses were male-sterile, and one cross was partially-fertile. One cross was not observed.

In 1984 the fertility readings of the crosses of the 9E sterile by the six parental lines indicated male-sterile progeny from Wheatland, Martin, Tx2536, and TAM428. The progeny from Redlan and SC370 were partially fertile. The fertility readings of the crosses of 9E sterile by the F_1 tester lines indicated the following: five crosses were male-sterile (also sterile in 1980), two crosses were partially fertile (these were sterile in 1980). Eight crosses were not observed. The crosses of SC299 sterile by the six parental lines in 1984 gave partial

fertile progeny from Redlan (sterile in 1980) and SC370. Progeny from Wheatland and Martin were not observed. Crosses of the SC299 sterile and the F_1 tester lines in 1984 gave the following: eight crosses were male-sterile (also male sterile in 1980), three crosses were partially fertile (all sterile in 1980), and four crosses were not observed. The fertility reactions of the test crosses from the six parental lines onto 9E and SC299 sterile agreed within years. The reaction of the F_1 tester lines onto 9E and SC299 sterile showed a difference for the Martin*SC370 F_1 in 1980 and Martin*Redlan F_1 in 1984. These crosses involve Martin again.

To further determine the differences between the 9E and the SC299 sterility systems, both were crossed by the ten publicly released lines. In 1980, the crosses of 9E and SC299 sterile by the ten publicly released lines were all sterile as shown in Table XI. However, two crosses were not observed. In 1984, the crosses of the 9E and SC299 sterile systems produced a range of reactions from fertile to sterile as shown in Table XII.

Readings from the two steriles differed for OKY8 and OKY10, only. The 9E sterile crossed by OKY8 gave all male-sterile progeny while the SC299 sterile crossed by OKY8 gave partially fertile progeny consisting of nine sterile panicles and one fertile panicle. When the OKY10 pollinator was crossed onto the 9E sterile and SC299 sterile, the fertility readings of the SC299 hybrid were male-fertile, but the 9E hybrids consisted of 9 male-fertile panicles and one male-sterile panicle. The readings agreed, then, except for one aberrant plant in each comparison.

Pollen Studies

Observations of starch-fill of pollen cells from the crosses of 9E and SC299 steriles by the six parental lines and by the ten publicly released lines for 1980 are shown in Table XIII. Starch fill was read as grains filled with starch, partially filled, and grains empty from the iodine test for starch. The percentages of pollen grains filled with starch were relatively similar for 9E and SC299 hybrids. If a 9E hybrid had a high percentage of grain filled with starch, so did the SC299 hybrid. This relationship held for grains partially filled and grains empty, but there were exceptions. Hybrids with 9E and SC299 not only have nondeshiscent anthers, but the pollen grains tend to be less than completely filled with starch.

In 1984, the material was grown under a more favorable environment and pollen samples were classified as shown in Table XIV. The results showed less of a tendency for 9E and SC299 hybrids to be similar, but there was some tendency for the partially filled category to be largest.

Statistical differences could not be estimated on these observations, but the 9E and SC299 CGMS systems were not shown to be different.

Disease Observations

The two sterility systems were compared as to their disease reactions at Tivoli, Texas in 1980. Head smut and downy mildew were the only diseases observed. Check rows observed indicated that head smut and downy mildew inoculum were present. The crosses of the two

TABLE XIII

STARCH-FILL OF POLLEN GRAINS AS MEASURED BY STAINING FROM THE 9E AND SC299 STERILES CROSSED BY SELECTED LINES IN 1980

Selected lines	Starch-fill in hybrids					
	Grains filled		Partially filled		Grains empty	
	9E	SC299	9E	SC299	9E	SC299
	-%-					
B9E Martin	0	17	76	76	24	7
Wheatland	21	53	68	47	11	0
Redlan	56	53	44	36	0	11
Tx2536	24	2	58	89	18	9
TAM428	14	22	63	56	23	22
SC370	26	77	61	8	13	15
ROKY8	93	89	7	11	0	0
ROKY10	18	14	58	75	25	11
ROKY15	0	39	100	43	0	18
ROKY34	-[1]	-	-	-	-	-
ROKY62	73	11	22	68	5	21
ROKY76	-	-	-	-	-	-
ROKY78	-	18	-	71	-	11
Tx2567	2	17	76	21	22	62
Tx2568	-	26	-	61	-	23
Dwarf Redlan	-	18	-	71	-	11
Mean[2]	29.7	35.8	57.6	48.2	12.8	16.0

[1]Not observed.

[2]Mean of pollinators observed on both females.

TABLE XIV

STARCH-FILL OF POLLEN GRAINS AS MEASURED BY STAINING FROM THE STERILES 9E AND SC299 CROSSED BY SELECTED LINES IN 1984

Selected lines	Starch-fill in hybrids					
	Grains filled		Partially filled		Grains empty	
	9E	SC299	9E	SC299	9E	SC299
	%					
B9E Martin	30	-[1]	21	-	49	-
Wheatland	26	-	74	-	10	-
Redlan	12	13	86	12	2	75
Tx2536	4	21	13	56	83	23
TAM428	4	1	82	23	12	76
SC370	16	30	53	52	31	18
ROKY8	1	15	84	49	15	36
ROKY10	61	42	35	26	4	31
ROKY15	6	3	57	65	37	32
ROKY34	83	-	14	-	3	-
ROKY62	27	11	60	43	13	46
ROKY76	41	-	33	-	26	-
ROKY78	61	-	36	-	3	-
Tx2567	0	-	0	-	100	-
Tx2568	-	0	-	83	-	11
Dwarf Redlan	26	31	53	43	21	26
Mean[2]	28.6	18.6	58.1	41.0	24.2	40.3

[1]Not observed.

[2]Mean of pollinators observed on both females.

sterility systems by the six parental lines and three of the ten publicly released lines were observed and the data are compared in Table XV. Of the nine selected lines used to make crosses on the two sterility systems, 9E and SC299, only one (TAM428) produced hybrids with a disease-free reaction on both steriles, while the other eight produced hybrids which varied in disease ratings from 0 to 10%. Statistical differences could not be calculated, but 9E and SC299 could not be declared different on the basis of these disease observations.

Disease Reaction of Paired Progenies (A- and B-lines)

The twenty paired progenies (A- and B-lines) were also grown at Tivoli, Texas in 1980, as shown in Table XVI. Head smut and downy mildew were observed on the different paired progenies. For downy mildew some pairs showed more disease in the A-line while others showed more disease in the B-line. The pairs which were most susceptible to downy mildew had identical readings. However, the incidence was so low in general that a trend could not be established. For head smut some pairs had higher readings for the A-line and some had higher readings for the B-line. Several pairs had identical readings, but the incidence was low in general and no trend could be established.

TABLE XV

DISEASE OBSERVATIONS OF 9E AND SC299 STERILES CROSSED BY SELECTED LINES, TIVOLI, TEXAS, 1980

Pollinator	Diseased plants[1]			
	Head smut		Downy mildew	
	9E	SC299	9E	SC299
	- - - - - - - - - - -%- - - - - - - -			
Wheatland	0.0[2]	2.0	0.0	0.7
Redlan	0.0	2.0	2.0	3.5
Tx2536	3.3	5.0	0.0	0.0
TAM428	0.0	0.0	0.0	0.0
SC370	4.0	0.0	4.5	0.0
B9E Martin	0.6	0.0	1.8	2.0
ROKY10	0.0	0.0	2.0	0.0
ROKY15	10.0	2.0	0.0	0.0
ROKY62	2.0	3.0	6.0	3.0
Mean	1.92	1.02	2.21	1.56

[1]Checks A7169 and R102 averaged 33 and 16% head smut, respectively, and Piper averaged 36% downy mildew.

[2]Single observation.

TABLE XVI

DISEASE OBSERVATIONS OF PAIRED PROGENIES (A- AND B-LINE) FOR DOWNY MILDEW AND HEAD SMUT, TIVOLI, TEXAS, 1980

Pedigree	Diseases[1]			
	Downy mildew		Head smut	
	A-line	B-line	A-line	B-line
	%			
KS56	0[2]	2	6	8
KS57	0	0	0	0
KS65	2	0	4	4
KS50	50	50	0	0
OK8	4	4	0	2
OK11	0	0	2	2
OK12	0	0	8	0
OK24	2	0	2	4
WD4	4	0	2	0
WD18	0	0	0	0
OKY54	0	2	0	0
OKY55	0	4	0	4
Redlan	0	2	7	4
Wheatland	0	0	0	0
Dwarf Redlan	0	2	0	0
Tx2754	0	2	2	0
TX2755	6	6	0	6
SC299 Sterile	2	6	0	0
9E Martin	1	1[3]	3	3[3]
A2TAM428	0	0[4]	0	0[4]
Mean	3.55	4.05	1.80	1.85

[1]Checks A7169 and R102 averaged 33 and 16% head smut, respectively, and Piper averaged 36% downy mildew.

[2]Single observation

[3]Means of 10 observations on A- and B-lines.

[4]Means of 2 observations on A- and B-lines.

CHAPTER V

SUMMARY AND CONCLUSIONS

Steriles from four cytoplasmic-genic male-sterility (CGMS) systems were crossed with three groups of testers: six parental lines; 15 F_1 tester lines (made by intercrossing the six parental lines); and ten publicly released lines. These crosses were grown out to obtain data on sterility in 1980 near Perkins, Oklahoma and in 1984 near Aiken, Texas. Backcross ratios were determined for crosses of the F_1 tester lines onto the A1 milo-kafir CGMS system and they were tested by Chi-Square for goodness-to-fit to a one, two, three, or four gene ratio in order to estimate the number of genes involved.

The inheritance of the A2Tx428 CGMS system was not determined, but the system was determined to have a cytoplasm different from the A1 milo-kafir, the 9E, or the SC299 system based on the results of the crosses. Also the expression of sterility appeared to be influenced by the environment.

The 9E and SC299 CGMS systems (nondehiscent anther character) were compared for sterility throughout the test crosses, for pollen starch-fill, and for disease reaction. Also, twenty paired progenies (A- and B-lines) were observed for reaction to naturally occurring head smut and downy mildew in 1980 near Tivoli, Texas.

In the inheritance study, the phenotypic ratios from backcross data indicated 1, 2, 3, or 4 independent recessive genes controlling male sterility. Estimates from the data seemed to indicate fewer genes

involved in sterility in 1984 than in 1980. Inter- or intra-allelic interaction, the environment, or a combination of these factors may have influenced the expression of sterility.

The 9E and SC299 CGMS systems were similar for fertility readings, pollen starch-fill and reaction to head smut and downy mildew.

Data accumulated were very similar on the reaction to head smut and downy mildew of pairs of A-lines and B-lines (paired progenies).

CONCLUSIONS

1. The inheritance of the Al milo-kafir CGMS systems is controlled by one to four nuclear genes in the presence of sterile cytoplasm.

2. A2Tx428 CGMS system is different from Al milo-kafir, 9E, and SC299 CGMS systems. The number of genes involved was not determined, but it appears that caution should be exercised in the use of this system because of the influence of the environment on its expression.

3. 9E and SC299 CGMS systems reacted very similarly in the test crosses for fertility, in the pollen analysis, and in the reaction to head smut and downy mildew. Additional data are needed to determine if differences exist for pollen starch-fill.

4. Because of the concern over genetic vulnerability, the A-lines and B-lines of 20 paired progenies were evaluated to head smut and downy mildew, but none of the A-lines appeared to have disease susceptibility associated with sterility.

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VITA

Jimmy Mack Ritchey

Candidate for the Degree of

Doctor of Philosophy

Thesis: INTERRELATIONS OF CYTOPLASMIC-GENIC MALE-STERILITY STYSTEMS IN SORGHUM

Major Field: Crop Science

Biographical:

Personal Data: Born in Colorado City, Texas, June 4, 1946, the son of Mack and Irene Ritchey.

Education: Graduated from Colorado High School, Colorado City, Texas, May 1964; graduated from Texas Technological University, Bachelor of Science degree in Agronomy, August, 1968; graduated from Texas A & M University with a Master of Science degree in May 1976; completed the requirements for Doctor of Philosophy degree at Oklahoma State University, December, 1985.

Professional Experience: Employed by ACCO Seed Company, sorghum and pearl millet breeding - Agronomist, July 1968 to January 1975; employed by the Soils and Crop Science Department, Texas A & M University, College Station, Texas January 1975 to July 1976. Employed by George Warner Seed Company, Hereford, Texas, sorghum and small grain breeder, July 1976 to August 1978. Employed by Sorghum Breeding Project in the Agronomy Department at Oklahoma State University, August 1978 to August 1980. Employed by Arkansas Tech University, Russellville, Arkansas, Assistant Professor of Agriculture, August 1980 to June 1982. Employee of Eastside Church of Christ, Director of Christian Student Center, Western Texas College, Snyder, Texas, also part time instructor in Agriculture, June 1982 to present.