PRODUCTION OF COMMERCIAL F_2 COTTON (Gossypium) HYBRIDS UTILIZING A SELECTIVE MALE GAMETOCIDE

by

James Michael Olvey

A Dissertation Submitted to the Faculty of the

DEPARTMENT OF PLANT SCIENCES

In Partial Fulfillment of the Requirement
For the Degree of

DOCTOR OF PHILOSOPHY
WITH MAJOR IN AGRONOMY AND PLANT GENETICS

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Production of commercial F_2 cotton (*Gossypium*) hybrids utilizing a selective male gametocide

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GRADUATE COLLEGE

As members of the Final Examination Committee, we certify that we have read the dissertation prepared by James Michael Olvey

entitled Production of Commercial F_2 Cotton (Gossypium) Hybrids Utilizing a Selective Male Gametocide

and recommend that it be accepted as fulfilling the dissertation requirement for the Degree of ______________.

Warner D. Fisher — Date: August 2, 1991

Elgar L. Turcotte — Date: August 2, 1991

Lee S. Stith — Date: August 2, 1991

Hiroshi Muramoto — Date: August 2, 1991

Robert E. Briggs — Date: August 2, 1991

Final approval and acceptance of this dissertation is contingent upon the candidate's submission of the final copy of the dissertation to the Graduate College.

I hereby certify that I have read this dissertation prepared under my direction and recommend that it be accepted as fulfilling the dissertation requirement.

Lee S. Stith
Dissertation Director

August 6, 1991
Date

STATEMENT BY AUTHOR

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SIGNED: James M. Olvey

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I am dedicating this dissertation to my mother, Mrs. Eleanor Louise Olvey and my brother, Mr. John Wesley Olvey.

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ABSTRACT

Literature was reviewed to substantiate the authors' concept that the F_2 hybrid in Upland cotton (Gossypium hirsutum L.) is a usable product. Obstacles to hybrid cotton production include effective emasculation techniques, economical methods to produce F_1s, including pollen transfer by insect vectors, and identification of parental combinations that demonstrate useful heterosis.

F_1 hybrids useful in commercial agricultural crops became the focus of attention of plant breeders in the 1940's when, through mechanical emasculation of one monecious parent, a hybrid could be easily produced and the maximum expression of heterosis exploited. The complete flower of cotton, however, dictates chemical or biological rather than mechanical emasculation and the techniques available create problems of phytotoxicity, cytoplasmic incompatibility, and/or restoration. The author therefore abandoned the use of the F_1 hybrid concept for cotton hybrids and began to evaluate an alternative, the F_2 hybrid. The problems associated with genetic segregation in F_2 generations in other crops delayed acceptance of a F_2 hybrid concept for cotton until the 1980's when the research discussed herein and supported by University of Arizona, Pennwalt Corporation, and American Cyanamid

Corporation was made. Trade secret constraints allow only the reporting of summarized data and not the detailed information appropriately on file with the companies.

In the 26 year period between 1947 to 1973, only 70 hybrids were created by cotton researchers and evaluated in the F_2 generation for yield performance. Olvey and team created 467 hybrids using chemical emasculation techniques which were evaluated and reported in 1985 and 1986. Other researchers throughout the cotton belt have now studied 69 F_2 hybrids since 1986. The acceptance of the F_2 hybrid concept traces directly to the specific program developed by the author.

Research cited substantiates that the chemical TD-1123 (3,4-dicloroisothiazole-5-carbolic acid) is an effective emasculator, that production costs can be reduced considerably by marketing the F_2 hybrid, and that extensive F_2 hybrid yield testing has shown that the F_2 hybrid has promise as a commercially feasible product.

CONFIDENTIALITY STATEMENT

All information in this dissertation is based on published information references, including my own publications, in order to ensure the protection of trade secrets of CHEMBRED, INC.[R], a subsidiary of American Cyanamid Company.

CHAPTER 1

INTRODUCTION

Over the past 30 years, a great deal of effort has been devoted to the production of cotton hybrids on an experimental basis. The cotton hybrids have been both inter- and intraspecific. Many of the reports on these efforts indicate the benefit of hybrid cotton for commercial production (El-Adl and Miller, 1971; Jones and Loden, 1951; Kime and Tilley, 1947; Marani, 1968a; Meredith and Bridge, 1972; Meredith, et al., 1970; Miller and Marani, 1963; Miller and Lee, 1964; Thomson, 1971; Turner, 1953a; Turner, 1953b; White and Richmond, 1963).

The objective of this dissertation is to explain the utilization of the F_2 hybrid concept, as conceived by the author, to develop a commercial product, utilizing a selective male gametocide.

Most of the published material that was reviewed was used to develop this objective; and to put all the essential parts together, not only to substantiate but to document. The essential component parts are a chemical hybridizing agent (CHA) and its effective utilization, and the economical production of F_1 and F_2 seed, and testing the F_2 hybrid across environments to arrive at a viable commercial product.

Muramoto (1958) stated that the prerequisites for commercialization of cotton hybrids, the following problems must be solved before hybrid cotton can become a commercial reality:

1. Emasculation by the application of a selective male gametocide or the use of male sterile lines.
2. Effective cross-pollination by insects.
3. Selection of high combining parents which will give the desired hybrids.

If hybrids can be a potentially effective commercial product, each of these problems must be solved or negated. The prime incentive for hybrid cotton production is to increase yield and/or improve fiber properties in varieties of cotton by taking advantage of the considerable heterosis known to exist within the crop. For several decades, numerous scientific studies have been published which document significant amounts of heterosis in cotton (Davis, 1978) and thus, the potential agronomic value of hybrid cotton (Table 1.1). Davis (1978) in Table 1.2 summarizes the heterotic response in certain agronomic and fiber properties of G. hirsutum x G. barbadense L. hybrids.

Several obstacles have limited the direct exploitation of hybrid vigor in cotton on a commercial scale. Some of the difficulties include the time-consuming effort of hand-emasculation of the female parent to produce F_1 seed, the deleterious effects of the sterile cytoplasm within Gossypium harknessii Brandegee, pollination techniques, development and identification of parent combinations showing significant levels of heterosis and justification of the cost to produce hybrid cottonseed (Sheetz, 1984).

The road to commercial use of hybrid vigor (or heterosis) in cotton has proven to be filled with a great deal of unanticipated or unexpected detours.

An F_2 hybrid as described in this thesis results from a cross between two parental lines resulting in at least 95% hybrid plants in the F_1, then the F_1 generation is increased under conditions maximizing self-pollination resulting in an F_2 hybrid. The F_2 hybrid is the second filial, which retains some hybrid vigor.

Cotton is normally defined as a self-pollinating crop. To produce hybrid seed, pollen must be removed from the female parent prior to anthesis in order that the pollen from only the selected male parent will fertilize the female parent. This mechanism of pollen removal from the female parent has been a major obstacle for cotton breeders; however, with the utilization of CHA, this is no longer a major concern.

Hybrid cottonseed is popular in India and is grown on a considerable number of acres throughout the country (Munro, 1987). Manual labor is used to hand emasculate and hand-pollinate cotton flowers which makes the cost of hybrid seed approximately 20 times higher than conventional seed, however, hybrid cotton seed can be produced cost effectively where labor is inexpensive.

The discovery of cytoplasmic male sterility (CMS) within the Gossypium harknessii Brandegee species (Meyer, 1975) circumvented the problem of hand-emasculation, but produced other obstacles. Since 1975, the CMS system has predominated as a means to hybridization. A considerable amount of effort has been put into researching CMS hybridization of cotton including the okra leaf versus normal leaf system developed by Texas Agricultural Research Center cotton breeder LeVon Ray (personal communication). In this case the F_1 hybrid is distinguishable by the heterozygous okra-leaf shape, an intermediate leaf shape between the parent having okra-leaf shape and the other parent having normal leaf shape. This presence of heterozygous leaf shape insures that hybridization has occurred and is an excellent means of determining percent hybrid plants. Gannaway, et al., (1986) reported some yield improvement evident in hybrids, however, fiber quality was slightly inferior to normal inbred varieties. It is the opinion of this author that use of the okra-leaf trait with its inherent lower yield should be avoided. Meyer (1976) was the first to report that there may be some possible deleterious effects as a result of using the CMS G. harknessii Brandegee cytoplasm, which may explain the inconsistent heterotic effects (Schoenhals and Gannaway, 1990).

With discovery of a selective male gametocide by the author (Olvey, et. al. 1981), the chemical sterilization of pollen of the female parent for the production of hybrid seed became a more desirable alternative. This method would obviate the need for hand emasculation as well as bypass the anomalies associated with G. harknessii Brandegee cytoplasm.

The lack of control of the insect vectors for pollination makes F_1 seed production uneconomical and impractical, even utilizing the CHA method. The initial concept of a commercially feasible F_2 hybrid was demonstrated by Olvey (1986).

Within the scientific community as well as the cotton industry, there is excitement about increasing F_1 seed and marketing the F_2 hybrids for commercial use. Through this procedure, at least a partial heterosis may be utilized for commercial gain.

There has been major concern that there is high variability within the F_2 hybrid in appearance and in its fiber properties. It is the opinion of this author that these concerns are unwarranted, particularly when parental selection for the F_2 emphasizes productivity and limits divergence between parents.

CHAPTER 2

LITERATURE REVIEW AND DISCUSSION

Extensive literature reviews have been placed throughout appropriate sections of this dissertation. Since each section can stand on its own merits, the literature review and discussion are embodied therein, and summarized in the conclusion. This format was used to address separate issues that unite the F_2 hybrid concept as proposed by the author. Due to the constraints imposed by copyright restrictions, the section of materials and methods has been omitted and the above mentioned concept approach has been followed in this discussion. The statistical details discussed are on file in the archives of the sponsoring agency so copyright information may be legally protected. Published research results that has been statistically verified are presented where appropriate.

CHAPTER 3

EMASCULATION TECHNIQUES

The cotton flower is botanically classified as perfect in that both male and female reproductive parts are located in the same floral structure. In order to produce hybrid plants, the male portion of the flower, the anthers, must be removed or be sterile while the female portion remains fertile. Presently, the only means of accomplishing emasculation in cotton is hand removal of the anther sacs, an extremely labor-intensive method. Hand emasculation has been done only in China and India on a commercial scale and is too expensive to be economically feasible in the United States. The method most commonly proposed in utilizing hybrid vigor in cotton (Christidis and Harrison, 1955) involved genetic and/or cytoplasmic male sterile plants. Those who have reported genetic male sterility within Upland (G. hirsutum L.) cotton are Turner (1948), Justus and Leinweber (1960), Fisher (1961), Justus, et al., (1963), Allison and Fisher (1964), Meyer and Meyer (1965) and Weaver and Ashley (1971). Genetic male steriles also have been reported in Pima (G. barbadense L.) cotton (Turcotte and Feaster, 1985).

Cytoplasmic male sterile plants have been developed by Meyer (1969) but they present numerous problems regarding fertility restoration within the hybrid and a great many production problems (Fisher, 1979). Meyer (1969) was the first cotton geneticist to develop a stable cytoplasmic male sterile cotton, making 3,000 test crosses, which resulted in only two male-sterile offspring. The source of Meyers' cytoplasmic male sterility was from the wild cotton species Gossypium harknessii Brandegee.

Chemical hybridizing agents (CHAs)

Another means of obtaining male sterility is the use of a selective male gametocide or chemical hybridizing agent (CHA) which can be applied to almost any crop and is an effective means of obtaining male sterility.

CHA refers to a genera of chemicals that selectively render the male portion (pollen) of the flower non-functional. Cotton pollen in CHA-treated plants is either underdeveloped, dysfunctional or does not dehisce. Dehiscence is the spontaneous opening of a structure, such as anthers sacs, permitting the escape of reproductive entices (or pollen) contained in the dehiscing structure. CHAs are useful as a breeding tool to eliminate the fertility of the male portion of the flower thereby allowing for cross pollination with another pollen source. Examples of other CHAs include SC1056 and SC1271 on wheat (Schultz and Almeda, 1988); Hybrex ™, RHOOO7 (McRae, 1983) for small grains; Ethrel used for a number of crops, but primarily grain cereals (Rowell and Miller, 1971); A3C (azetidine-3-carbolic Acid) produced by Shell and shown to be an effective CHA for small grain cereals; and TD-1123 in cotton (Olvey, 1983).

Both Moore (1950) and Naylor (1950) demonstrated that male sterility in grains can be obtained by applying maleic hydrazide. Since that time, numerous other chemical hybridizing agents have been developed and tested. One of the main difficulties observed with the application of chemical hybridizing agents is that along with male sterility, there is an accompanying adverse effect upon female fertility. Most CHA's are not selective for just male sterility but also induce some female sterility. Another shortcoming is the fact that many of these chemicals are phytotoxic and affect the plant physiologically. Maleic hydrazide stops terminal growth. Some CHA's induce significant bract burn and phytotoxicity on foliage. Many crops require numerous CHA applications in order to obtain complete male sterility throughout the effective flowering period, and repeated dosages further aggravates the female fertility problem.

In order for the CHA technology to be used as an efficient breeding tool in the development of hybrids, at least 95% sterility must be obtained and maintained throughout the entire effective flowering period. Other details to be addressed must include:

1. determination of application rates,
2. timing on the selected crop,
3. determination of varietal differences in reaction to CHA within the crop,
4. environmental conditions affect in CHA utilization,
5. development of an effective production scheme.

The gametocide TD-1123 was compared to OMT L-0-methyl thyronine and SD-227559 which were reported to produce male sterility in all dicotyledonous crops (Ladyman et al., 1990). Both TD-1123 and OMT demonstrated selective CHA activities at dose rates of 0.9 and 0.45 kg/ha^{-1}. Both chemicals were phytotoxic based on reduced plant stature at the highest dosage rate of 1.8 kg/ha^{-1}. TD-1123 treatments at 0.9 and 0.45 kg/ha^{-1} had significantly higher numbers of hybrid seed than the controls. TD-1123 proved to be phytotoxic to some extent at all rates. Leaf necrosis and inhibition of flower development were observed for several weeks after spraying. At the lower dose rates, TD-1123 was less phytotoxic to the plant and therefore resulted in more effective treatment (Table 4.1, appendix A). Bull and Shaver (1980) found that TD-1123 was relatively stable over an extended period of time within three soil types. After 6 months post-treatment, recoveries of the parent compound (TD-1123) from the soil were 81, 92, and 83% of the applied dosage. It also was found that TD-1123 leached readily within these same soil profiles. Post-harvest soil residues, after being treated with one application of TD-1123 at the rate of 1.12 kg/ha^{-1}, declined to less than 0.1 ppm after 1 year; and residues of radioactive carbon within the rotational crop study were insignificant. CHA use greatly simplifies cotton breeding and production procedures for the utilization of hybrid cotton. The expense and operational time in the development and increase of male sterile lines can be completely avoided, and a requirement for cytoplasmic incompatibility and a restorer system is eliminated when using the CHA system. The time involved in development of new female parental inbreds compatible with restorer genes in a cytoplasmic-male sterile system is avoided. In principle, using the CHA technique allows any cotton germplasm to be used as the female parent. Additionally, the evaluation of combining ability is greatly simplified because the preliminary work to develop A- and R-line parents becomes unnecessary.

Use of the CHA requires consideration of a number of aspects, including the interaction between the genotype and the chemical itself, as well as the effect of environmental conditions upon the effectiveness of the CHA.

One effect that seems to be prevalent in most CHA's is that this chemical treatment is phytotoxic to the plant and may be detrimental to seed quality (Brandes, 1958; and Olvey 1981). For this reason, it became the opinion of this author that marketing an F_1 hybrid developed by use of a CHA (TD-1123) is not desirable; however, by growing out the F_1, any detriment to seed quality should be removed in the resultant F_2.

CHA application appears to require complete peripheral coverage on a bi-weekly basis, in most cases. Any delays in the timeliness of the chemical application (i.e, inclement weather), resulting in male fertile flowers would lower the percent hybrid of your cotton crop (Olvey, et al., 1981).

Other CHAs

Most CHAs affect pre-meiosis except for A3C. Mogensen and Ladyman (1989) determined the mode of action of A3C on grain. They found that spraying the entire grain plant, the quantity or quality of pollen per spike was not adversely affected. This is unlike Ethrel, Hybrex and TD-1123, cause a disruption in pollen development. (Colhoun and Steer, 1983; Jensen, 1984; and Olvey, et al., 1981). The A3C mode of action in wheat was in prevention of normal pollen tube growth, therefore, inhibiting fertilization and resulting in male sterility.

Scott (1961) applied ^{14}C labeled FW-450 and Dalapon to dark-conditioned cotton plants. The inhibition in translocation of the gametocide chemicals by preliminary day-conditioning was reversed by pantothenic acid, D-ribose, and adenine compounds. The compounds were found to be readily translocated to the reproductive tissues and reversed the non-dehiscent anther response produced by the gametocide chemicals. McRae and Usdin (1958) demonstrated that the presence of ^{14}C-labeled FW-450 was consistently higher in the anthers than in the ovules.

Feaster, et al., (1958) found that FW-450 is not a selective male gametocide. Although the chemical causes pollen inhibition (or male sterility), it also causes female sterility. For this reason, FW-450 as well as Dalapon have not gained wide acceptance as breeding tools. FW-450 affects the synthesis of pantothenic acid, a component of coenzyme-A within the carboxylate metabolism, which may explain why it causes both male and female sterility.

Hilton (1958) suggested that FW-450 competes with pantothenic acid for a site on pantothenic synthetase and Dalapon also interfered with pantothenic acid metabolism. Hilton et al., (1958) showed the beta-alanine partially reversed the growth inhibition in yeast caused by FW-450 or Dalapon.

Chauhan and Kinoshita (1982) made a review of chemical hybridizing agents. Their findings concluded that plants of most CHA-treated crops showed greatly reduced yields when compared to non-treated plants, largely due to considerable female sterility.

Patterson, et al., (1966) reported that the induction of male sterility in cotton by spray application of FW-450 manifested itself in the formation of a large amino acid pool in the anthers. The gametocide is also selectively concentrated in the anthers; the largest increases were observed in aspartic acid, glutamic acid, serine, and threonine. No methionine or cystine was found among the free amino acids of the anther, before or after treatment. Lesser differences were observed with the protein and non-protein amino acids fractions from the ovules, calyx, and bracts.

In 1982, Pennwalt Corporation which owned TD-1123, was originally going to merchandise TD-1123 to seed companies as a chemical hybridizing agent. The author placed several F_2 hybrids in the 1984 state cotton yield trials grown throughout the United States. These F_2 hybrids showed a 10% increase in yield (Olvey et al., 1985). After the promising F_2 yield results the author was able to convince Pennwalt Corporation it would be economically advantageous to retain control of their CHA (TD-1123), to produce F_1 hybrids, using them to generate F_2 seed for commercial use. In 1985, Pennwalt Corporation went into the cotton seed business and started to support a cotton breeding program.

The F_2 hybrid concept was developed by the author (Olvey, et al., 1985) through the discovery of the chemical effects of TD-1123 and identification of opportunities for use of the CHA as a breeding tool. The F_2 concept was derived, in part, by observation of the detrimental effects of lowered seed viability. In an F_1 hybrid test at Marana, Arizona in 1981, poor seed viability invalidated the test (Olvey, 1986). Because the F_1 hybrid test was destroyed due to low seed viability, F_2 seed was saved and subsequently yield tested to determine which hybrid combination was the most preferred. Thus, the development and use of the F_2 hybrid concept was essentially dictated by discoveries and observations that were made in a thwarted attempt to utilize F_1 hybrid vigor in cotton.

Numerous techniques were investigated to determine an effective means of monitoring and regulating male sterility in TD-1123 sprayed cotton plants. The techniques to determine the rate and timing of TD-1123 were; the degree of leaf phytotoxicity, nectar concentrations, timed intervals, plant growth, heat units, irrigation scheduling, and bract burn. The degree of bract burn was the most effective indicator.

CHAPTER 4

SEED PRODUCTION

Pollination Methods

The bumblebee has been shown to be the most efficient pollinator of cotton, but Grout (1955) demonstrated that the use of supplemental colonies of honeybees in hybrid seed production fields would also enhance cross-pollinations. Dr. J. B. Weaver (personal communications) felt that the problem with bumblebees is their solitary habit, small populations and unmanageability prevent their use as effective pollinators although they are very efficient.

Meade (1915) demonstrated that hand pollination caused a yield increase over natural pollination in Durango and Acala cotton varieties of 11 and 5%, respectively. He suggested that beekeeping might increase cotton yield.

Srinivasan, et al., (1972) reported hand pollinations are used in India to produce hybrid cotton on a large scale. Researchers and seed companies feel that it is economically worthwhile to produce the hybrid seed despite the high cost.

Seeds for Tomorrow, a California-based company, has proposed making F_1 crosses via emasculation and hand pollination in India, growing out the F_1 in the United States, and selling the F_2 seed, thereby circumventing the problems of fertility restoration with the CMS system and the unavailability of an efficient CHA. This company views F_2 hybrids as a practical commercial approach to utilizing heterosis within cotton (Vince DeCarlo, personal communication). A possible roadblock is the regulated importation of large quantities of F_1 seed into the U.S. from India.

Meredith and Bridge (1973b) in Mississippi reported that a number of studies have been conducted to determine the percentage of natural out crossing. They reported that out crossing ranged from 0 to 47% in the 1950's and 1960's to as low as 2% in a 1972 study. Natural crossing has been reduced because the advent of aerial application of insecticides has drastically reduced wild bee populations in certain cotton-growing regions. Biological controls of harmful insects may alter this trend in the future.

Bee Pollination

As Muramoto (1958) indicated, hybrid cotton production requires effective cross-pollination by insects. Unlike other crops such as corn that are wind pollinated, cotton is primarily a self-pollinated crop and requires insect vectors for pollen transfer.

Grains of cotton pollen are quite large, from 81 to 143 microns (Kaziev, 1964), and are covered with a viscid material which causes them to adhere to each other and for this reason, the pollen grains are not transported by wind.

Because cotton pollen is spiny and very large, it tends to be difficult for honeybees to pack and transport, and also lacks any attractive chemicals. For these reasons, honeybees rarely gather cotton pollen. Honeybees in search of nectar have been known to exit flowers and brush cotton pollen from their bodies on leaves and other plant surfaces. Utilization of honeybees for production of hybrid cottonseed may necessitate a pollen substitute, which would be preferable to having the bees forage for weed pollen and for pollen from flowers of other crops.

Stith (1970) addressed the utilization of honeybees in hybrid cotton production.

Moffett et al., (1976b) identified numerous effective pollinators on cotton. However, he concluded that in order to make production on a commercial scale feasible, hybrid cotton would require honeybees for pollination since they are manageable (Moffett et al., 1978).

Waller (1982) concluded that two honeybee colonies per acre would provide adequate pollination in cotton.

Nectaries are produced on cotton plants in five different areas (Trelease, 1879). These different areas of nectar secretion are: floral, circumbractal, subbractal, leaf, and additionally may be found in microscopic areas on the flower peduncles and young leaf petioles. Nectar secretion may begin a few hours or a few days before the flower opens depending upon which gland is involved. Usually early secretions are of minimal volume. Nectar reaches its maximum accumulation by mid-afternoon. Nectar secretions are strongly influenced by soil fertility (McGregor, 1976).

Moffett et al., (1975), Waller and Moffett (1981) and Loper (1984) agree that male-sterile flowers were preferred by honeybees over pollen-bearing flowers presumably because the bees avoid cotton pollen. Loper (1984) indicated that further much less Pima (G. barbadense L.) pollen was deposited on the Upland (G. hirsutum L.) cytoplasmic A-line stigmas than pollen from Upland plants. There was an 18 to 26% sugar concentration in floral nectaries of Pima, whereas the flowers from nectariless plants had 41±6% sugar. They suggested that a high sugar concentration may increase bee visitation. For purposes of cross pollination the pollen parent was genetically nectariless. Flower color was also observed to influence honeybees' behavioral patterns which in turn impacts on pollen dispersion.

The use of nectarless (leaf) cotton has been proposed to attract bees and to increase cross-pollination. The floral nectary is located at the base of the staminal column and is only located on the inner and lower surface of the calyx. This nectary is necessary to attract bees down the staminal column where pollen is collected and carried for cross-pollination. Eliminating other nectaries from the plant would narrow the bees' choice in its search for cotton nectar.

Moffett, et al., (1978) conducted a hybrid production study in Aguila, Arizona, during 1977, at Farmer's Investment Company property. This study utilized the honeybee as pollinator. The row configuration used was: two female or A-line rows, one skip row, four male or R-line rows, one skip row, and repeat pattern. Four hundred colonies of honeybees were placed within 1 mile of approximately 750 acres of cotton. Bee visitations on the cotton flowers were determined by slowly walking through the field at various time intervals throughout the day and counting the number of bees visiting within the open cotton flower utilizing McGregor's (1959) method. Bee visitation rate was excellent through the fifth week of bloom; however, after the first application of insecticide (Acephate and Chlorodimeform), bee visitations dropped by 94%. Although these insecticides were sprayed at night and the hives covered, these sprays still had a major impact on bee visitation. It also was observed that the A-line flowers were much more attractive to bee visitation than their male counterpart, 4.36 vs. 3.48% respectively.

Bees are attracted primarily to an A-line (or a CHA-sprayed plant) because in the male sterile line the absence of pollen grains, which act as irritants to bees, in their path to the floral nectaries.

Moffett, et al., (1978) recommended against using a skip row between male and female parents because the honeybees did not readily move from one parent to the other across a vacant space. The bees move readily to adjacent plants. Findings also indicated that wild bees were scarce and therefore provided little value as pollinators on this large F_1 production system within Arizona. Synchronization of flowering became a problem because the male ceased flowering earlier in the season (due to boll load) whereas the A-lines continued to flower. With the CHA method, the flowering will not completely synchronize but it should not detrimentally influence yield.

Moffett (1978) concluded that hybrid cottonseed can be successfully produced in Arizona using honeybees as pollinators. Overall yield on female rows was 62% of the adjacent male rows; however, the yield could be greatly enhanced with increased bee visitations which could be accomplished by eliminating detrimental sprayings, changing row configuration, and synchronizing the flowering of both parents. Yield on female parent rows were found to be up to 25% less due to the inefficiency of honeybees as pollinators (Olvey, 1986).

McGregor (1976) found adequate levels of honeybee visits to attain a full seed set in the boll to be about 1 bee per 100 flowers. It appears that from one to three hives are needed per acre of cotton. To make this determination, the total area of pollination must be considered plus the addition of vegetation or crops in the surrounding areas--both factors being equally important.

Moffett, et al., (1976b) reported female row yields equal to 79% of male row yield due primarily to higher bee visitations. The effect on seed production of distance from pollen source was determined using male-sterile cotton. Moffett's 1975 planting pattern was 2 male rows to 14 female rows; in 1974, it was 2 male to 2, 4, or 6 female rows. The planting pattern of 2-6 provided satisfactory seed yields on the female rows with an average bee visitation of at least 0.5% or higher. The 2-14 row configuration in 1973, did reduce seed yields. The honeybees appeared to travel no further than 3 rows from the pollen source.

Under the CHA method of hybrid seed production, the 2-4 row configuration has been successfully utilized; however, going to 2-6 row configuration could be accomplished if adequate bee populations were available.

Loper (1984) also conducted a row configuration study using 2-2, 2-4, 2-6, and 2-9. He determined pollen dispersion by counting pollen grains per stigma, and determined that there was an average of 52% reduction in pollen grains per stigma in the third row away from the male parent versus the row(s) adjacent to the parent. This study concluded that a 2-4, possibly a 2-6, row configuration would be the optimum to ensure adequate pollination.

Moffett, et al., (1974) concluded that honeybees are the essential pollinating agent for the commercial production of hybrid cotton seed. Instead of determining the number of hives per acre, Moffett recommended a more effective means of determining the number of bee visits to certain number of flowers. Findings indicated that one to ten bees seen in 100 flowers (as the observer walks down the row of cotton), would provide adequate pollination. The number of hives varies greatly depending upon the area, field size, location, and stage of flowering. Moffett recommended that hives be shaded and provided with an adequate water supply within one-quarter mile of the hive. Most importantly, hives must be protected from pesticides.

Loper, et al., (1987) conducted field and greenhouse studies during 1984 and 1985 to study the response of TD-1123 to the cotton plant and to honeybees. They found that the CHA, TD-1123, when fully applied as recommended, was systemic and translocated to both the floral and bract nectaries of the plant. The concentrations of the chemical ranged from 10 to 12 parts per million in nectar from the floral nectary.

Floral visitation by foraging honeybees was not observed to be affected by the gametocide under field conditions. The gametocide was observed in nectar of the treated cotton plants; however, it did not pose a threat to pollen grain germination and development. They also observed that foliar application of the gametocide initially showed some degree of phytotoxicity; however, it did not severely inhibit normal growth of the plant. When the floral nectar levels of TD-1123 dropped below 25 to 35 mg L^{-1}, the plant would begin, at least partially, producing male fertile flowers. The TD-1123 concentration of 75 mg L^{-1} in a sucrose solution consumption by honeybees actually increased. Part of this attraction may be explained by the presence of potassium salt content of TD-1123 which honeybees are known to prefer. The flowers of the treated plants were at least as attractive to the foraging honeybees as those of the untreated plants. Because TD-1123 and a metabolite were present in the nectar, a study was conducted to determine if TD-1123 appeared in the ripened honey. Under normal field conditions where the workers are collecting nectar from a large foraging area, there may be no traces of TD-1123 in the honey; however, to avoid any possible human health problem, all honey produced from colonies foraging on the gametocidally treated cotton must not be sold or distributed for human consumption.

An important aspect of utilizing honeybees as pollinators is the selection of locations for growing cotton that require little or no insecticide during the flowering season.

Normal production practices must be modified to accommodate hybrid cottonseed production. Irrigation, for example, must be scheduled to allow accessibility to fields for foliar application of CHA (Brandes, 1958; and Olvey, et al., 1981). Time intervals between irrigations may need to be shortened to accommodate the stress produced from the chemical applications. Insecticide use and the timing of applications (night) must be adjusted to prevent harm to bee populations.

Production of hybrid cottonseed is labor intensive and requires a thorough knowledge of the factors essential for successful seed production. Some of these factors are:

1. constant monitoring of degree of male sterility (visual observation of flowers),
2. maintaining a high degree of male sterility (95%) during flowering,
3. proper chemical application (complete peripheral cover), and
4. proper selection of parents.

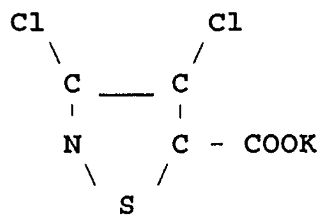
Cotton is predominantly self-pollinating unlike corn and sorghum, which are wind pollinated. In order to commercially produce hybrid cotton, insect pollination is essential and honeybees, the insect vectors of pollen, must transfer pollen from flowers of the male to the female staminal column. There is an observed 25% reduction in yield due to the inefficiency of honeybees to cross pollinate as compared to normal self-pollination production acreage (Olvey 1981). Honeybees have been shown to be an effective pollinator (Waller, et al., 1982). Certainly using honeybees as vectors opens up a whole new set of challenges. First, the cotton breeder must select parental stocks for attractiveness to bees; second, beekeepers must provide quality honeybee colonies in sufficient number, at the proper time, and properly distributed to maximize pollen transfer; and third, and most serious, is the protection of honeybees from insecticides since cotton is one of the major recipients of insecticidal sprays.

T D - 1 1 2 3

Over the last 20 years, the chemical TD-1123 from Pennwalt Corporation, has been tested as an experimental growth regulator for:

1. preconditioning cotton prior to defoliation,
2. chemical termination of fruiting on cotton for insect control (Kittock, 1978), and
3. inducing male sterility in cotton flowers as a means of producing hybrid cotton seed (Olvey, et al., 1981).

TD-1123 is the trade name for the chemical 3, 4-dichloroiso-thiazole-5-carbolic acid, potassium salt. The empirical formula is C_4 Cl_2 NO_2 SK with a molecular weight of 236. The following represents the structural formula of TD-1123:



After several years of field trials, TD-1123 has shown that its application, prior to an application of cotton defoliants or desiccants, will act as a conditioner to improve the effectiveness of either the defoliant or desiccant. The use of TD-1123 as a cotton harvesting aid conditioner will result in a more complete defoliation or desiccation when compared to the use of a defoliant or desiccant alone. Research suggested that defoliants or desiccants be used 7 to 21 days after the application of TD-1123 (Kittock, et al., 1978). They stated that a mixture of TD-1123 and Maintain CF 125 (chloroflorinol) applied prior to harvest would terminate late season cotton fruiting without an adverse effect on yield or quality. The TD-1123 application eliminates the late season green bolls and immature squares which would normally provide oviposition sites for insects. The reduction of oviposition sites will in turn reduce the number of insects that will normally survive the winter to infest the next years crop.

To use TD-1123 as a selective male gametocide in cotton, the first application should be sprayed 2 to 3 weeks prior to first flower and re-applications made every 10 to 14 days thereafter until completion of the effective flowering period. Figure 4.4 (appendix B) shows a normal cotton flower on the left and CHA-treated male-sterile flowers in the middle and on the right. TD-1123 inhibits the development of the pollen sacs on anthers (Fig. 4.4, middle flower) so that pollen is incapable of dehiscing. The flower on the right of Figure 4.4 has fully developed anther sacs that have not dehisced. These flowers express the desirable range of sterility from TD-1123. Table 4.4 (appendix A) indicates the effects that TD-1123 has on various cotton plant parts under a desirable and a high rate. By rendering the flower male sterile, TD-1123 can serve as a breeding tool to produce hybrid cotton (Olvey, et al., 1981).

TD-1123 has been shown to have numerous growth regulating activities that might be applicable in benefitting the productivity of cotton. The application of TD-1123 either as a chemical terminator (at a rate of 0.75 to 1.5 kg of active ingredient or AI/ha.) or as a gametocide (at a total application of 1.0 kg AI/ha.) tends to effect the seedling vigor because of the adverse effect on the plant as a whole (Kittock, et al. 1978 and Olvey, et al., 1981).

United Kingdom Patent No. 2112617 (Olvey, 1983) describes the effects of TD-1123 on various characteristics of Upland cotton (Table 4.1, appendix A). Research with TD-1123, to provide data needed for the patent application, was conducted at the University of Arizona, Cotton Research Center, Phoenix. Treatments included an untreated control, four application rates of Dalapon, and fifteen application rates of TD-1123 applied on 2 July. Dalapon had been used in the past to achieve male sterility even though it also caused female sterility. Higher application rates of both Dalapon and TD-1123 maintained male sterility longer but produced more leaf phytotoxicity. The effect of a single application of Dalapon or TD-1123 on seedling vigor was minimal. One difference observed was the control averaged 87 flowers/plot whereas Dalapon averaged 53 flowers/plot. The higher application rates of TD-1123, however, averaged 108 flowers/plot. TD-1123 demonstrated an increase in reproductive growth in comparison to Dalapon or untreated checks. Boll size of plants treated with recommended rates of TD-1123 were 75 to 80% of the untreated check and seeds/boll were reduced from 25.8 in the untreated control to 20.4 with TD-1123. The reduction in the number of seeds/boll and size of boll is an indication of some degree of female sterility as well as a phytotoxic effect upon the whole plant. Plants treated with Dalapon tended to become vegetative whereas plants treated with TD-1123 were shorter in stature compared to the check due to shorter internode lengths. Bolls that did not set on plants treated with TD-1123 were later compensated by larger numbers of squares and additional late-season flowering compared to the control (Table 4.1, appendix A). Figure 4.1 (appendix B) shows the component parts of a typical cotton flower. Figure 4.1 2A through D represents the progression of normal bract development compared to the development showing bract burn or phytotoxicity. This is one of the most important aspects for monitoring the degree of sterility within the developing bud. The chemical TD-1123 demonstrates more specific phytotoxicity to the bracts than any other component of the cotton plant; therefore bract burn is an early indication of male sterility within the developing bud. Observation of buds similar to those shown in Fig. 4.1 2D is proof of having achieved male sterility, however, the most desirable degree of sterility and bract burn would be that demonstrated in Fig. 4.1 2C.

Because cotton plants are in numerous stages of boll development at any particular time (Figure 4.2 and 4.3), the degree of sterility can be easily determined by observing the amount of bract burn on any particular bud. This observation also can be used to determine the need for further applications, as well as the rate and time.

McDonald (1971) attempted to determine whether the environmental factors humidity and temperature exerted any influence on the expression of anther sterility. McDonald reported that pollen sterility would result when the maximum temperature 17 days before anthesis was above a critical level. High humidity was most damaging to pollen sterility 19 days before anthesis. A number of studies with the TD-1123 have been conducted in several environments including Arizona, California, Georgia and Texas. Arizona is a desirable location for applying the CHA because normally low humidity and high temperatures cause sterility even in a commercial variety. Temperature effects on pollen sterility are additive to the CHA effect by inducing complete sterility which is essential for large scale production of F_1 hybrids.

TD-1123 is affected by environmental factors including temperature (Walker, 1985). Six years were required to determine the proper rate and timing of applications for the different varieties of cotton. In addition, foliar spray has a phytotoxic effect by causing a red tinge along the periphery of the leaf.

Shaver, et al., (1979) found that TD-1123 was readily absorbed from the leaf surface and translocated throughout the plant (about 55% within the first 24 hours as indicated on Table 4.2). Appreciable residues of radioactive TD-1123 accumulated in the cotton seed at slightly less than 200 parts per million, and most of these residues were the parent compound. Even more important were the 430 parts per million of the parent compound found in the bracts (Table 4.3). This explains why the bracts are a key indicator of sterility. Because the bracts accumulated well over twice as much as any other location, the chemical seemed specific to the bract which results in phytotoxic burning of the bract tips (Olvey, 1983). Careful experimentation (Olvey, et al., 1981) has shown that when there is bract burn (Fig. 4.1), the developing bud will exhibit male sterility whether it opens in 1 day or 23 days (Fig. 4.2).

Shaver et al., (1979) also determined that TD-1123 was rapidly excreted in the urine of white rats. Within a 24-hour period, 95% of the parent compound was eliminated and there were only minimum concentrations (.01 to .17 ppm) within the remaining tissues after 24 hours. In treated plants, radioactive material was absorbed and reached its peak at 1 day post treatment and then declined due to utilization and translocation from the treated leaves. Unabsorbed TD-1123 on leaves was washed away with rainfall of even less than 1 centimeter. Since rainfall can easily wash away the TD-1123, it is important to reapply the chemical immediately after rainfall.

Figure 4.2 shows the various stages of cotton bud development. All plants have buds in various stages of development during the flowering season. TD-1123 is effective in producing male sterility on cotton buds from 12 to 21 days prior to bloom, when the plant is going through meiosis, allowing the chemical to inhibit normal anther and pollen development (microsporogenesis). About 11 days prior to bloom, the bud has developed beyond the stage of being influenced by TD-1123. The elongation of the stigma is the last structural development in a cotton flower, and high concentrations of TD-1123 can inhibit this process.

F_1 cotton hybrids produced by hand or chemical emasculation are identical products except that F_1 seed produced by TD-1123 contains 10 to 12 ppm CHA which may lower seed viability. (Shaver, et al., 1979; and Olvey, et al., 1981). An increase in planting rate and more desirable planting date can easily negate this potential problem.

Economics

Sheetz and Quisenberry (1986) noted that F_1 cotton hybrids are economically impractical because the additional income received for the increased yield and higher quality fiber does not compensate for the additional expenses involved in the current methods of producing F_1 hybrid seed, even when utilizing a selective male gametocide (Olvey, et al., 1981.)

The acceptance in economic terms of an F_2 hybrid would be influenced by the cost of the planting seed versus the potential increase in crop value that would be derived. Production costs of F_2 hybrid seed are minimal when compared to F_1 hybrid seed costs. Pricing should be flexible depending upon the level of improvement exhibited by the F_2 hybrid. Sheetz (1984) stated: "The higher the F_1 seed cost estimates, the more heterosis will be required to offset the added cost to the cotton grower". He also indicated that a 10% yield increase in certain high yielding areas would certainly be an adequate justification for hybrids and likewise a low yield area works against the hybrid concept. Cotton grown within the High Plains of Texas, a relatively low-yielding area, would require a minimum of 20% yield increase to justify the cost of F_1 hybrid seed.

One difference in the seed production increase phases between conventional cotton varieties and an F_2 hybrid is the additional step of F_1 production. Assuming a planting rate of 15 pounds/acre of F_1 seed for F_2 seed production, and assuming the F_2 production will yield an average of 1,500 pounds planting seed per acre, it follows that it will cost an additional 1 cent per pound for each pound of F_2 produced over conventional varieties (e.g. $1.00/lb. F_1 seed = 1 cent/lb. F_2 seed). If the additional F_1 seed production cost were as much as $5/lb., it would only cost an addition 5 cents/lb. to produce F_2 seed. Even though the F_1 production program is costly, the cost for the end product, F_2 seed is a small pricing factor (Dale, 1989). Production costs for using heterosis within cotton has been the major obstacle in the development and utilization of cotton hybrids. Production cost increase is not as important a factor in F_2 hybrids.

Stroman (1961) suggested that perhaps the use of cuttings and transplanting to produce the F_1 would be commercially feasible. He also suggested that during planting season the following year, these plants could be cut off or ratooned for the second year. Growing cotton as a perennial crop would greatly reduce production costs. Once the F_1 is produced and planted it would not have to be planted again. Simply harvest the fields planted to F_1 continuously to obtain the F_2 hybrid. In theory this ratooning concept would work very well; however, this practice has been used commercially with varieties in Arizona on two occasions, with major insect problems occurring in each instance. Since insects and disease pose such a threat to the cotton growers, the ratooning procedure is illegal in Arizona.

Stroman (1961) further indicated that there were significant differences in earliness with the intra- and inter-specific crosses. This indication of earliness was based on first pick of seedcotton when 12 crosses were significantly higher yielding than the commercial strain in a yield trial. The earliness factor is one of the definite benefits of hybrids. He further suggested that through the use of a gametocide to produce male sterility (Eaton, 1957), a method for collecting large amounts of pollen might be developed where the female parents would be dusted by hand with the pollen rather than using the insect vector method of pollination. Stroman's study is based on yields from five plants which is an example of some of the limitations placed on breeders in producing F_1 seed. Restrictions on the amount of hybrid seed limited full-scale research efforts.

The Southwestern United States provides several advantages for the production of cotton planting seed. These include:

1. seed quality is generally excellent
2. planting rates are low

3. seed yields are maximized

4. crop failure due to environmental conditions is less likely than several other locations across the cotton belt

Maximizing the rate of increase in F_1 production is important for F_2 hybrid development. When the favorable economic conditions of the southwest are weighted, it is easy to understand why all major cottonseed companies in the U.S.A. are growing a considerable amount of their cotton planting seed in the Southwest for sale in the Delta and Southeast regions of the U.S.A.

Percent Hybrid

A number of methods can be used to assess percent hybrid within the F_1 production program. These are:

1. Visual ratings which can be made by examining the stigma and anthers of open flowers to determine if the flowers are fertile or sterile, depending upon the amount of pollen produced from the anther sacs. Since the cotton flower is large, observations can easily be made while walking through several areas of the production fields which will provide a rating

for the entire field. If the flower is sterile with no pollen shed evident, the flower is considered receptive to cross pollination. If the flower is fertile or partially sterile, it is still considered fertile even though it may only have a few anther sacs with dehiscing pollen.

2. Selfing is a method to prevent cotton flowers from opening to ensure self pollination and pure seed development, and also is a tool to assess sterility. This method is accomplished by pinching the top portion of the flower closed with metal clips or cellulose acetate in the early morning and tagging the base of the flower for identification. If the plant has been sprayed with a CHA, pollen needed for self-pollination will be absent and the flowers will drop off the plant. Physiological shed not associated with induced sterility will also occur on both the normal (50%) and CHA-treated flowers, so non-CHA treated flowers must be utilized as a check. If the selfed flowers do set, fertility is indicated, so these flowers are tagged and the number of

tags present at the end of the season is recorded in order to calculate the percent sterility through out the field.

3. Under normal cotton growing conditions, glands are present and visible to the naked eye on leaves, stems, bolls and bracts, and they can be used as a genetic marker to assess sterility. In using a genetic marker, glandless cotton, condition by the recessive gene gl_1 gl_1, glandless cotton is placed within the female parent rows in representative areas to be sprayed with the CHA. The gl_1gl_1 glandless trait is expressed on the main stem or hypocotyl of the plant making it visible during the course of the season. All cottonseed from the glandless marker plants is harvested separately and grown out in sandflats in a greenhouse. The percent of glanded seedlings present compared to glandless seedlings, is indicative of the percent natural crossing occurring in the field. This procedure is enhanced by making at least four backcrosses to the female parent and isolating true-breeding lines before it can be used as a production tool for determining percentage hybrid.

McMicheals (1954) suggested the use of the glandless boll trait in Upland cotton as a useful tool in the study of natural crossing. In 1960, he reported that the glandless trait was conditioned by two recessive genes (gl_2 gl_2 and gl_3 gl_3) and was a double recessive. He determined that seeds which came from self-pollinated glandless plants all produced glandless seeds, whereas those seeds from cross-pollinations to a female glandless with glanded males would have glands. This technique is a means of determining natural crossing as well as percent hybrid within a production system. If the $gl_2gl_2gl_3gl_3$ glandless trait is incorporated into the female parent, it also can be used as a monitoring system to determine percent hybrid within cottonseed production fields.

McMicheals (1954) and Cross and Richmond (1959) proposed that glandless seed also was a desirable method of determining the degree of outcrossing by determining the presence or absence of the glands in the embryos. This can be done at the seed stage by cutting each seed open, and observing the presence or absence of glands. Other methods of determining percent outcrossing within cotton include mixing two stocks, one carrying a dominant marker gene such as a red-leaf or okra-leaf, and the other carrying its recessive allele. These seeds are harvested, germinated in sand flats and the proportion of red to green seedlings or normal to okra-leaf plants is a measure of outcrossing. The hybrid, which is the heterozygote in both of these cases, can be difficult to identify, particularly in the early stages of seedling development.

Parental Maintenance

In a study of the maintenance of cultivars that have seed up to 12 years old, Meredith and Culp (1979) reported no significant differences in the lint yield, the 50% fiber length, and fiber strength. They did, however, observe small but statistically significant differences in lint percent, boll size, seed index, 2.5% fiber length, elongation and micronaire. Even though they concluded that there were no major changes within cultivar maintenance programs, differences do exist.

Consistency and stability within an F_2 hybrid becomes a part of the maintenance program because it is necessary to go back to the original parents each time a seed increase is produced. This will result in a consistent product with little or no loss due to inbreeding, genetic shift, seed contamination, drift due to environmental pressures or any other factor pertaining to the purity or shifting characteristics of an established variety.

The maintenance program of the parents involves a very small seed volume which can be handled with intensity and strictness to ensure a uniform and consistent product.

CHAPTER 5

HETEROSIS

Introduction

Mell (1894) was the first to report the existence of hybrid vigor in cotton; however, it was not until Loden and Richmond (1951) that the yield potential of hybrid vigor was clearly demonstrated and triggered a great deal of interest in hybrid vigor studies using diallel crosses. The interest in hybrid cottons was heightened when genetic male sterility was discovered and even heightened further when cytoplasmic-male sterility was introduced by Meyer and Meyer (1965).

High yields are not the only possible goal of hybrid cotton. There are a number of cases in which the F_1 or F_2 hybrid can retain the yield of the more productive parent while assuming other important attributes from the other parent such as fiber quality, earliness, disease resistance, or stormproofness. While these attributes may be of use to the farmer, yield must remain the primary consideration in any attempt to manipulate characteristics for hybrid usefulness.

Yield is defined as the amount of useful plant material removed from a given area. Kerr's (1956) cotton model defined yield by bolls per unit area x seed cotton per boll x percent lint. An increase in one or more of these factors would represent an increase in yield and/or heterosis.

The increased yield that has been demonstrated in interspecific G. hirsutum x G. barbadense crosses is manifested by an increase in number of bolls (Marani, 1963, 1964 and 1967; Fryxell, et al., 1958; and Davis, 1974). Within the intraspecific crosses, however, most of the yield increase was due to an increase in boll size (Miller and Marani, 1963; Turner, 1953A; and Harris and Loden, 1954).

One aspect that has been somewhat ignored throughout most studies of heterosis is cottonseed which is an important byproduct. Cottonseed adds to the value of the crop when the cottonseed oil is extracted for human consumption or the seed used for animal feeds. The main value of cotton is, however, the fiber produced on the seed.

Most heterosis studies have focused on lint or seed production. The direct effect of heterosis is the enhanced vegetative portion of the plant. White and Richmond (1963) showed a greater dry matter production of the cotton plant. Muramoto, et al., (1965) suggested that the increase in production was due primarily to greater leaf area; whereas Porter and Jones (1977) indicated a greater leaf area partitioning attributes to the heterotic effect. Wells and Meredith (1986) and Olvey (1986) indicated that there is no single factor that results in heterosis. The accumulative effect and overall vigor within the plant results in yield increases and seedling vigor. Porter and Jones stressed the importance of early growth during the seedling and earlier stages of development.

Davis (1978) composited prior literature in the evaluation and potential of heterosis in cotton. Thus, it is not the intention of this author to restate this evidence since heterosis in cotton is commonly acknowledged. Rather, this paper attempts to concentrate on the F_2 hybrids as they have evolved and focus on their specific attributes.

One of the major problems in the literature regarding measurements of hybrid vigor in cotton is the variety of methods that have been reported. Numerous investigators evaluated heterosis based on mid-parent or high-parent values while others opted to compare to the best commercial variety (useful heterosis). Meredith and Bridge (1972) suggested useful heterosis as a true measure for comparison and compared hybrid yields with the highest yielding commercial variety as the check. In this manner there is a direct economic meaning that may be placed on heterosis.

Jones and Loden (1951) indicated that neither heterosis or inbreeding depression have been as dramatic or significant in cotton as has been demonstrated in corn.

Brown (1942), Young and Murray (1966), and Simpson and Duncan (1953) concluded that there is very little yield reduction through continuous self-pollination in cotton. Meredith and Bridge (1973a) reported negligible yield reduction and stated that the only purpose of inbreeding in a hybrid program is the production of uniform parental lines.

Evaluation of Heterosis

In this paper, evaluations of characteristics of F_2 hybrids are confined to useful heterosis rather than mid-parent or high-parent values. Useful heterosis indicates a demonstrated advantage over the best commercial varieties. This reflects the need to surpass the best varieties available in order to realize beneficial gain. This dissertation also is confined to those attributes that are commercially valuable in cotton--yield per area, fiber properties and seed. Heterosis is any advantage conferred by hybrid vigor in any generation until such time that the germplasm is said to be inbred or is no longer showing a heterotic effect. Each successive filial selfed generation produces additional homozygosity resulting in fewer combinations of heterozygous pairs of loci in the total genetic background in a favored hybrid combination.

Heterotic Behavior

New World species of cotton are tetraploid (2n=52) and contain two sets of genomes, A and D, from different species. According to Fryxell (1979), cotton tetraploids are amphidiploids, and Hutchinson, et al., (1947) used the term allopolyploid. Amphidiploids behave genetically as diploids. Manning (1955) has shown that there is little reduction in genetic variability in inbreeding. The unique behavior of cotton in that it is an allotetraploid which behaves like a diploid, may offer the promise of improved productivity as a commercial product (Olvey, 1986).

Heterosis assumes a cross between pure line varieties or homozygous parents. This author proposes to differ in that most cotton varieties are composites of similar phenotypic characteristics, that can be separated out into a number of different and genetically distinct inbred lines. The opinion of this author is that most commercial varieties are heterogenous collections of relatively homozygous genotypes.

Endrizzi (1962), Kimber (1961), and Al-Rawi and Kohel (1970) established that cotton, a polyploid, undergo diploid segregation at meiosis. Reciprocal crosses within Gossypium hirsutum L. generally do not demonstrate significantly different characteristics. White and Richmond (1963) reported no significant differences between reciprocal crosses for fiber fineness, strength, or length.

Adaptation

Meredith, et al., (1970) indicated that both F_1 and the F_2 generations tend to be more consistent yield performers than their parents as tested over several environments. In theory, the F_2 hybrid should be more widely adapted than either of its parents, however, further testing is warranted. Data must be accumulated over additional locations and environments to substantiate the performance of a particular F_2 hybrid.

Bridge, et al., (1969) and Miller, et al., (1962) investigated the environmental and genetic variances of cotton cultivars and found that genotype x environment variation was greatest for yield. Also, as the interaction of genotype x environment for fiber properties was frequently significant; the variety component assumes a greater importance; it becomes of significant importance to use a variety that is widely adapted. Fiber properties can vary greatly between environments.

Dobzhansky and Wallace (1953) reported that heterozygosity in cross-pollinated species gives greater adaptation and stability over varying environments than does homozygosity. If this is true, a predominantly self-pollinated crop such as cotton would be expected to be more adaptable in the F_1 and F_2 than its parents (Meredith et al., 1970). Kohel (1969) compared individual F_1 hybrid plants that were from crosses of double haploids and found that the hybrids were not as adaptable as the parents. He concluded that heterozygosity in cotton probably does not reflect greater adaptability.

Dobzhansky and Wallace (1953) also stated that another factor adding to increased stability may be polymorphism in which a population that is genetically heterozygous would be expected to be more stable than one that is completely homozygous, such as a doubled haploid.

The difference between the findings of Kohel (1969) and Meredith, et al., (1970) was that Meredith evaluated populations while Kohel evaluated individual plants. Another factor that could contribute to the different response is the use of different genetic materials grown in different environments.

Hand-pollinated F_1s

Dr. J. B. Weaver, University of Georgia, has been a long-time advocate of F_1 cotton hybrids. In a personal communication, with Dr. Weaver, he stated that due to significant problems within the cytoplasmic-male sterile system

(CMS) with regard to pollen fertility restoration and production, the F_2 offers a more viable means of capitalizing on some heterosis in cotton until such time as commercial F_1 hybrids become practical. Weaver has documented cases of 15% increase in heterosis within the F_1 above the high parent with a retention of up to 10 to 12% heterosis in the F_2. He also has proposed that initial crosses be made by hand in India and transported to the United States where F_1 seed would be increased to produce F_2 seed. He feels, however, that prohibition on the importation of large lots of hybrid cotton seed into the U.S. is a major stumbling block to this approach.

Seeds for Tomorrow, a California-based seed company, has also proposed hand-pollination to produce F_1s overseas, which then would be increased from the F_1 to the F_2 in the U.S.A., where F_2 seed would be sold for commercial production.

Variety Mixtures

Another avenue to establishing a broad genetic (adaptation) base is the practice of mixing varieties, lines, or strains of cotton (Richmond and Lewis, 1951; Ramiah and Panse, 1941; Sawhney and Narayanayya, 1941). Ramiah and Panse (1941) indicated that yields of the seed mixtures were equal to or better than the pure varieties and produced superior lint and spinning qualities. Sawhney and Narayanayya (1941) concluded that the value of mixing varieties was due to an increase in yields on a consistent basis from year to year probably due in turn to a wider adaptation base. Richmond and Lewis (1951) saw the merits of providing greater flexibility of response to the environment. In their report, yields did not differ significantly from the pure line varieties; however, a benefit was improved fiber properties with fiber mixing, especially fiber strength.

On the 1990 Delta Breeders' Tour (sponsored by the National Cotton Council of America, Memphis, TN) it was noted that because of the advent of high volume instrumentation (HVI) testing of fiber by classing offices, some farmers were beginning to mix varieties. Mixing Deltapine 50 with Deltapine 90 in a 9:1 ratio obtained yield and earliness from Deltapine 50 and increased fiber quality from Deltapine 90. Thus, variety mixtures can be desirable, however, the advent of F_2 hybrids provides the opportunity to utilize desirable plant characteristics in the selected parents.

Peebles (1956) obtained a 25.5% increase in yield over the best parent in a first generation (F_1) hybrid between two American-Egyptian cottons. When he planted a 50-50 mixture of the hybrid and the best parent seed, the yield was 18.5% rather than the expected 12.75% Peebles attributes this yield increase to more rapid seedling development and to subsequent dominance of the hybrid plants in the field.

Utilizing F_2 hybrids would result in a product that more directly and efficiently provides desired characteristics with a higher degree of certainty and would negate the need for mixtures. In other words, a hybrid can be "tailor-made" to meet market demand.

F_1 Hybrids

Muramoto (1958) suggested using a top cross method to predict successful parents to be used in a hybrid breeding program. Also, through use of general and specific combining abilities of parental lines that produce the greatest gains in the F_1, the preferred parents can be utilized as a homozygous tester. This is the same approach pursued by this author in the evaluation of parents used in hybrid combinations (Olvey, 1986). The use of a top cross to accurately predict the best combiners can save time and prove highly successful within a screening program.

Meredith and Bridge (1972) indicated that the improved conditions of growth tends to narrow the advantages of hybrids in Upland cotton.

In a review of 14 hybrid studies on cotton, Meredith and Bridge (1972) reported that F_1 hybrids demonstrated an 18% yield increase over the mid-parent value due primarily to higher individual boll weights and an increase in the number of harvested bolls per area. With regard to fiber properties, heterosis has been shown to have less effect, ranging from 0 to 2% heterosis for fiber properties.

Stroman and Fryxell (1960) indicated that within an F_1, particularly an interspecific cross, plant height is usually greater. Plant height of the F_1 can be desirable as long as the increase is not due to an increase in internodal length.

Earliness can be determined by the stratified method of harvesting using the method of Richmond and Radwan (1962), and significant differences in earliness can be detected within the hybrids.

Sheetz and Quisenberry (1986) conducted an evaluation of F_1 hybrids and concluded that an average yield increase was 15%, and on an individual basis, 33% above the high-parent. The increase in yield may be attributed to heterosis.

F_2 Heterosis

Shull (1952) found in his early corn experiments that the average F_1s yielded 285% more than the inbreds, and the F_2 produced 174% more than the inbred parents. These phenomenal F_1 yield increases were expected as yields of inbred lines of corn at that time were extremely low.

In 1948, Simpson proposed the use of advanced generations as a practical means of growing hybrid cotton by circumventing the production problems of the F_1 hybrid. He tested this theory by intercrossing varieties using the natural bee population in Tennessee in small "cotton patches". He reported that half the seeds were selfed and half were F_1 hybrids. Based on his results, he obtained between 5.7 to 44.2% yield increases of the F_1 over the inbred. Simpsons' method is not repeatable since there is no control of parental material or insect visitations. It currently is not recommended to be used as a means of producing advanced generational materials. Simpson also indicated that under completely random mating, as approximated in corn, there is no further decrease beyond the F_2 in yield. With partial selfing or partial interbreeding as would occur in corn, there would be some intermediate result. He further stated that the heterosis evident in the F_2 populations would be partially continued through several subsequent generations and that the excess yield obtained in the F_2 would be largely maintained. Simpson (1952) later found an 11% increase in yield in one F_2 hybrid over the mid-parent value, which decrease to 5% in F_4 (See Table 5.1). Another hybrid decreased from 9 to 4%. Fiber length also decreased with each successive generation as did fiber strength. Within the U5, length increased in each successive generation.

Wright devised a formula that estimates expected performance in the F_2 generation from any given number of inbred lines:

$$F_2 = F_1 - \frac{F_1 - P}{n}$$

where F_2 is the expected yield; F_1 is the average yield of the F_1 hybrids from all combinations of inbreds as can be expected where random mating is accomplished; P is the average yield of the inbred parents, and n is the number of parental lines involved. The formula indicates the expected yield of an F_2 would be one-half that of the F_1 yield attributed to heterosis. The higher yielding the inbred parents, the more productive the F_2 hybrid, according to Wright's formula. This is a good reason to produce high yielding parents with good specific combining ability. This is perhaps one of the major barriers in the acceptance of the F_2 hybrid concept in that it is not the ideal product; however, it has been shown that it can be a superior product over the parental lines. The other significant factor is that there are still a great many barriers to the commercialization of F_1 hybrids. Use of the cytoplasmic system or even the chemical hybridizing (CHA) system to produce F_1 hybrids does not appear economically feasible because of biological and production restrictions, and the cost is prohibitive at this time. If F_1 hybrids are not economically feasible, then the next logical approach is to develop the most productive product possible without restrictions of high production costs which is the F_2 hybrid. Another pertinent genetic principle is the Hardy-Weinburg rule that says there should be no further decline in the vigor in generations successive to the $F_{2,}$ provided that mating is completely at random and there is no differential selection. This principle is not particularly applicable in cotton since cotton is considered to be a self-pollinating species, in which outcrossing may occur, depending upon the insect populations.

Turner (1953b) demonstrated a consistent decline in heterosis from the F_1 to F_2 in numerous traits in 21 hybrid combinations (Table 5.2). Yield of seed-cotton showed an average increase of 33% in the F_1 over mid-parent value; however, this increase dropped to only 9% in the F_2 generation.

Dever and Gannaway (1990) conducted a study to determine whether more fiber variability had been introduced in the F_2 generation than would normally be present within a commercial variety or an F_1 hybrid. Their research showed that there was more variability in the F_2 than in the F_1 hybrid, particularly with regard to strength and standard fineness, if there was high environmental influence. The variability of fiber length and fineness disappears, however, when environmental influences are minimized. They also indicated that whatever variability would occur within an F_1 or F_2 hybrid appears to be a function of the variability within the original parents selected, especially in fiber fineness and agronomic properties. When variability is low within the original parents, variability in F_2 strength and fineness is minimal. Dever and Gannaway concluded that whenever fiber variability occurs within F_2 hybrids, it should be no greater than the variability observed in a single plant.

There are certain limitations as to the diversity of parents used to make an F_2 hybrid (Olvey 1986). Selected parents should not be greatly diverse in yielding ability as well as in agronomic properties or fiber properties.

Meredith (1990) studied a half diallel which encompassed seven Delta-type parents, 21 F_1 hybrids and 21 F_2 hybrids which were evaluated in 1987 and 1988 at three sites, using two different planting dates, a total of 12 environments (Fig. 5.7). Yield, fiber properties, and yield components were all determined in study. Meredith indicated that F_2 hybrids have the genetic potential for increasing cotton yields and fiber quality. The F_2 hybrids, besides having only 50% of the F_1 heterozygosity, consist of a very heterogeneous population which might result in a greater range of adaptation than either of their parents or F_1 hybrids. The parents selected were superior varieties or market share leaders. The use of productive commercial parents caused a lower heterotic expression, 11.8%, compared to the 18% in 14 studies that were reviewed by Meredith and Bridge (1972).

In a diallel experiment, Al-Rawi and Kohel (1970) measured heterosis as departure from the average mid-parent value. For fiber length, it was 4 and 8% for the 50% and 2.5% span, respectively; for fiber strength, 5.6%; and for fiber elongation, it was 8.5%. No heterosis was observed for fiber fineness. General and specific combining abilities were highly significant for all fiber properties. The F_1 hybrids had higher means for yield on average than the mid-parent values and both F_1 and F_2 means were close for all fiber properties. It is significant to note that no reciprocal differences were found for any of these characters. In this study, the nine parents used were quite diverse with regard to fiber properties.

Fiber

Miller and Marani (1963) reported significant additive genetic variance for fiber length and fiber strength which would allow for improvement of these traits through recombination and reselection. Ware, et al., (1944) conducted research that showed the long cotton fiber were dominant to short fiber. Ware and Harrell (1944) reported that fiber strength is inherited in a partially dominant manner. Verhalen and Murray (1967) reported that fiber fineness was governed by overdominant gene action with less additive gene variance than fiber length and strength. Young and Murray (1966) indicated that there is predominantly non-additive gene action for lint yield.

Al-Rawi and Kohel (1970) and Ware and Harrell (1944) reported that fiber properties might be controlled by partially dominant gene action but mainly in reference to fiber elongation. Baker and Verhalen (1973) disagreed with several earlier reports by stating that there was complete dominance for fiber length and strength and partial dominance for fiber fineness. Al-Rawi and Kohel (1970) reported no significant inbreeding depression detected in the fiber properties tested in their nine cultivar diallel inheritance study. Inbreeding depression, measured as a performance reduction by the F_2 below the F_1, was not significant for any of the fiber properties measured.

Meredith, et al., (1970) found no significant differences between F_1 and F_2 production although the F_1 had better overall fiber quality and yield. Significant inbreeding depression for fiber properties is further disputed by Meredith and Bridge (1973a) who reported that fiber strength, length, and elongation in F_2 selections were indicative of later generation performance. In interspecific hybridization, it is anticipated that fiber properties will diverge more widely and heterosis and inbreeding depression will become more pronounced. Fiber length is superior to the high parent in the F_1 but not between parents in the F_2 (Marani 1968a). Marani also found that fiber strength and fineness showed no F_2 deviation. Early genetic studies (Hardy, 1908) indicated that the F_2 generation can be expected to have only half of the heterozygosity of the F_1 and will consist of a very heterogeneous population.

Meredith (1990) found that the average yarn strength tenacity for the parents, F_1 , and F_2 hybrids were 130, 134, and 132 kN m kg^{-1}, respectively (Table 5.3). Another finding was that both the F_1 and F_2 hybrids had significantly lower short fiber content when compared with the parental lines. Meredith also indicated that the F_1 and F_2 hybrid of DES 119 x Delcot 344 showed a significant increase over its parents in T_1 fiber strength.

In a recent paper investigating yield and quality of F_2 hybrids, Meredith (1990) indicated a good potential for higher yields as well as benefits in lower short fiber content and higher yarn tenacity.

Standard practice of spinning mills with their elaborate routine in the blending room is an indirect tribute to the heterogeneity of cotton. The inherent fiber variability within cotton varieties is well documented (Moore, 1941) and shows highly significant differences for most fiber traits between plants in a pure line variety as well as between regions on an individual seed. Ninty-eight percent of fiber variability in a commercial Pima strain is attributed to the individual seed (Richmond and Fulton, 1936). Rigney and Nelson (1951) conducted a study to determine optimum sampling techniques for studying cotton fiber properties. They found that variability on a plot to plot basis was evident for all fiber properties in as related to fruiting position on an individual plant. Kerr (1966) indicated that variation in fiber properties can be caused by environment, heredity, and lint processing. The sampling and analytical techniques can measure the degree of variability among cotton fibers (Worley and Krowicki, 1966). Cotton processing systems have been designed to adapt to normal variation; however, if that variation is too great, the difficulties may be compounded rather than corrected.

The two highest yielding F_2 hybrids involving Pima strains (G. barbadense L.) had longer, stronger, and finer fiber with greater 22's count yarn strengths compared to Pima S-6 (Turcotte and Percy, 1990).

Simpson, et al., (1955) claimed that wide genetic variability in fiber properties could be accepted because of the desired uniformity of the proper blends can be attained as long as desirable levels of individual properties available for blending. They further concluded that the utilization of advanced generation hybrids would maintain vigor without causing insurmountable spinning problems.

The bulk harvesting of F_2 plants, which are genetically variable, can be compared to blending different lots of cotton as far as fiber property is concerned (Dever and Gannaway, 1990).

Yield

Marani (1963, 1964, 1967, 1968a and 1968b) conducted numerous studies on combining ability within and between Gossypium hirsutum L. and Gossypium barbadense L. Within G. hirsutum L., he reported a 19% yield increase in the F_1 (Table 5.10); and within the F_2, he reported 10% increases (Table 5.9). The percent deviation of the mean, of the F_2 yield from the average of the F_1 and mid-parent performance indicates how much the decline in yield is due to inbreeding in the F_2 and fits the expected loss of 1/2% of the F_1 increase due to heterosis. This would suggest based on the lower numeric values, that F_2 performance is what would be expected, and that the additive and dominant gene effects were more important than epistasis for the traits listed. Within G. barbadense L. hybrids (Fig. 5.1), heterosis for the F_1 was more evident. Again, the F_2 deviations weren't statistically significant; therefore, agreeing with the theoretical expectations of the inbreeding effect. Marani also conducted some studies (Table 5.4) in interspecific G. barbadense x G. hirsutum L. crosses in which there was significant deviation within the F_2 which is anticipated from an interspecific cross.

Marani (1968a) stated that heterosis for lint yield in his experiments was 8 to 38% in the Gossypium hirsutum L. intraspecific crosses and 12-41% in the G. barbadense L. intraspecific crosses. He also indicated that F_2 performance compared to the average of the mid-parent and F_1 performances were as anticipated. Thus, performance of the F_2 hybrid looked promising in comparison to the commercial varieties, again demonstrating useful heterosis. Figure 5.2 also indicates that the F_2 populations in the intraspecific combinations of G. hirsutum L. as well as G. barbadense L. show a superior performance with regard to lint per acre compared to its commercial parents.

Marani (1968b) indicated the F_2 performance of interspecific cross was 39 to 44% lower than the lowest yielding parental variety. Crossing of different species of cotton results in a segregated F_2 population. He further stated that when no epistasis is present, F_2 performance is expected to be near the average of F_1 and mean parental performance which is similar to results expected in combinations of G. hirsutum x

G. hirsutum L. With interspecific crosses, however, there is an epistatic gene action due to the significant F_2 deviations in all of the interspecific studies (also cytological breakdowns). For these reasons, an interspecific F_2 would be uneconomical and not a useful product.

Yield trials were conducted over a 3 year period comparing F_1 and F_2 generations in six parental combinations by Hawkins (1965) (Table 5.12). The best F_2 hybrid tested was Empire x Stoneville 7 which was 11% higher yielding than the high-parent value.

Meredith and Bridge (1972) found that heterosis for yield was present in F_1 yields ranging up to 15% more than the commercial variety Deltapine 16, whereas the F_2 yields ranged up to 10% useful heterosis (Table 5.8). They reported that heterosis in each of the nine traits studied was determined primarily by dominant gene action. Of the 54 possible tests, additive x additive epistasis was significant in only four instances. Dominance was particularly evident in larger boll size. The interaction of additive effects with locations was usually of greater magnitude than the dominant x location interaction. The F_2 hybrid of Deltapine 16 x Stoneville 603, demonstrated a 10% increase over the top commercial variety tested--Deltapine 16. This is certainly an indication of the potential of an F_2 hybrid. During the 1984 and 1985 seasons at Maricopa, Arizona the F_2 hybrid, HYP 81, demonstrated a

10.1% yield increase over the highest yielding commercial variety tested, Deltapine 90. Also, in Yuma, Arizona, for the 1984 and 1985 seasons, HYP 65, another F_2 hybrid, showed a 16.3% yield increase over Deltapine 90. The yield performance of F_2 hybrids indicate potential for commercialization of F_2s (Table 5.5, Olvey, et al., 1986). It was only after these yield trials that Pennwalt Corp. was convinced not to sell the CHA TD-1123 to seed companies, but get into the breeding/seed business via the F_2 hybrid concept.

Schoenhals and Gannaway (1990) concluded that their F_1 hybrids produced more lint than the five parental lines, however, the F_2 did not show a consistent yield to be competitive. They did indicate that the selection of top parental lines would be essential to produce an F_2 hybrid. Schoenhals and Gannaway's parents consisted of B-lines, two R-lines, Deltapine 50, Acala 1517-77 and a Dr. Luther Bird (Texas Agricultural Experiment Station) line. None of the parents were suitable for the High Plains of Texas especially when compared to the commercial variety Paymaster HS26 which was not used as one of the parents.

Lee (1983) stated that the basic pattern of cotton cultivars had not changed substantially in years. He also stated that the determination of performance on a one-meter row system has its limitations. He felt that breeders were approaching the practical limits in plant breeding, and that the best a hybrid may be able to do is to slightly increase yields and this increase may be due to crop earliness. He concluded that useful heterosis seems to come down to a very thin margin between the hybrids and the top ongoing efforts of the doctrinaire plant breeder.

The parents, F_1 and F_2 had total yields of 953, 1065, and 1025 kg/ha^{-1}, respectively (Meredith, 1990). The superior F_2 hybrids demonstrated 8% higher yield than the best parents DES 119 and Deltapine 50 as shown in Table 5.6. Figure 5.3 shows the level of yield of parents in relative proportion to the F_1 vs. F_2 vs. parental lines across 12 environments. As indicated, several of the crosses showed little inbreeding depression as indicated by Fig. 5.3. An F_2 hybrid between Deltapine x Stoneville produced yields 20 kg/ha^{-1} greater than the F_1 and 84 kg/ha greater than Deltapine. Meredith further indicated that epistasis is relatively small in comparison to additive and dominant effects within this test.

Since Chembred Incorporated is the only commercial seed company currently selling F_2 hybrids, the results of tests involving F_2 hybrid CB-1135 from the 1988, 1989 and 1990 Georgia and Tennessee state testing programs are summarized in Tables 5.13 and 5.14, respectively. CB-1135 outyielded the widely grown commercial varieties, Deltapine 90 and Deltapine 50, respectively by an average of 10 and 12%. Table 5.15 presents the rank by yield of several Chembred F_2 hybrids in various state tests from 1984 to 1989. The F_2 hybrids presented in Table 5.15 show that they were at or near the top of every yield test.

In summary, several studies of the yield performance of F_2 hybrids demonstrates superior yields (Table 5.16) as compared to well established and market share leaders, and this conclusion is supported by state and federal research as well as that by Chembred, Inc.

Utilization

One useful aspect in which the F_2 hybrid might be utilized is with the $\underline{B_t}$ gene for Heliothis resistance in one parent and conventionally incorporated resistance germplasm in the other parent. This could provide a two-way mechanism of resistance in the hybrid. Utilizing this method could delay the development of resistant types of Heliothis as compared to using one system alone, since insects would have to overcome both types of resistance mechanisms.

Germplasms that contain high levels of resistance to tobacco budworm are currently available to breeders. This germplasm is not being used by commercial seed companies primarily because the resistant germplasm does not yield as well as commercial varieties.

Jenkins, et al., (1991) indicated a negative relationship between genetically determined tobacco budworm resistance and yield. This study demonstrated the ability to make increases in both resistance and yield in F_2 hybrids as compared to each parental line (Fig. 5.6). The hybrid MHR-11 x DES 119 is more resistant than either parent and the hybrid shows heterosis for resistance. The F_2 MHR-117 x Stoneville 825 is more resistant than either parent. The F_2 hybrid MHR-16 x DH-126 was considerably higher in yield than DH-126 yet retained the resistance of DH-126. Jenkins results indicated three of the tested F_2s did indeed combine resistance with higher yields. The F_2 hybrids had a higher range of yield and a narrower range of resistance which was skewed toward resistance. In the F_2 hybrid Deltapine 50 x MHR-11, yield was as good or better than either parent. The F_2 hybrid, Stoneville 453 x DH-126, showed good resistance and equal yield to the Stoneville parent. Also, Deltapine 50 x MHR-11 maintained good resistance and was comparable in yield to the Deltapine parent. This study showed that acceptable levels of resistance to tobacco budworm can be maintained and yields can be improved while utilizing the resistant germplasm in crosses with commercial cultivars via the F_2 hybrid concept. Using the CHA to produce the F_2 hybrids within a cotton breeding program, the tobacco budworm resistant germplasm could be used to capitalize on this resistance trait.

Rooney and Stelly (1991) analyzed six monosomic-race stocks and found the same alien chromosome, designated C1- A through D, was transmitted through the female gamete in 23 to 90% of their progenies. None of the four chromosomes was transmitted through male gametes. This report indicated that the C1- A to D and other preferential transmission systems might be useful in the improvement of cotton. This system could be used as follows:

1. through the transmission of certain sets of genes
2. in genetic studies
3. in introgression
4. in the specialized use of genes responsible for this preferential transmission

This report also mentioned that if the F_2 hybrid became a commercial reality, this mechanism can be used to achieve uniformity among the F_2 plants for key selected genes (those that are engineered into one or both parents). A phenotypically uniform F_2 hybrid that is highly productive can be achieved through the proper selection of parents under closely controlled conditions. These conditions include maintaining 95% hybrid in the F_1 which is then increased to the F_2 within a low outcrossing environment.

The maternal effects from the F_1 parent would enhance F_2 performance to a degree, in terms of seed quality and physiological condition as well as seed coat characteristics. The F_2 hybrid seed is composed of an F_2 embryo with an F_1 seed coat. For this reason the F_2 hybrid seed which the farmer is planting would be as uniform as any variety currently on the market (Fig. 5.5).

Most major crops like Gossypium can be genetically vulnerable to disease or insects because they have a narrow genetic base. The use of an F_1 or F_2 hybrid affords the breeder/seed company the opportunity of interjecting any necessary germplasm through the choice of parent.

The 1990 Cotton Improvement Conference portion of the Beltwide Production-Research Conferences proved to be personally gratifying to those supporters of the F_2 hybrid concept because of the numerous reports from independent state and federal researchers verifying the worth of the F_2 hybrid. The acceptance of F_2 hybrids in the cotton industry appears to be advancing. The research being conducted by a number of independent sources in addition to the commercialization of the F_2 verifies that the F_2 hybrid concept is viable.

F_3 Populations

One aspect that would be of major concern to the seed company as well as the industry as a whole, is the tendency of farmers to "save-back" seed for planting rather than purchasing planting seed each growing season. In this case, if the F_2 were planted, the "save back" would be the F_3 generation. The F_2 generation provides a maximum range of genetic variability and F_2 populations are heterogenous, and individual plants are heterozygous. If there are high levels of intermating within the F_2, gene frequencies will tend to be maintained in the F_3 and the phenotypic makeup of both generations would be quite similar. Because cotton is predominately self-pollinating, this would suggest that inbreeding of the F_2 would result in partial fixation of the alleles and could have the affect of increasing the frequency of contrasting phenotypes, thus accentuating population variability and diluting heterotic affect that may have existed within the F_2. Many cotton breeders do make selections in the F_2 generation, however.

Meredith and Bridge (1973a) and Olvey (1988) found that the range of yield within the F_3 was far wider than the F_2. Meredith and Bridge concluded that making plant selections would be more desirable in the F_3 generation and beyond, rather than the F_2.

Another issue that the farmer must consider is how much phenotypic variability can be tolerated and anticipated within an F_2 as well as successive generations. Assuming a narrow scope of diversity between the parents, there should be few phenotypic differences evident within the F_2s, with potentially increasing differences in the F_3s. Also, and more importantly, a degradation in yield of 50% may be expected with each successive generation after the F_1 hybrid.

Inbreeding Depression

Inbreeding depression is the decline in plant vigor with each successive self-pollination among the subsequent generations following the F_1 cross between two genetically different lines.

Simpson (1948) reported that even though cotton can be and often is cross-pollinated, inbreeding depression does not manifest itself to a very high degree.

Jones and Loden (1951) indicated that both heterosis and inbreeding depression have not been nearly as dramatic or significant in cotton as has been demonstrated in corn.

Brown (1942), Young and Murray (1966), and Simpson and Duncan (1953) all concluded that there is very little yield reduction through continuous self-pollinations. Meredith and Bridge (1973a) reported negligible yield reduction. The only purpose of inbreeding in a hybrid program is to produce non-segregating parental lines.

Allotetraploid cottons show less response for heterosis and inbreeding depression than diploids and wild cottons because many favorable genes are carried in duplicate on different chromosome sets. Manning (1955) theorized that inbreeding depression is low due to the infrequent pairing of homologous chromosomes from the different genomes and the interaction between the duplicate genes. Based on this theory, there may be an explanation for the phenomenon which appears in many cotton diallel and heterosis studies in which heterosis is present in the F_2 as well as the F_1 generation. Basic genetic inheritance would dictate that F_2 hybrids exhibit 50% of the heterosis of the F_1 as defined as performance over the mid-parent performance present the F_1 hybrid. This percentage heterosis would be even less when heterosis is defined by comparing it with the highest yielding parent and the principle is more relevant and consistent when applied to simple hereditary or qualitative traits. Unfortunately agronomic characteristics in cotton are not simply inherited and most of the economically important traits, including yield and fiber properties, are quantitative with very complex inheritance patterns.

Cotton breeders generally agree that too much inbreeding is detrimental to a variety. As early as 1942, Brown

(1942) and O'Kelly (1942) concluded that inbreeding in Upland cotton reduced production by decreasing the number of flowers and producing smaller bolls. Simpson and Duncan (1953) selfed several cultivars for 10 years and found that they produced 15% less cotton than the original plants. A certain degree of heterozygosity is essential to the viability of a variety.

Al-Rawi and Kohel (1970) determined that inbreeding depression measured by the reduction in F_2 below F_1 performance, was not significant for any of the fiber properties; however, they did find that general and specific combining ability were highly significant for all fiber properties (Table 5.7). All of the fiber properties were within the range of partial dominance except fiber fineness which showed over dominance, possibly caused by repulsive linkage. Table 5.7 shows that F_1 hybrids had higher means on average than the mid-parent and F_1 means were very close to F_2 means for all fiber properties. Also, no reciprocal differences were found for these characters.

Young and Murray (1966) indicated that G. arboreum L., a diploid species, was more responsive to inbreeding than G. hirsutum L., an allotetraploid species. They concluded further that G. hirsutum L. hybrids exhibited less heterosis than the G. arboreum L. hybrids and were less responsive to inbreeding. This lack of reponse to inbreeding depression would indicate that the allotetraploid species may carry an accumulation of dominant genes in duplicate resulting in a type of built-in heterosis within polyploids. Because of the polyploid characteristic for heterosis and inbreeding, one may conclude that hybrids within cotton probably will not have the potential for hybrid vigor or inbreeding depression demonstrated in corn and tomatoes, although, there may be enough to be considered commercially beneficial. The significant finding of Young and Murray is that any heterosis found within a G. hirsutum L. hybrid combination would persist for several generations and would be important in synthetic variety production, which indicates that perhaps the F_2 hybrid would be a potential product. An F_2 hybrid is equivalent to a Syn-1 or first generation of a synthetic variety.

Darlington (1932) discussed some of the breeding problems in polyploids, particularly those that are dependent upon seed fertilization for reproduction. He found that normally the chromosomes unite in pairs at reduction- division stage of meiosis. Traits are inherited in a diploid fashion when plants are selfed because most of the mutations are masked due to the presence of at least two sets of independent factors for any particular character.

Kearney (1923) observed no inbreeding depression for yield in his five successive generations of inbreeding Pima cotton. Meyer and Justus (1961) found that the cotton plant was tolerant to inbreeding. Utilizing double haploids, which are theoretically completely homozygous, fiber and yield properties were produced that were comparable to commercial varieties. If cotton were sensitive to the effects of inbreeding, the doubled haploids would be inferior in performance as compared to commercial varieties. There are two hypotheses that would explain the lack of expression of heterosis in inbreeding of allotetraploid cottons verses corn and tomatoes. One hypothesis is that plants which are self-pollinated normally do not express a high degree of inbreeding depression of hybrid heterosis compared to those plants that are cross-pollinated. The reason for this lack of inbreeding depression, as explained by Dobzhansky (1946), is because the deleterious recessive and unfavorable combinations are quickly eliminated from the population. Also, Mather (1943) suggested that those plants that are strongly inbred achieve an internal chromosomal balance and as a result are not greatly affected by inbreeding depression. A second hypothesis is that cotton is genetically in a polyploid condition composed of A and D genomes. The diploid parents of the allopolyploids each carry many genes that have identical functions and, with the new amphidiploids, can be expected to carry more duplicate genes at each locus. There had been duplications found for several genes with qualitative effects upon the tetraploid (AD_1) cotton (Murray, 1965; and Rhyne, 1957) resulting in a duplication of many dominant, favorable genes. Jones' (1917) theory on heterosis indicated that inbreeding effects would be expected to be less in tetraploids because the segregates lack a dominant favorable allele at a particular duplicated locus and would be less frequent than is the case within a diploid.

Hertzsch (1959) demonstrated that the new polyploids were less sensitive to inbreeding than their diploid parents, similar to the case in cotton. The duplication of favorable genes must be present if the polyploid condition does reduce inbreeding depression. Young and Murray (1966) concluded that with certain hybrid combinations, considerable heterosis could be found for several generations beyond the F_1.

Parentals

Mendel (1865) stated: "In this generation there reappear, together with dominant characters, also the recessive ones with their peculiarities fully developed..." From Mendel's observations came the foundation of basic plant breeding systems of increasing variability via hybridization and selecting improved plants from the F_2 generation on.

Typically in cotton, the F_2 generation has been used primarily for selection because it has maximum genetic segregation. Since pre-Mendelian time, plant breeders have adopted the concept that wide adaptability within agricultural varieties is desirable. Johansons' "pure-line" theory of using the selection/progeny-row method of breeding was widely adopted, particularly in cotton. Many present day breeders have developed varieties based on this progeny-row method; however, the potential flaw of this method is that selection for one plant characteristic may be done at the expense of other plant characteristics. An adaptive base or population can be maintained with a certain degree of heterogeneity. The preservation of this broad adaptation has led most cotton breeders to put together composite mixtures or populations consisting of strains that are similar in major agronomic characteristics but respond differently to major environmental changes. These broadly adapted strains of cotton are usually composed of mixtures of relatively inbred biotypes.

Stroman and Fryxell (1960) indicated that an interspecific hybrid of _G. barbadense_ x _G. hirsutum_ L. produced a very large F_2 plant that was of little practical value. This accents similiar limitations with the F_2 hybrid concept in that it cannot be descended from as wide a cross as species x species. Fryxell (1958) conducted a literature review attempting to pinpoint how to select the best parents in development of the hybrid. His basic conclusion was that:

1. the parents cannot be genetically incompatible
2. the parents cannot be widely dissimilar--like crosses between species except maybe in _G. hirsutum_ x _G. barbadense_ L.

3. rely on parents that are similar but unrelated

4. rely on parents that are very closely related and

5. that it is unrealistic to work with unproductive parents in the hope of discovering a dramatic and spectacular example of specific combining ability effects which would be expecting too much from the material as Turner (1953b) has demonstrated

Logan and Richmond (1951), Fryxell (1958), and White and Richmond (1963) all agree that the greater the productivity of the parents, the smaller the heterotic effect shown in the hybrids. Working with parents that are very diverse or less productive, may require a very large amount of heterosis to place a hybrid within the range of commercial usefulness. When working with parents that are highly productive, a moderate expression of heterosis may be all that is commercially necessary.

Hawkins, et al., (1965) suggested that in breeding for heterosis, the genetic diversity of parents appears to be as important as combining ability. The selection of parents is critical.

Feaster and Turcotte (1970) found that after a few generations from the initial cross, the potential of the strain was established making further selections ineffective. They concluded that crosses between varieties rather than selection within a variety showed greater potential for a new variety.

El-Adl and Miller (1971) crossed two parental lines and showed a yield increase of 32.6% in the F_1 above the mid-parent value and exceeded the high parent by 13.3%. Based on high yield, six inbred lines were selected, carried through three cycles of recurrent selection, and were then evaluated at three locations for 2 years. The six selected lines exceeded the F_1 by 5.5%, indicating that transgressive segregation had occurred. After three cycles of recurrent selection, the F_{n+1} showed a 9.6% above the mean of F_n (Figure 5.4). Figure 5.4 is an example of generations affect on cotton yield. When crossing two parents that contribute both fiber properties and yield, the F_1 definitely shows heterosis from which improvements can be made in successive generations of individual plant selections similar to Chembred's parental development program (Olvey, 1988).

Successfully tested cotton hybrids utilizing parents of extreme backgrounds (Brown, 1948) as well as closely related lines (Feaster and Turcotte, 1970) have occurred despite the commonly held concept that hybrid vigor is positively correlated with the dissimilarity of parents (Brewbaker, 1964).

Stroman (1961) crossed a Tanguis (coarse, long fiber cotton) with an Acala 1517C (fine, medium staple cotton); the resultant F_1 hybrid more closely resembled the Acala type. The F_2s resembled more of the Tanguis with very few Acala-type plants. This might indicate that there is too wide a diversity between these two germplasms for their hybrids to prove beneficial. Another explaination could be that there was little homology at the loci and pairings or crossover did not occur. The two simply segregated out in the successive generation. In addition, an F_2 from the interspecific cross Tanguis (G. barbadense) x Acala 1517C (G. hirsutum) L. would not be expected to produce a desirable product.

Miller and Lee (1964) showed, after 3 years of testing, that there were several combinations higher yielding than the commercial variety, Coker 100-A, one of which yielded up to 25% more lint. Findings also indicated a highly significant correlation between fiber yield of one parent (example Coker 100A) in the performance of its hybrid which is further proof that in order to obtain a superior hybrid, superior parents are needed. It was recommended that at least one parent be well-adapted,in order to achieve useful heterosis. Brandes (1958), Olvey, et al., (1981) and Lee (1983) emphasized that a conventional cotton breeding program (parental development) and cotton hybridization programs be operated concurrently.

Meredith and Bridge (1983) in a study related to genetic effects for yield concluded that since nonadditive genetic effects were not detected in the F_3 generation and the lint yield range in the F_3 was much greater than that of the F_2, selection in the F_3 or later generation should be more effective than in the F_2.

Meredith and Bridge (1973a) support making selections in the F_3 or later generations verses the F_2 because greater phenotypic variability exists. They further stated that the only progeny by the F_7 generation that was superior to Deltapine 16, the leading variety at the time, descended from the highest yielding F_2 hybrid. This finding supports the use of replicated yield trials of F_2 hybrids as a good starting point in the new parental selection programs.

Chembred, Inc. conducted multi-year, multi-location replicated yield trials on F_2 hybrids (Olvey, 1988). From those tests, highest yielding F_2 hybrids with other desirable traits were selected, bulk harvested, and increased in 300 foot rows during the next growing season for an F_3 population. From this population, individual plant selections were made from which fiber sample test data further eliminated approximately 50% of the selections. Those remaining selections were grown out in F_4 progeny row increases. Harvested F_5 samples were placed in preliminary strains tests and selected candidates advanced to an advanced strains test and then elite strains test. After 3 years of testing, the new parent is placed in the crossing program to develop a new F_2 hybrid (Olvey, 1988).

Also, on a theoretical basis, it is assumed by this author that variability is desirable within cotton. The logic lies in that most commercial seed companies develop and market a variety from a composite consisting of two to five different strains or lines. Cotton breeders will devote a great deal of their efforts to develop a very homogeneous inbred line only to composite a number of those to give him that variability in combination that would be necessary to perform commercially. The F_2 hybrid can provide a direct combination of desirable traits to the cotton industry. Identifying, accepting, using, and incorporating that variability into an F_2 hybrid program is critical.

The trend toward improving cotton through genetic manipulation (Meredith and Bridge, 1983) is that breeders are paying closer attention to local adaptation rather than "beltwide" adaptation and are breeding more intensely for improved fiber properties. Lint percentage has increased; yields have increased; micronaire has increased, while the size of bolls has decreased. Yield increase is primarily due to increased numbers of bolls per area along with the increased percent of lint and higher micronaire.

The evolution of cotton breeding has led to tailor-making varieties for specific local needs. This is much easier to accomplish through the F_2 hybrid concept. Meredith and Bridge (1983) also indicated that the increase in lint yield has been from 7 to 10.4 kg/ha/year (0.84% annual gain).

Discussion

Baker and Verhalen (1973) noted that epistasis was not detected as a significant factor for any of the agronomic and fiber property traits studied. Overdominance governed lint percent, earliness, 50% span length, and uniformity index. Partial dominance was operative for fiber fineness and complete dominance was indicated for the 2.5 span length and fiber strength.

Wells and Meredith (1986) conducted growth analysis research comparing the parents with the hybrids. Results indicated that heterosis of the hybrids was greatly influenced by the early physiological development of the plant. Leaf area was greater within the hybrids than the parents, however, the leaf area development remained proportional to the dry weight growth of the plant. Both parents and hybrids had similar leaf area partitioning (LAP coefficient). The increased leaf area index of the hybrids would result in greater net assimilation rate thereby assimilating growth due to increased interception of light and photosynthetic production prior to the advent of interplant competition which is a major factor in cotton.

Varieties developed by composite strains as well as variety mixtures are all attempts to do something the F_2 hybrid concept does inherently. Does this substantiate the place for an F_2 hybrid?

CHAPTER 6

CONCLUSIONS

It appears to this author that F_2 hybrids were not considered a viable commercial product in the past because:

1. cotton breeders were pursuing the more desirable F_1 hybrid
2. the lack of an effective breeding tool/method to produce F_1 hybrids
3. most of the F_2s that were in breeders' nurseries were purposely quite diverse to select desirable recombinantes, not the type of crosses desirable to produce an F_2 hybrid
4. most seed companies make their F_1s in their nurseries, send them to winter nurseries in Tecoman, Mexico to increase and then the next growing season plant them in their fields, getting two generations in 1 year by using the winter nursery can result in low quality F_2 generation seed that may produce a less productive F_2 plant

It should be remembered that high-yielding F_2 hybrids will very likely be the exception rather than the rule in that every hybrid will not outyield its parents. There is every reason to believe that for cotton, as with corn, extensive and competent research programs will produce outstanding hybrids. These research programs will require an elaborate breeding system with extensive screening to select the few desirable hybrids.

Stith (1974) indicated that there is no limit to the potentials for tailor-making cottons if the proper tools and methods are available. He also cited the advantages of hybrids in increased yields, maturity, ability to manipulate dominant genes, provide disease and insect resistance, and the ability to "combine quantitative genes into a hybrid, thus utilizing additive effects due to dominance". Several conclusions can be drawn:

1. TD-1123 is an effective and selective male gametocide on Upland cotton
2. there is considerable heterosis within the F_1 cotton hybrid particularly for yield
3. generally, yield will decline within the F_2, but not necessarily
4. the production costs for the F_2 hybrids are substantially lower than for any F_1 hybrid system which makes it economically feasible for commercialization

After extensive yield testing, the F_2 hybrids show promise as a commercial product. The utilization of a CHA in cotton appears feasible.

Chembred, Inc. is the only cottonseed company currently selling F_2 hybrids. They have sold small quantities in 1990 and 1991 and hope to sell a substantial amount in 1992.

Meredith (1990) amply stated that "The commercial use of F_2 hybrids is most likely to depend upon the logistics of seed production and the willingness of the cotton industry to accept change."

APPENDIX A

TABLES

Table 1.1 Heterosis for Yield. Superiority of the Best F_1 Hybrid over the Best Commercial Check in Net Yield and Percentage Increase.

Investigator	Commercial check comparison	Check yield level (kg/ha)	Best F_1 hybrid over check (kg/ha)	Performance percentage increase
A. Interspecific Hybrids (G. hirsutum x G. barbadense L.)				
Marani (1967)	Coker 100 A	1040	520	50
Barnes and Staten (1961)	Acala 1517-C	890	394	44
Katarki (1971)	Laxmi	579	198	34
Fryxell et al. (1958)	Acala 1517-C	895	189	21
Omran et al. (1974)	Coker 100 WR	-	-	41
Stroman (1961)	Acala 1517-C	-	-	38
Karev (1969)	Bulg. 3279	-	400	-
Christidis (1955)	Local cultivars	-	-	7
B. Intraspecific G. hirsutum L. Hybrids				
Patel (1971)	Gurjurat 67	662	915	138
Thomson (1971)	Stoneville 7A	1622	271	17
Marani (1968)	Coker 100A	1640	260	16
Hawkins et al. (1965)	Pope	875	192	22
Meredith and Bridge (1972)	Deltapine 16	913	138	12
White and Richmond (1963)	Acala 4-42	1040	105	10
Jones and Loden (1951)	Pandora	572	77	14
Miller and Marani (1963)	Coker 100	888	NS	
Turner (1953a)	Pandora	-	-	34
Kime and Tilley (1974)	Stoneville 4B	-	-	13

SOURCE: Davis, 1978.

Table 1.2 Generalized Heterotic Response in Certain Agronomic and Fiber Properties of *G. hirsutum* x *G. barbadense* L. Hybrids.

Character	Response evaluation	Source
	Plant characters	
Seedling vigor	Asset--early attainment of adequate framework for fruiting.	Barnes and Staten (1961)
Overall plant height	Liability or neutral--depends on SCA	Ware (1930), Barnes and Staten (1961), Marani (1967), Davis (1973)
Node Number	Neutral	Ware (1930), Kearney (1923b)
Node length	Liability--plant too rangy	Ware (1930), Kearney (1923b) Davis (1973)
Leaf size	Liability--leaf/fruiting index too high	Kearney (1923b)
Petiole hair	Neutral	Kearney (1923b)
Bract size	Liability--may contribute to trash	Kearney (1923b)
Boll size	Neutral--compensations made in flowering, shedding rates	Marani (1963, 1967), Davis (19-73), Fryxell et al. (1958), Barnes and Staten (1961)
Boll number	Asset--primary yield component	Marani (1963, 1967), Fryxell et al. (1958), Davis (1973), Omran et al. (1974),
Lock number	Neutral	Kearney (1923b)
Seeds per boll	Liability--increases number of bolls required to produce 1 kg. of lint	Marani (1963, 1967)
Lint percentage	Liability--more seed cotton required to pro-duce 1 kg. of lint	Marani (1963, 1967), Fryxell et al. (1958) Davis (1974), Omran et al. (1974)
	Fiber properties	
Fiber fineness	Variable--depends on end-use requirements	Fryxell et al. (1958), Marani (1968d) Davis (1974)
Fiber length	Neutral to liability--depends on end-use requirements	Fryxell et al. (1958), Kearney (1923), Barnes and Staten (1961)
Fiber maturity	Neutral--depends on SCA	Fryxell et al. (1958)
Length uniformity	Neutral	Fryxell et al. (1958), Davis (1974)
Fiber strength	Asset--high strength important to most end uses	Fryxell et al.(1958),Marani (1968d), Davis (1976)

SOURCE: Davis, 1978.

Table 4.1 Effects of TD-1123 on Various Characteristics of Upland Cotton

	Treat-ment	Rate (lbs /Acre)	Plant Height (cm)		Node Number (No.)		Flower Counts (No.)		Total Dry Weights (grams)		Number of Squares (No.)	
Date			7-16	8-6	7-16	8-6	7-27	8-3	7-16	8-6	7-16	8-6
	Control	0	89.7	113.3	18.7	24.7	94	81	97.3	198.3	52.3	26.3
	Dala-pon	1.73	86.3	116.0	18.7	25.0	56	56	77.0	127.3	42.7	43.3
		2.64	--	--	--	--	47	60	--	--	--	--
		6.09	91.7	120.0	20.3	24.0	22	14	113.7	151.2	55.7	36.7
		12.69	75.0	98.0	17.3	21.3	6	16	61.6	136.7	35.0	25.7
	TD-1123	0.04	94.0	109.3	19.7	26.3	82	71	91.6	208.8	59.0	76.3
		0.09	--	--	--	--	74	88	--	--	--	--
		0.17	--	--	--	--	73	103	--	--	--	--
		0.42	--	--	--	--	81	108	--	--	--	--
		0.65	88.7	117.0	19.0	26.3	68	145	99.0	180.8	56.7	73.3
		0.81	--	--	--	--	67	119	--	--	--	--
		1.07	--	109.0	--	25.3	57	140	--	108.4	--	69.3
		1.10	--	--	--	--	44	138	--	--	--	--
		1.46	--	--	--	--	48	168	--	--	--	--
		1.47	83.3	100.3	18.3	25.3	40	119	90.8	102.1	31.7	58.0
		1.52	--	--	--	--	27	118	--	--	--	--
		3.00	--	--	--	--	8	40	--	--	--	--
		3.18	--	--	--	--	2	5	--	--	--	--
		6.77	--	--	--	--	0	9	--	--	--	--
		11.78	69.3	61.7	15.3	18.7	0	3	58.8	58.0	1.3	2.1

Table 4.1 Effects of TD-1123 on Various Characteristics of Upland Cotton (Continued)

Treatment	Rate (lbs /Acre)	Number Mature Bolls (No.)		Green Boll Weight (g)		Square Weight (g)		Leaf Weight (g)		Stem Weight (g)		Root Weight (g)	
Date		7-16	8-6	7-16	8-6	7-16	8-6	7-16	8-6	7-16	8-6	7-16	8-6
Control	0	5.7	27.0	8.5	87.8	5.6	3.7	38.0	41.8	38.2	58.0	6.8	7.0
Dalapon	1.73	6.3	9.7	6.3	25.5	5.5	6.0	28.6	35.6	30.9	53.0	5.7	7.2
	2.64	--	--	--	--	--	--	--	--	--	--	--	--
	6.09	6.3	6.7	10.7	11.8	7.0	3.6	40.9	59.0	47.6	67.1	7.5	9.7
	12.69	3.3	7.3	2.9	22.4	3.8	2.7	23.7	44.3	26.1	57.7	5.1	9.7
TD-1123	0.04	7.7	18.0	5.6	56.8	7.1	10.0	34.4	56.5	38.3	74.3	6.2	11.2
	0.09	--	--	--	--	--	--	--	--	--	--	--	--
	0.17	--	--	--	--	--	--	--	--	--	--	--	--
	0.43	--	--	--	--	--	--	--	--	--	--	--	--
	0.65	5.7	14.7	10.4	39.1	6.8	8.9	36.1	49.7	38.7	72.4	7.0	10.8
	0.81	--	--	--	--	--	--	--	--	--	--	--	--
	1.07	--	4.0	--	7.7	--	8.1	--	35.5	--	48.7	--	8.4
	1.10	--	--	--	--	--	--	--	--	--	--	--	--
	1.46	--	--	--	--	--	--	--	--	--	--	--	--
	1.47	2.7	2.7	5.7	6.9	3.6	6.4	34.1	34.5	39.6	45.6	7.8	8.8
	1.52	--	--	--	--	--	--	--	--	--	--	--	--
	3.00	--	--	--	--	--	--	--	--	--	--	--	--
	3.18	--	--	--	--	--	--	--	--	--	--	--	--
	6.77	--	--	--	--	--	--	--	--	--	--	--	--
	11.78	1.0	2.0	1.3	3.1	0.2	0.6	22.5	18.1	28.5	28.7	6.3	7.5

SOURCE: Olvey, 1983.

Table 4.2 Fate of foliar applied ^{14}C-labeled potassium 3, 4-dichloro-5-isothiazolecarboxylate on individual cotton leaves in the field (100 ug/leaf)

Days post-treatment	% of dose in indicated fraction			
	external rinse	internal extract	unextractable	loss[a]
0	97.5	2.2	0.3	0.0
2	44.9	23.2	5.5	26.4
3	22.6	18.8	10.2	48.4
7	11.2	9.5	15.4	63.9
14	3.5	4.8	10.8	80.9

[a] Reflects volatilization, weathering, and translocation to other parts of the plant.

SOURCE: Shaver, et al., 1979.

Table 4.3 Distribution of radioactivity in cotton plants sprayed with ^{14}C-labeled potassium 3, 4-dichloro-5-isothiazole-carboxylate and harvested 43 days posttreatment.

plant sample	ppm (dry wt) ^{14}C-labeled PDIC equiv (±SE)	dry wt, g
stems	16.9 ± 0.9	113.2
roots	3.3 ± 0.2	15.5
leaves (on ground)	83.0 ± 4.7	115.5
leaves (on plant)	145.7 ± 5.4	70.8
bolls		
calyx	45.0 ± 2.6	43.8
bracts	429.7 ± 19.1	3.0
lint	4.9 ± 1.8	44.7
seed	233.7 ± 23.8	86.3
hulls	24.5 ± 4.8	

SOURCE: Shaver, et al., 1979.

Table 4.4 Effects of TD-1123 on Various Cotton Plant Parts

PLANT PART	HIGH TD-1123 RATE	DESIRED TD-1123 RATE
Plant Height	Reduced	Slightly reduced
Leaves:		
Developing leaves	Much smaller; no distinct lobes; burned margins	Slightly reduction
Older leaves	Reduction in size due to burning of margins-burn spots where high concentrations landed on leaf	Little or no effect
Terminal Growth	Severely stunted; initiates lateral growth	Slight inhibition
Internode Spaces	Much shorter	Slightly shorter than normal
Flowering	Initially inhibits flowering then flowers excessively; flowers easily abscise	Slight reduction initially; then flowers heavier than normal; flowers abscise if not cross-pollinated
Flower	Considerable variation in expression of all parts of flower	Similar to cytoplasmic male sterile flowers
Petals	Smaller; red color on margins	Slightly smaller than normal; possible pink coloration
Bracts	Bracts burned	Tip of bracts slightly to moderately burned
Bud	Small and red tipped	Slightly smaller; may be pinkish
Stigma	From no stigma; varies in sizes--small to too tall	Close to normal
Filaments	Very small to normal sized	Small to normal
Anthers	Very underdeveloped to normal size; but do not dehisce	Very underdeveloped to normal size; but do not dehisce
Number of Ovules	Reduction	Reduction
Locks per boll	Two to three	Three to four (4 to 5 normal)

Table 4.4 Effects of TD-1123 on Various Cotton Plant Parts (Continued)

PLANT PART	HIGH TD-1123 RATE	DESIRED TD-1123 RATE
Number of Seeds	Reduced and Immature	Slightly reduction in number
Fiber Quality	Slight	Slight
Percent Set	Reduced	Slightly reduced
Leaf Phytotoxicity	Severe	Slight
Number of Days 100% Male Sterile	25+ days	14 days

SOURCE: Olvey et al., 1981.

Table 5.1 Lint yield, fiber lengths, and fiber strength in advanced generations of Ute 4 and Ute 5 hybrids.

Populations*	Lint yield %MP**	Fiber length in.	Pressley index
Ute 4B	111	1.18	8.17
Ute 4C	110	1.19	8.07
Ute 4D	106	1.16	7.93
Ute 4E	105	1.16	7.41
Ute 5B	109	1.17	7.48
Ute 5C	104	1.18	7.64
Ute 5D	105	1.15	8.23

* B = F_2, C = F_3, D = F_4, E = F_5.
** Percent of mid-parent

SOURCE: Simpson, 1952.

Table 5.2 Heterosis in F_1 and F_2 generations.*

Trait	F_1 % MP*	F_2 % MP*
Seedling vigor	17	10
50 % bloom date	6	0
Shedding rate	35	0
Number of bolls	25	4
Grams per boll	7	0
Seeds per boll	12	3
Lbs. seed cotton per plot	33	9

* Heterosis measured as percent of mid-parent.

SOURCE: Turner, 1953.

Table 5.3 Average parental, F_1, and F_2 cotton fiber properties* from a seven-parent half-diallel across 12 environments.

Genotype	Span length						Short fiber	
	50%	2.5%	T_1	E_1	Mic.	Yarn tenacity	no.	wt.
	mm		kN m kg^{-1}	%		kN m kg^{-1}	%	
Parents	14.4b**	29.4c	21.1c	7.8a	4.02a	130c	7.3a	3.5a
F_1	14.5b	29.9a	21.5a	7.6b	3.97c	134a	6.2b	2.9b
F_2	14.5b	29.7b	21.3b	7.6b	4.00b	132b	5.8b	2.8b

* T_1 = fiber strength; E_1 = elongation; Mic. = micronaire reading.

** Within columns, means followed by the same letter are not significantly different at the 0.01 probability level, as indicated by a t-test.

SOURCE: Meredith, 1990.

Table 5.4 Mean heterosis and F_2 deviation in three experiments with Gossypium hirsutum x Gossypium barbadense crosses.

Trait	F_1 % MP*	% F_2 deviation**
Lint yield	62.7	57.7
Lint %	-8.7	8.4
Boll weight	-3.4	26.9
Boll number	68.5	40.3
Seeds per boll	-14.2	21.1
Number flowers	17.7	13.4
% boll retention	30.8	23.8

* Heterosis measured as percent of mid-parent.
** Percent deviation from average of F_1 and mid-parent.

SOURCE: Marani, 1968a.

Table 5.5 Yield comparisons of F_2 hybrids (HYP #) vs Deltapine 90 (DP 90) in Arizona yield trials for the 1984 and 1985 seasons.[1]

	MARICOPA				YUMA			
	YIELD		Aver-	Percent	YIELD		Aver-	Percent
Entry	1984	1985	age	Increase[2]	1984	1985	age	Increase[2]
	(Lbs/A)	(Lbs/A)	(Lbs/A)	(%)	(Lbs/A)	(Lbs/A)	(Lbs/A)	(%)
HYP 49	2085	2028	2057	6.2				
HYP 81	2209	2056	2133	10.1				
DP 90	2041	1832	1937		1402	1558	1480	
HYP 1					1512	1720	1616	9.2
HYP 53					1458	1810	1634	10.4
HYP 65					1715	1727	1721	16.3
HYP 85					1650	1753	1702	15.0
HYP 290					1636	1730	1683	13.7

[1] Compiled from University of Arizona Annual Cotton Reports.

Table 5.6 Average parental, F_1, and F_2 yield and yield components in cotton, from a seven-parent half-diallel across 12 environments.

	Lint yield			Weight	
Generations	Total	First harvest	Lint	Boll	Seed
	kg ha^{-1}		%	mg	
Parents	953c*	594c	35.7a	500a	104a
F_1	1065a	688a	35.9b	541c	106c
F_2	1025b	643b	35.7a	522b	105b

* Within columns means followed by the same letter are not significantly different at the 0.01 probability level, as indicated by a t-test.

SOURCE: Meredith, 1990.

Table 5.7 Average performance of F_0, F_1, and F_2 generations, and overall heterosis and inbreeding depression of fiber properties.

	Generation mean			Highest parent			No. of crosses significant, .05	
Character	F_0	F_1	F_2	Lowest parent	Heterosis	Inbreeding depression	Heterosis	Inbreeding depression
50% span length	0.466	0.484	0.476	1.23	4.0*	1.6	9	0
2.5% span length	1.022	1.051	1.036	1.27	2.8*	1.4	8	0
Strength	19.187	20.269	20.249	2.15	5.6**	0.1	7	0
Elongation	6.341	6.882	6.866	2.33	8.5**	0	8	0
Fineness	4.154	4.214	4.215	1.28	1.4	0	1	0

*, ** Significant at .05 and .01 levels, respectively.

SOURCE: Al-Rawi and Kohel, 1970.

Table 5.8 Heterosis for lint yield in F_1 and F_2 population from six crosses.

Population*	Generation	%MP**	%HP**
DPL X Q	F_1	47	10
	F_2	28	-4
DPL X DC	F_1	20	0
	F_2	16	3
DPL X FTA	F_1	15	-8
	F_2	8	-14
DPL X A	F_1	38	0
	F_2	24	-10
DPL X Mo	F_1	17	15
	F_2	9	7
DPL X Stv	F_1	7	7
	F_2	9	10

* DPL = Deltapine 16, Q and FTA = Pee Dee Strains, A = Acala 3080, Mo = Missouri strain 277-396, Stv = Stoneville 603

** MP = mid-parent; HP = high parent

SOURCE: Meredith and Bridge, 1972.

Table 5.9 Mean performance of the parents and their F_2 hybrids in the 1968 diallel.

Entry	Lint Yield kg/ha	Lint %	Boll Size	Seed Index	50% SL	2.5% SL	T_1	E_1	Mic.
DPL 16	942	38.6	5.34	10.4	0.54	1.16	20.4	8.1	4.0
Stv 508	836	34.6	5.62	11.0	0.56	1.18	20.3	7.1	3.9
Coker 4104	862	35.7	5.52	11.0	0.52	1.12	19.1	6.9	3.8
NM 9608	823	36.2	5.51	10.7	0.57	1.14	23.1	5.8	4.2
PD 3967	850	40.5	6.00	11.5	0.53	1.10	21.0	5.5	4.7
DPL x Stv	915	36.3	5.51	10.4	0.57	1.18	20.2	7.5	3.7
DPL x Cok	1,032	37.5	5.66	10.7	0.55	1.15	20.5	7.4	3.8
DPL x NM	945	38.0	5.19	10.8	0.57	1.15	21.2	7.1	3.8
DPL x PD	924	39.2	5.45	10.2	0.55	1.15	20.7	7.1	4.0
Stv x Cok	916	35.7	5.93	11.2	0.55	1.17	20.0	7.1	3.8
Stv x NM	930	36.7	5.91	11.3	0.57	1.15	21.6	6.6	3.9
Stv x PD	907	37.8	5.99	11.1	0.55	1.16	19.9	6.6	4.1
Cok x NM	907	36.2	5.96	11.4	0.56	11.5	22.3	6.2	4.2
Cok x PD	848	38.1	5.73	11.2	0.53	1.15	19.8	6.5	4.1
NM x PD	900	38.8	5.97	11.6	0.59	1.16	22.9	5.7	4.3

SOURCE: Marani, 1968a.

Table 5.10 Mean heterosis and F_2 deviation in two experiments with _G. hirsutum_ crosses.

Trait	F_1 % MP*	% F_2 deviation**
Lint yield	19.6	1.8
Lint %	2.4	-1.4
Boll weight	7.2	-2.3
Boll number	8.8	4.0
Seeds per boll	0.8	1.5
Number flowers	1.3	3.1
% boll retention	7.3	1.7

* Heterosis measured as percent of mid-parent.
** Percent deviation from average of F_1 and mid-parent.

SOURCE: Marani, 1968a.

Table 5.11 Mean heterosis and F_2 deviation in two experiments with G. barbadense crosses.

Trait	F_1 % MP*	% F_2 deviation**
Lint yield	24.6	5.6
Lint %	1.8	0.5
Boll weight	4.8	2.2
Boll number	16.2	3.0
Seeds per boll	2.2	1.8
Number flowers	10.8	3.6
% boll retention	4.9	-1.0

* Heterosis measured as percent of mid-parent.
** Percent deviation from average of F_1 and mid-parent.

SOURCE: Marani, 1968a.

Table 5.12 Three-year mean heterosis for yield in F_1 and F_2 generations from six parental combinations.

Population	Generation	% MP*	%HP*
Empire x Pope	F_1	30	22
	F_2	-13	-18
Empire x Plains	F_1	21	20
	F_2	4	4
Empire x St 7	F_1	27	24
	F_2	13	11
Pope x Plains	F_1	25	18
	F_2	6	0
Pope x St 7	F_1	22	12
	F_2	2	10
Plains x St 7	F_1	21	18
	F_2	-7	-10

* Heterosis measured as percent of mid-parent (MP) and high parent (HP).

SOURCE: Hawkins, et al., 1965.

Table 5.13 Yield comparisons of Chembred 1135 (CB 1135) F_2 hybrid vs Deltapine 90 (DP 90) in Georgia State Yield Trials for the 1986-1990 seasons.[1]

	YEAR		1989		1990		AVERAGE	
	Yield	Percent	Yield	Percent	Yield	Percent	Yield	Percent
	(Lbs/A)	(%)	(Lbs/A)	(%)	(Lbs/A)	(%)	(Lbs/A)	(%)
Midville	1986							
DP 90	479	100	1327	100	545	100	784	100
CB 1135	441	92	1408	106	658	121	836	107
Plains								
DP 90			1572	100	789	100	1181	100
CB 1135			1511	96	1012	128	1262	107
Tifton	1987							
DP 90	1190	100	1262	100	789	100	1080	100
CB 1135	1264	106	1234	98	918	116	1139	105

[1] Compiled from Georgia state yield test data.

Table 5.14 Yield comparisons of Chembred 1135 (CB 1135) F_2 hybrid vs Deltapine 50 (DP 50) in Tennessee State Yield Trials for the 1988-1990 seasons.[1]

	1988		1989		1990		AVERAGE	
	Yield	Percent	Yield	Percent	Yield	Percent	Yield	Percent
	(Lbs/A)	(%)	(Lbs/A)	(%)	(Lbs/A)	(%)	(Lbs/A)	(%)
Milan								
DP 50	654	100	486	100	1118	100	754	100
CB 1135	650	99	633	129	1219	109	834	111
Jackson								
DP 50	1160	100	1346	100	945	100	1150	100
CB 1135	1265	109	1383	103	1087	115	1245	108
Ames								
DP 50					509	100	509	100
CB 1135					700	138	700	138

[1] Compiled from Tennessee state yield test data.

Table 5.15 Success of F_2 Hybrids in State Tests From 1985 to 1989.

STATE	LOCATION	RANK IN TEST*				
		1985	1986	1987	1988	1989
ALABAMA	Monroeville	-	2 & 3	4 & 5	7	1
	Prattville	-	1 & 2	3	7	2
CALIFORNIA	Screening	-	-	2,6,8	2,3,8	1,2,3
	Variety	-	-	-	-	4 & 5
GEORGIA	Athens	-	1	-	-	-
	Midville	-	1	-	4 & 5	7
	Tifton	-	1 & 2	2 & 3	7 & 8	9
	Plains	-	-	-	3	5
LOUISIANA	Bossier City	2 & 3	1 & 2	-	7	8
	Winnsboro-Irr.	-	-	-	5	-
	-Dry	-	-	-	4	2
MISSISSIPPI	Stoneville	2 & 3	1 & 3	1,3,5	-	7
MISSOURI	Portageville	-	2	2,4,5	2,5,8	3
	Senath	-	-	-	-	2
NEW MEXICO	Artesia	-	2	2	3	7
	Las Cruces	2	-	3	5	2
	-Adv. Str.	-	2	-	1,2,3	-
	-Strains	-	-	-	1,3,5	1
OKLAHOMA	Altus	1	5	4	-	-
	Mangum	1	3	1 & 2	-	-
S. CAROLINA	Florence	1 & 3	1 - 6	1 - 6	1 - 4	2 - 5
TENNESSEE	Ames	-	1,3,5	-	-	-
	Jackson	1	1,2,4	1	8 & 9	6
	Milan	-	-	-	5	2 & 4
TEXAS	College Station	7	-	-	-	2 & 5
	Corpus Christi	-	-	2	-	7
	Dallas	-	-	-	1,3,5	3,4,5
	Halfway:					
	Dryland	-	3	2 & 3	2	-
	Irrigated	-	-	4	4	-
	Lubbock:					
	Dryland	6	2	1 & 2	2	-
	Irrigated	-	-	1	2	-
	Pecos	-	-	-	3 & 4	-
	Thrall	1	-	1	-	2 & 5
	Weslaco	-	2	-	-	1

* F_2 hybrids from Chembred Inc. were directly compared to best commercial varieties in respective regions. Number of entries per test average 24 to 30.

\- Dash indicates not entered, test lost or data not received.

SOURCE: Olvey, 1991.

Table 5.16 Useful heterosis in F_2 Cotton Hybrids reported in literature reviewed.[1]

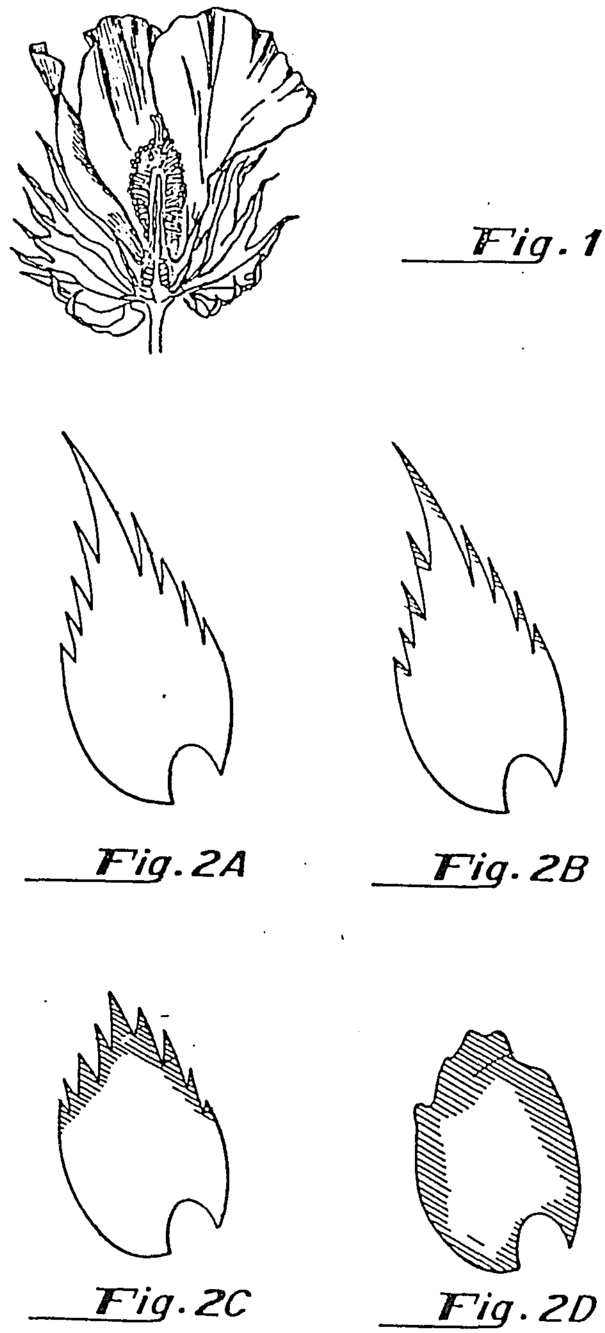
Data Source: Year	Data Source: Author(s)	No. of F_2 Hybrids Tested	Percent Increase
			(%)
1947	Kime and Tilley (MP)	na	5
1952	Simpson (MP)	na	11
1953	Turner (MP)	21	9
1958	Muramoto	7	4
1963	Miller and Marani	8	none
1965	Hawkins, et al.	6	2-14
1968	Marani (b)	6	9
1968	Marani	6	7
1972	Meredith and Bridge	6	7-9
1973	Meredith and Bridge	10	10
1985	Olvey, et al.		
	Maricopa, Arizona	262	8
	Yuma, Arizona	85	24
1986	Olvey, et al.		
	Maricopa, Arizona	60	12
	Yuma, Arizona	60	16
1986	Weaver		
	Athens, Georgia	10+	12
	Midville, Georgia	10+	6
1990	Meredith	21	8
1990	Turcotte and Percy (b)	15	8
1991	Jenkins	13	11

[1] All F_2 hybrids were from Gossypium hirsutum L., except for two authors who reported on Gossypium barbadense L., noted by (b). All were compared to the top commercial variety in the test unless indicated as mid-parent (MP) value.

APPENDIX B

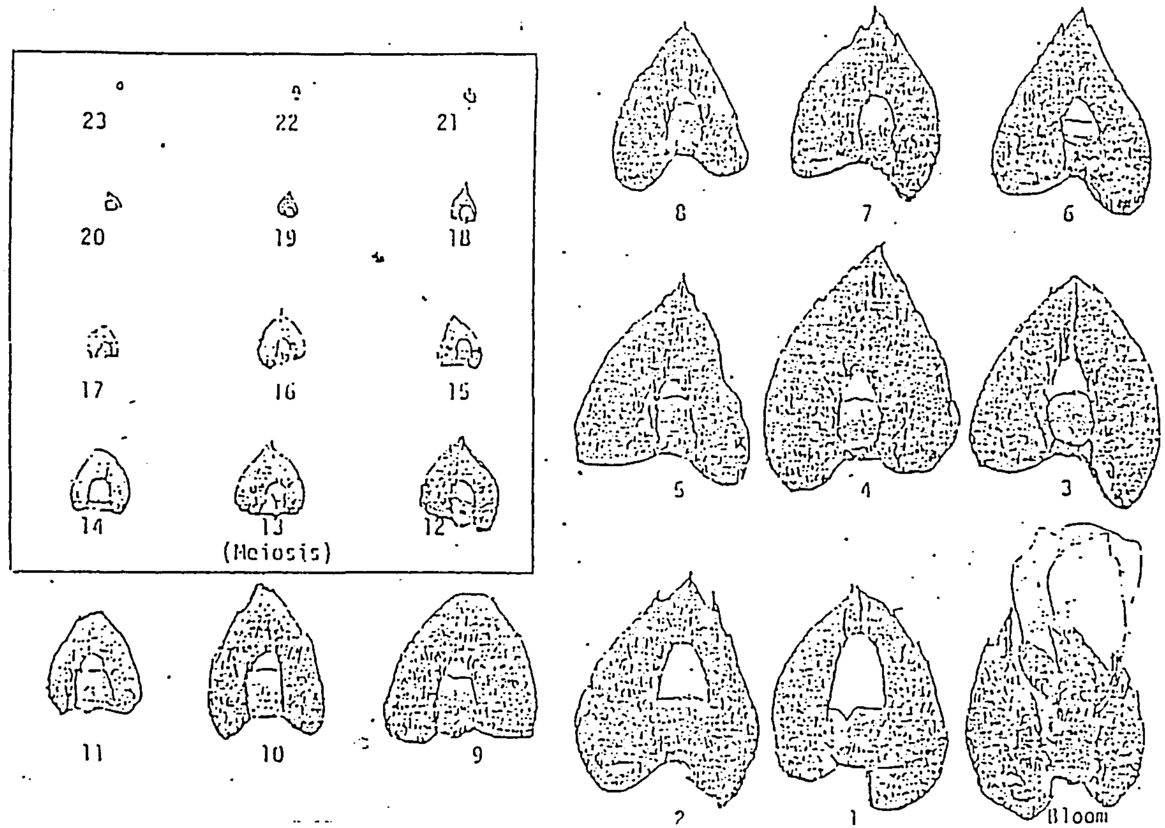
FIGURES

Figure 4.1 Brack Burn Identification - A Key to Determining Male Sterility



SOURCE: Olvey, 1991.

Table 4.2 Stages of Bud Development of Cotton



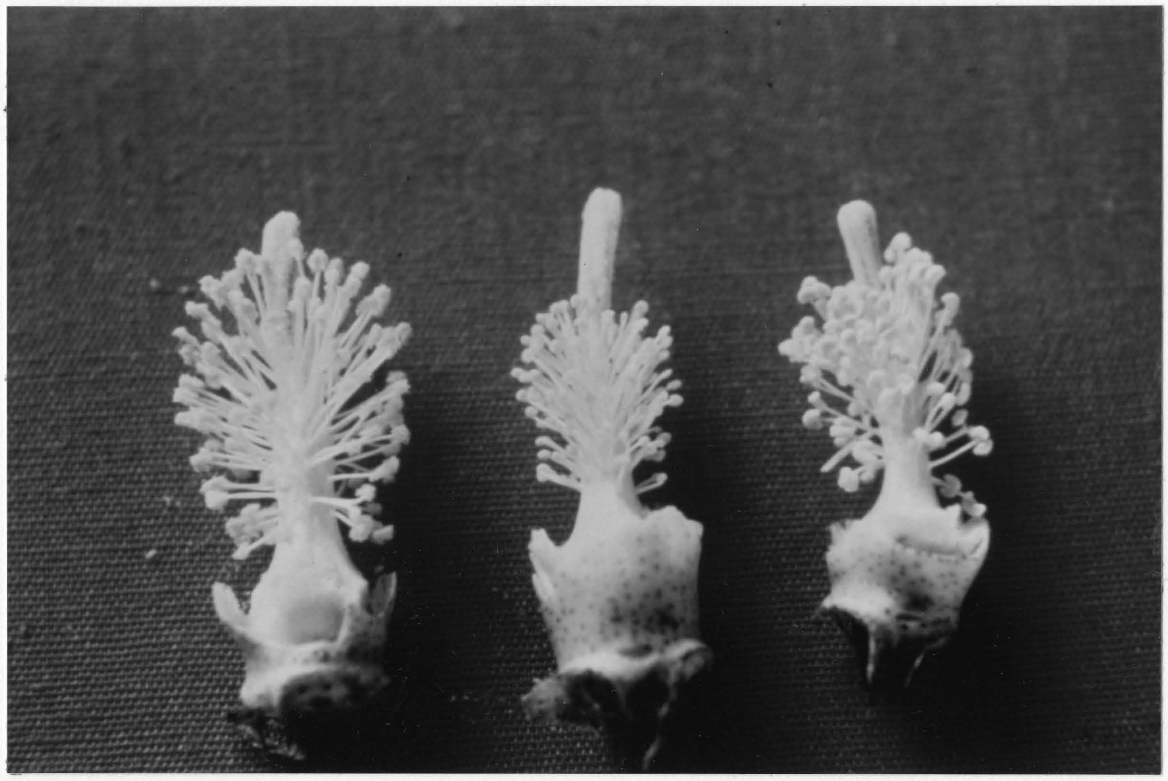
Floral buds of Garo Hill cotton, showing the size of the floral buds from 23 days preceding bloom until bloom (23 to 9 - natural size and 8 to bloom - x 9/10 size). Boxed area is the stage of development in which gametocide is most effective in inducing male sterility in flowers.

SOURCE: USDA ARS.

Figure 4.3 Developing Squares on a Fruiting Branch of a Cotton Plant

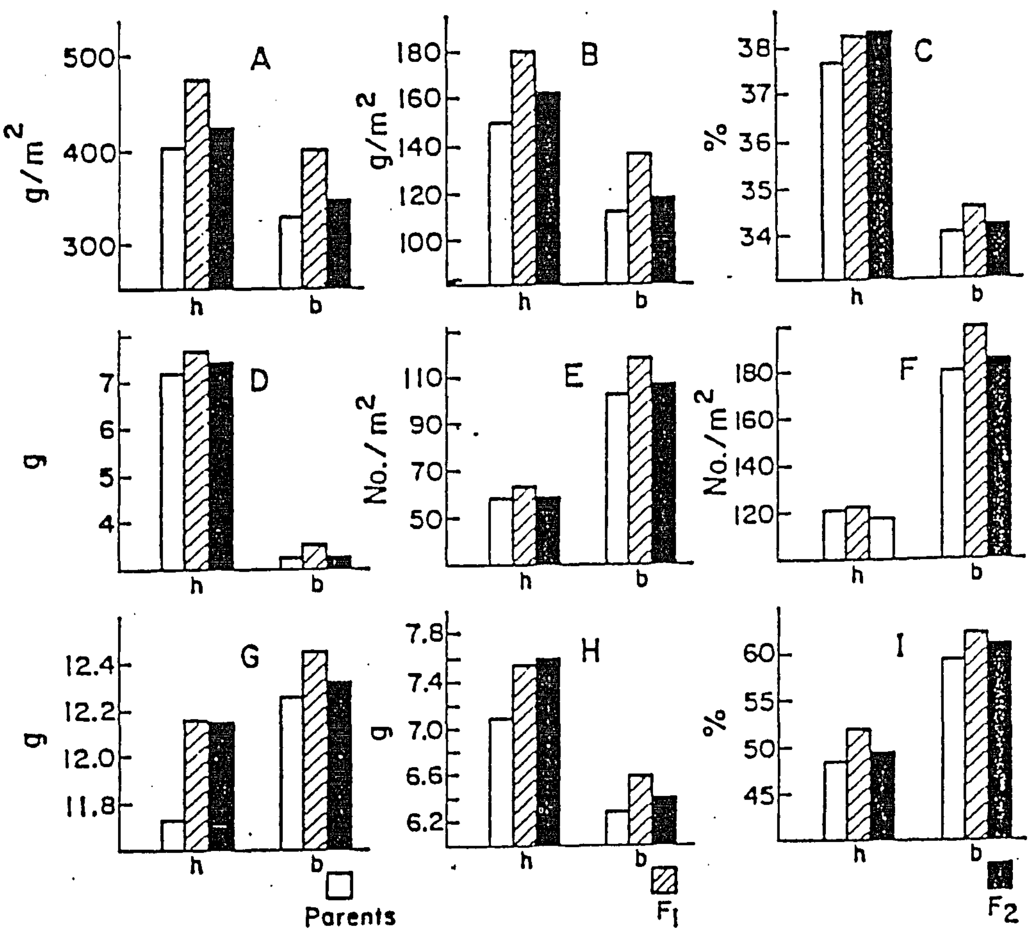
SOURCE: Olvey, 1991.

Figure 4.4 Normal and Two CHA-Treated Male-Sterile Cotton Flowers



SOURCE: Olvey, 1991.

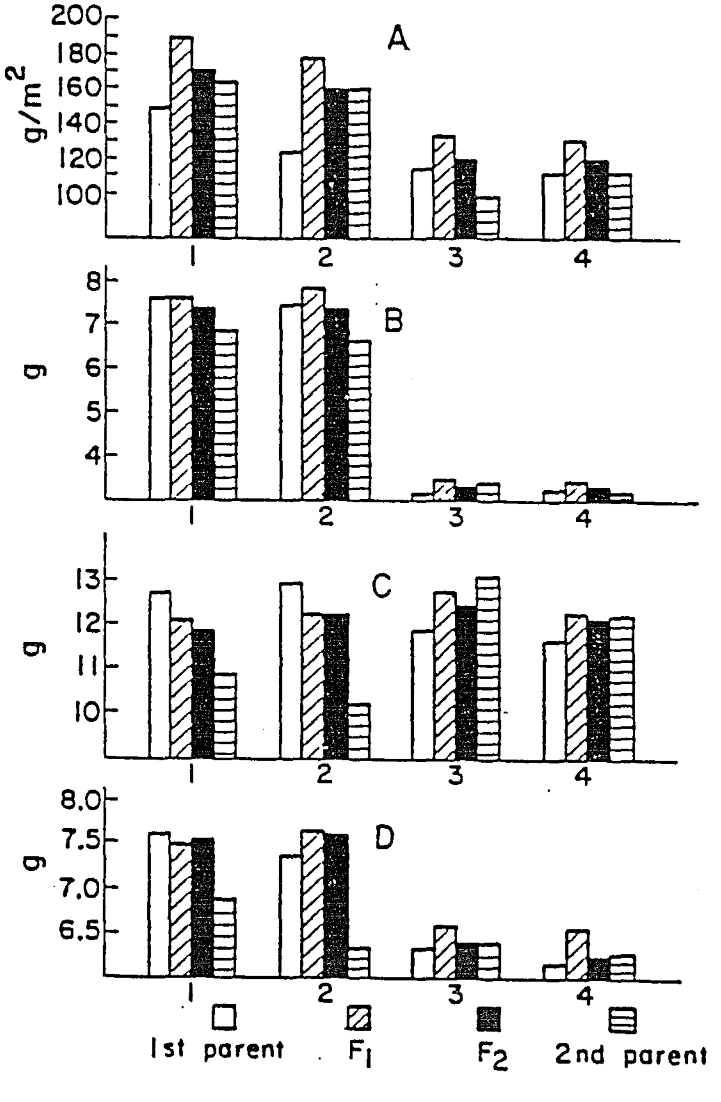
Figure 5.1 Average Performance of Parental Varieties and Their F_1 and F_2 Hybrids, of G. hirsutum L. and G. barbadense L.



Average performance of parental varieties and their F_1 and F_2 hybrids, of G. hirsutum L. (H) and G. barbadense L. (b). A. Yield of seed-cotton. B. Yield of lint. C. Lint percent. D. Boll weight. E. Boll number. F. Flower number. G. Seed index. H. Lint Index. I. Percentage of boll retention.

SOURCE: Marani, 1968a.

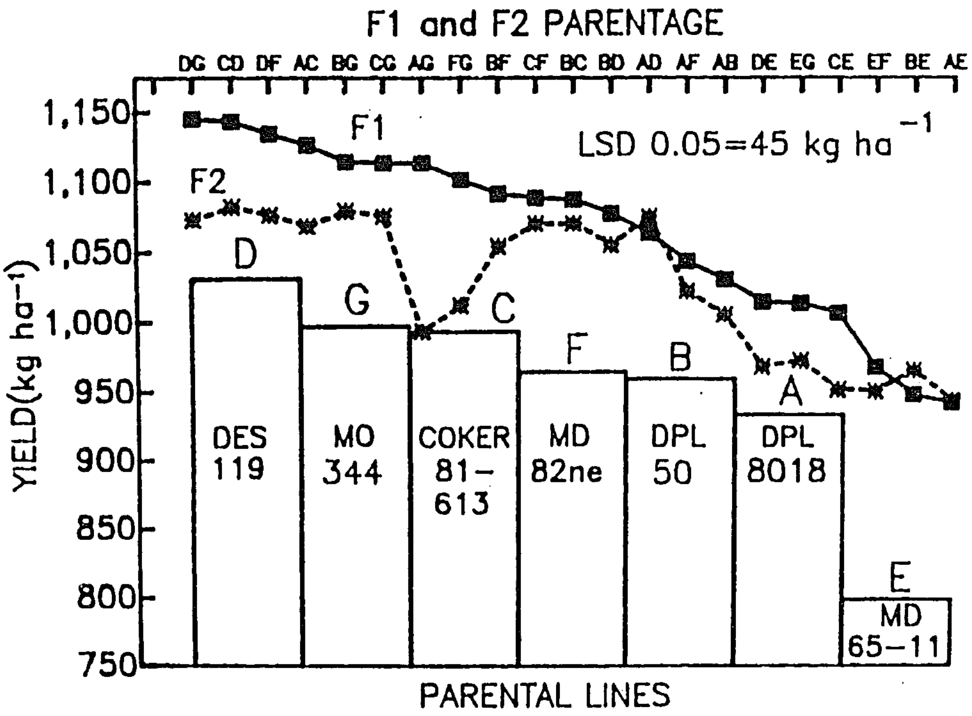
Figure 5.2 Performance of Parental Varieties and Their F_1 and F_2 Hybrids in Some Crossing Combinations



1. Acala 1517C x Coker 100A. 2. Acala 4-42 x Empire W. 3. Karnak x Malaki. 4. Giza 7 x Pima 32. A. Yield of lint. B. Boll weight. C. Seed index. D. Lint index.

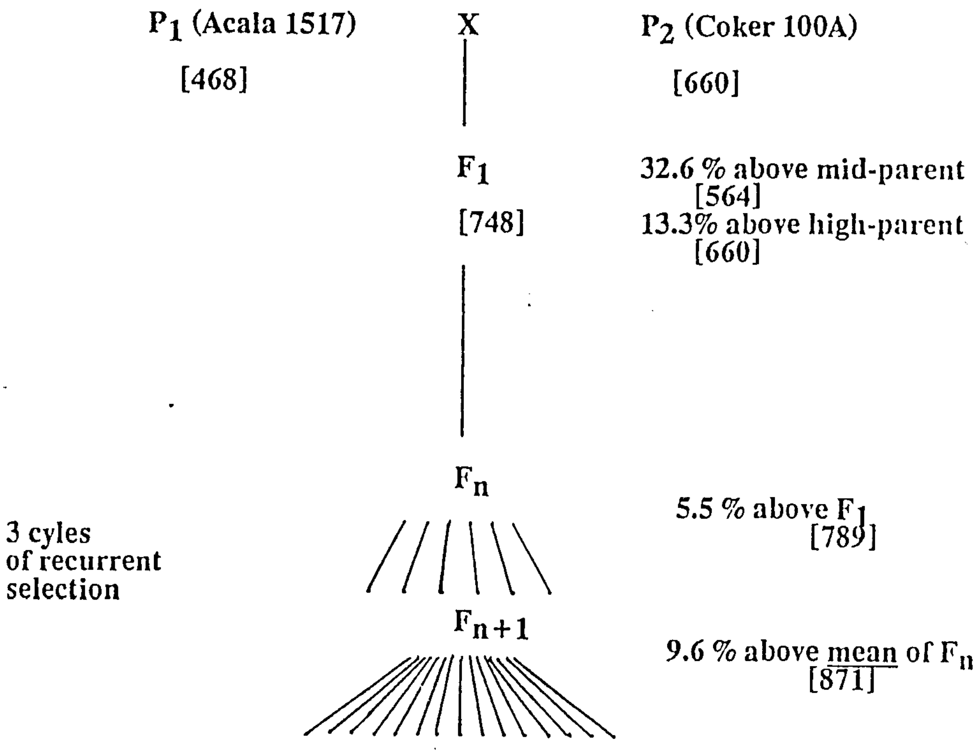
SOURCE: Marani, 1968a.

Figure 5.3 Average Yield of Cotton Parents and F_1 and F_2 Hybrids Across 12 Environments



SOURCE: Meredith, 1990.

Figure 5.4 An Example of Generations' Effect on Cotton Yield



Yield measured in kg/ha shown in [ ].

SOURCE: Olvey, et al., 1981.

Figure 5.5 Maternal Effects on Mean Phenotypic Values Upon Generation·

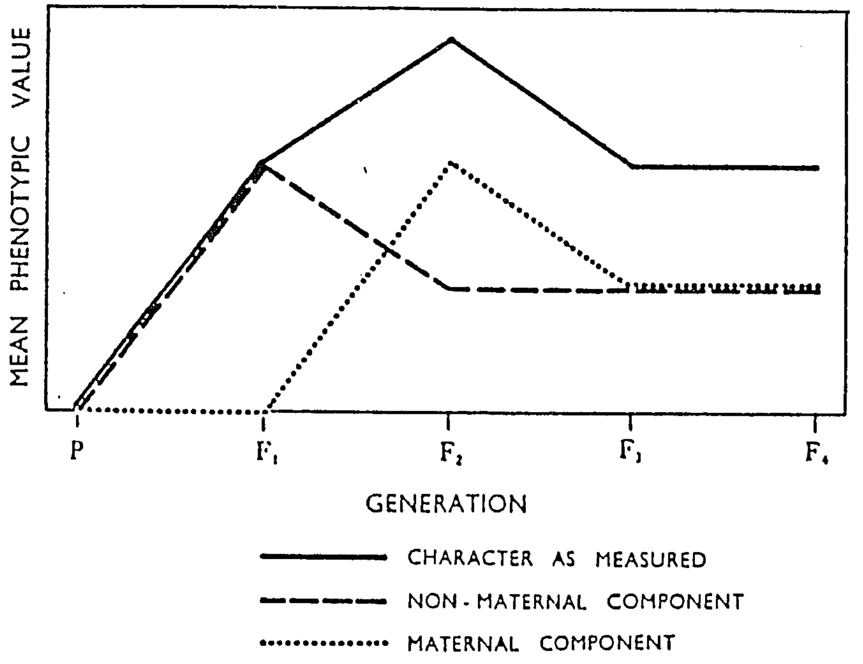
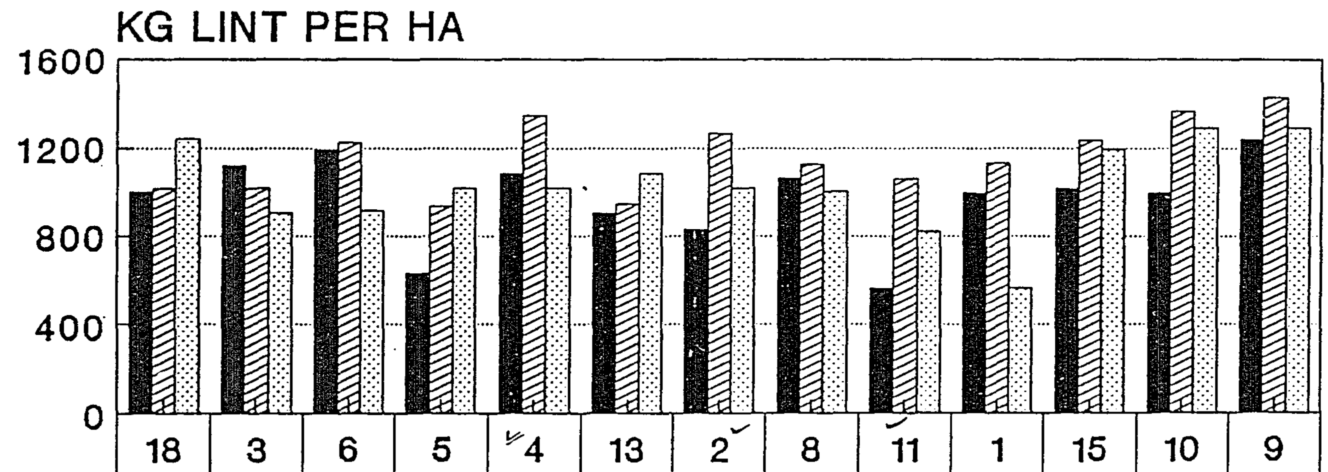


Diagram of the heterosis expected in a character subject to maternal effect, when two lines are crossed and the F_2 is made by random mating among the F_1. The maternal and non-maternal components of the character separately are here supposed to show equal amounts of heterosis, and to combine by simple addition to give the character as it is measured.

SOURCE: Roach and Wulff, 1987.

Figure 5.6 Yield of Non-Selected Parents and F_2



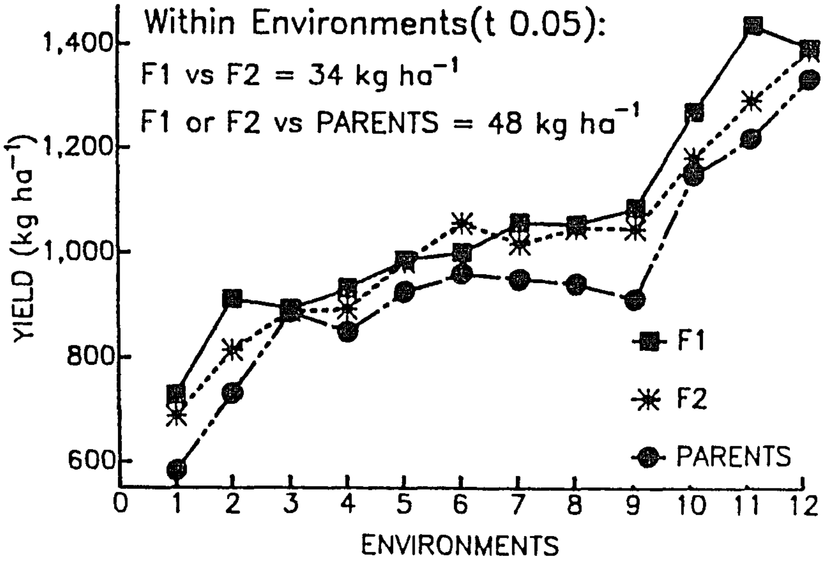
CROSSES	18	3	6	5	4	13	2	8	11	1	15	10	9
P 1	1000	1123	1195	636	1083	902	828	1064	570	998	1017	998	1241
F 2	1019	1018	1223	933	1343	944	1267	1125	1058	1131	1236	1366	1430
P 2	1241	902	912	1017	1016	1083	1016	1000	820	570	1195	1293	1293

CROSSES

P 1 F 2 P 2

SOURCE: Jenkins, 1991.

Figure 5.7 Average Yield in Each of 12 Environments for the Cotton Parents and 21 F_1 and 21 F_2 Hybrids in a Seven-Parent Half-Diallel Crossing Design



SOURCE: Meredith, 1990.

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