DIALLEL ANALYSIS OF WITHIN-BOLL SEED YIELD COMPONENTS AND FIBER PROPERTIES IN UPLAND COTTON (*Gossypium hirsutum* L.) AND BREEDING POTENTIAL FOR HEAT TOLERANCE

A Dissertation

by

PAUL IRWIN RAGSDALE

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

August 2003

Major Subject: Genetics

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Approved as to style and content by:

C. Wayne Smith (Chair of Committee)	Javier Betrán (Member)
J. Tom Cothren (Member)	James L. Starr (Member)
Mark A. Hussey (Head of Department)	Geoffrey M. Kapler (Chair of Genetics Faculty)

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ABSTRACT

Diallel Analysis of Within-Boll Seed Yield Components and
Fiber Properties in Upland Cotton (*Gossypium hirsutum* L.) and
Breeding Potential for Heat Tolerance. (August 2003)
Paul Irwin Ragsdale, B.S.; B.S., Louisiana State University
Chair of Advisory Committee: Dr. C. Wayne Smith

A diallel analysis of eight upland cotton (*Gossypium hirsutum* L.) genotypes was conducted in the field over two years to determine the potential for improvement in within-boll seed yield components and fiber quality parameters. Four exotic germplasm lines from the converted race stock (CRS) collection and four commercial types representing Texas, mid-South, and Eastern production regions were crossed and evaluated in a diallel with parents but without reciprocals according to Griffing's Model I, Method 2. Significant variation for genotypic, general combining ability (GCA) effects, and specific combining ability (SCA) effects ($P \leq 0.05$) were identified for all traits studied indicating potential for improvements through selection. Significant interactions of these parameters with years were also observed, suggesting that selection should be based on multiple years and/or locations. In addition to effects on yield, individual seed number traits were found to respond to heat stress under controlled growth chamber conditions, suggesting their potential for use in screening genotypes for heat tolerance. These traits were not found to interact with temperature, which indicates that selection for improvements in these traits could be conducted in any environment.

Improvements in seed yield components and, putatively, in heat tolerance could be achieved using CRS M-9044-0162. As expected, CRS accessions reduced fiber quality parameters in addition to other agronomic traits, suggesting that improvements for within-boll seed yield components and heat tolerance should be made utilizing a backcross approach. Also observed in this population was a superior hybrid for fiber length and fiber strength from the cross of TAM 94L-25 with PD 6186. This combination could lead to improved fiber length and strength potential in upland cotton.

DEDICATION

This dissertation is dedicated to my Aggie grandfather, Wayne Gilbert Irwin (Dairy Science, ‘43) who inspired me to go to A&M. It is dedicated also to his daughter, my mother, Sandy Irwin Ragsdale--a fellow academic, a fifth-generation Texan, and an Aggie in spirit who home-schooled me when it became necessary, who shepherded me through early college admissions and my subsequent academic path, and who helped make a goal become a reality--a degree from Texas A&M.

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Advice--from design and implementation to analysis and interpretation--was provided by the members of my doctoral committee, Dr. Javier Betrán, Dr. J. Tom Cothren, and Dr. James L. Starr. These committee members unfailingly made time to advise me regardless of their busy schedules and were always warm and supportive.

Finally, support for every aspect of my graduate education has been provided by the chair of my committee, Dr. C. Wayne Smith. He has been an uncommonly helpful advisor, supporting my own initiative while providing the expertise and resources to ensure successful project completion. He can truly be considered a personal and professional example.

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CHAPTER I

INTRODUCTION

Background

Modern genetics can be traced to the rediscovery of Gregor Mendel's research in the early 1900s. Mendel recognized that organisms have two copies of each gene (alleles) and that one allele is contributed by each parent to offspring. This phenomenon is observed in diploid organisms, those which have two sets of each chromosome in the genome. Mendel also concluded that alleles displayed dominance and recessiveness. However, today we recognize that other types of allelic interaction can exist in which alleles are additive (the heterozygote value is the average of the two homozygotes), incompletely dominant (the heterozygote value lies closer to one of the two homozygotes), or overdominant (the heterozygote value exceeds either of the two homozygotes), as well as dominant.

Linkage is a key genetic phenomenon impacting plant breeding. Linkage violates Mendelian independent assortment due to arrangement of genes on chromosomes. Every gene on a chromosome is inherited together. Many traits are said to be linked because the genes controlling them lie close together on a chromosome and therefore have a higher than random probability of being transmitted together to progeny.

Many other genetic phenomena influence expression of traits. First, multiple

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This dissertation follows the style and format of Crop Science.

alleles for each gene can exist in a population. Each individual may possess only two copies but those copies can differ among individuals (e.g., leaf shape in upland cotton, *G. hirsutum* L.). Second, epistasis is a phenomenon in which the expression of one gene is affected by the genotype of a gene at a separate locus (e.g., expression of AA, Aa, and aa depends on the genotype at locus B). Third, pleiotropy is a phenomenon in which a single gene can affect multiple traits. Fourth, heterosis is a phenomenon in which progeny between unrelated parents perform better than would be expected based on the average performance of the parents; this is the phenomenon which has led to hybrid seed production for yield improvement in maize (*Zea mays* L.) and grain sorghum (*Sorghum bicolor* [L.] Moench) and can be a result of combinations of the previous genetic phenomena. Finally, environment is a crucial modifier of gene expression.

Quantitative Genetics

Qualitatively inherited characters are those traits which have discrete categories in populations, such as flower color. Quantitatively inherited characters are those traits which vary continuously in a population. Quantitative traits are often controlled by many genes and can be modified extensively by the environment. Quantitative genetics is of great interest to plant breeders because many target traits, including yield and quality, are controlled by multiple genes.

The genetics of quantitative traits are controlled in the same fashion as qualitative traits (i.e., single gene or Mendelian traits). The genetics are simply an extension of Mendelian genetics to multiple genes (loci). However, the phenotype of each trait is also influenced by the environment: $P = G + E + G \times E$ where P represents

the phenotype of a trait, G represents genotype, E represents environment, and G×E represents the interaction of genotype with environment. These influences can obscure the underlying genetic factors which leads to a crucial component in researching quantitative genetics and breeding plants, i.e., control of the environment.

Plant Breeding

Crop improvement requires the ability to select higher-performing individuals from a population. Three key phenomena pose difficulties when selecting for improvements in quantitative traits. First, identification of superior individuals requires variation in the population. This is usually overcome by crossing unrelated strains to create variation followed by phenotypic screening as described in many plant breeding texts such as Allard (1960), Fehr (1993), Poehlman and Sleper (1995), and Stoskopf et al. (1993). However, many crops have a fairly narrow genetic base relative to their undomesticated progenitors. In cotton, progenitors of many modern cultivars were related, which further narrows the gene pool (Van Esbroeck et al., 1999). Breeders commonly have used the same parents to develop new cultivars which also narrows the gene pool (Van Esbroeck et al., 1998). This narrowed genetic base in cotton germplasm results in a limited supply of alleles for traits of interest that can only be expanded by introducing novel alleles (introgressing) from other populations. Bowman et al. (2003) note that the shift in production to transgenic cultivars has exacerbated the narrowing of the genetic base of modern cottons, threatening to reduce potential for genetic gain in lint yield. These authors point out that all transgenic cultivars were the products of

backcross introgression into genetically related cultivars and also that many transgenic cultivars have the cultivar Coker 312 as the donor parent.

Second, traits controlled by numerous genes can be difficult to improve because the probability of finding an individual with beneficial alleles at all of the genetic loci influencing the trait is often very low. A common approach to overcome this phenomenon is to select parents based on the likelihood of improving traits of interest and then hybridize to produce large populations of progeny. Traits of interest can be evaluated in these populations and used to select individuals and/or families to advance in traditional plant breeding schemes.

The environment is the third component affecting trait performance. Attempts are made to minimize or to maximize environmental effects by choice of location or sampling unit where possible. A good genotype evaluated under poor growth conditions could be overlooked. In all cases, replication of experimental units is employed to allow identification of experimental error. Additionally, many quantitative traits display interactions between genetic and environmental effects known as genotype by environment interaction (G×E). This phenomenon can pose difficulties in selecting superior genotypes that are adapted to wide geographic areas, a goal of most cultivar/hybrid development programs.

Cotton Genetics

Domestic cottons such as upland and pima cotton (*Gossypium barbadense* L.) are tetraploid (4x), i.e., they harbor two complete sets of chromosomes arising from the hybridization of two diploid (2x) species (Brubaker et al., 1999). The progenitor

genomes differed enough in the resulting allotetraploid (2n = 4x) to facilitate appropriate pairing of each set of chromosomes at meiosis as in a normal diploid species. Endrizzi et al. (1984) and Percy and Kohel (1999) reviewed qualitative genetics in cotton, and it is clear that many genes are inherited in a functionally diploid manner. According to Kearsey and Pooni (1996), quantitative genetics in such organisms can be analyzed as diploids using standard methods.

Cotton Germplasm

Expanding the genetic base of crops requires utilization of unrelated sources of genetic material (germplasm). Such an approach tends to have negative consequences in terms of agronomic performance. Undomesticated relatives of the same species tend to have traits that are undesirable for crop production such as shattering of seed, late maturity, photoperiodism, and tallness. When different but related species are used, there is often meiotic pairing or other incompatibility issues leading to fertilization failure or infertile progeny. Thus, the first step for increasing genetic variation in a crop is often to use germplasm resources within the same species.

In upland cotton, land race cultivars have been collected by the USDA and others as part of the National Germplasm Collection. These race stock accessions are photoperiodic, requiring a particular light and dark regime to flower. Seventy-nine of the accessions have been converted to a day-neutral flowering type to facilitate their use in cotton breeding (McCarty and Jenkins, 1993). Day-neutrality was introgressed into race stock accessions by backcrossing. The day-neutral cotton cultivar Deltapine 16 was used as a donor parent in a backcross breeding scheme with individual race stock

accessions serving as recurrent parents. The resulting BC_4F_4 converted race stocks (CRS) represent a useful source of exotic genetic variation, capturing much of the variation present in the race stock accessions in a form readily accessible to cotton breeders.

While CRS are useful sources of genetic variation, they do have limitations in cotton breeding and genetics. First, genetic linkage leads to incorporation of rather large tracts of chromosomes in the regions harboring desired traits (e.g., day neutrality) from the donor parent. In terms of germplasm, this linkage drag may reduce the amount of novel genetic variation from the race stock source in the converted descendants. Moreover, there can be inadvertent selection for donor parent content in other regions of the genome leading to additional reductions in novel genetic variation (Liu et al., 2000). Variation in donor parent genome contamination within and among CRS accessions (Liu et al., 2000) can cause individuals to be chosen that have considerable commercial genome contamination, negating the benefits of a germplasm introgression approach. Second, CRS tend to be heterozygous and heterogeneous (Liu et al., 2000) which can impair phenotypic evaluation and violate genetic model assumptions (Griffing, 1956).

Tools for Crop Improvement

Parental selection for crop improvement requires knowledge of the likelihood of improving traits of interest. This likelihood is based on the amount and type of genetic control of the trait as described by $P = G + E + G \times E$. The amount of genetic control is influential because improvement of a trait with very small genetic control relative to environmental influences will be difficult. An expression of this phenomenon is

heritability in the broad sense (h^2_{BS}), the ratio of genetic to phenotypic variation: $h^2_{BS} = V_G/V_P$. Traits with high heritability experience greater improvement in the trait resulting from selection than those with low heritability. The type of genetic control influences improvement because only certain types of genetic control can be reliably transmitted to progeny. In the formula for phenotypic expression ($P = G + E + G\times E$), the genotype term (G) can be expanded into additive (A), dominance (D), and interaction (epistasis, I) effects ($G = A + D + I$). The best alleles for additive, dominant, and epistatic loci can be captured in inbred lines, but this is not possible for overdominant loci which requires heterozygosity per se for maximal trait performance.

Tools exist to overcome difficulties in evaluating quantitative traits in plants (Bernardo, 2002; Falconer and Mackay, 1996; Mather and Jinks, 1971) and animals (Falconer and Mackay, 1996). Evaluation in many crop plants is more straightforward than in animals because plants can be inbred, replicated, and mated by design; several genetic mating designs exist to facilitate dissection of environmental and genetic control underlying quantitative traits in plants.

Diallel Analysis

Among the most common mating designs in crop improvement is the diallel analysis. This involves mating a set of parents in all possible combinations to produce a set of F_1 progeny. The analysis can be conducted with or without reciprocal crosses (using each line as both a male and a female parent) and with or without parental lines. Griffing (1956) described these basic methods of diallel analysis: Method 1 involving parents and all F_1 combinations including reciprocals, Method 2 involving parents and

all F_1 combinations without reciprocals, Method 3 comprising all F_1 combinations including reciprocals but without parents, and Method 4 involving only F_1 combinations without reciprocals or parents. Each method provides estimates of different genetic parameters as described by Griffing (1956). Method 2 (parents and F_1s without reciprocals) is used commonly in inbred crops because crossing is labor intensive and reciprocal effects tend to be less prevalent.

A diallel analysis can provide useful information regarding the genetic control of a quantitative trait, but two key assumptions must be made for interpretations to be valid (Baker, 1978). First, alleles for trait performance must be distributed randomly among the parents. Second, epistasis must not affect the trait. Failure of independent distribution of alleles among the parents and/or the presence of epistasis can bias genetic parameter estimates. Considering only independent distribution of alleles and epistasis, Baker (1978) advises researchers not to attempt to estimate additive and dominance genetic variance from any diallel. This suggestion also obviates determining heritability from diallel variance components.

The nature of the population under study affects diallel analysis and interpretation. According to Griffing (1956), two forms of analysis can be conducted: fixed or random effects. Fixed effects are required when the population is small (i.e., fewer than 10 parental lines) and/or the parental lines were selected prior to diallel mating. Such a model is limiting in two ways. First, the parameters that can be estimated with a fixed effects model are reduced; variance due to genetic sources (genetic variation, V_G) cannot be estimated, and no conclusions regarding genetic

control of the trait can be drawn. Second, the scope of estimates is reduced to the genotypes in the study, the parental lines and their F_1 progeny. No inferences can be made regarding the population as a whole.

Notwithstanding these limitations on genetic inferences, a fixed model diallel approach has utility in plant breeding because the combining ability of parents in the study can be evaluated. General combining ability (GCA) effects are the average performance of a parent in combination with all other parents, whereas specific combining ability (SCA) effects are the deviation of the performance of two parents in a particular hybrid combination from that expected from the GCA effects of each parent. While Griffing proposed that small numbers of parental lines negated the estimation of genetic variance, calculation of GCA and SCA effects should provide estimates of the additive and dominance genetic effects, respectively, or at least the practical breeding value, of a given parent within the set of parents studied.

Significant GCA and SCA effects provide information to help determine the efficacy of breeding for improvements in given traits and they can be used to identify lines to serve as parents in a breeding program for trait improvement (Kearsey and Pooni, 1996). The GCA effects reflect performance of parental lines in combination with all other lines, so the parents with the highest GCA effects should have the greatest impact on trait improvement. Specific combining ability effects identify the best hybrid combinations, but they also identify complementary alleles for trait performance (Kearsey and Pooni, 1996). Novel combinations of beneficial alleles at multiple loci could lead to new potential for inbred improvement. In maize and possibly other hybrid

crops, heterosis seems to be largely attributable to dominance or apparent overdominance (Stuber et al., 1992). However, in rice, which is inbred, there is evidence to suggest that the nature of heterosis does not depend on overdominance (Xiao et al., 1995; Yu et al., 1997). This suggests that hybrid performance could be captured in elite inbreds. Xiao et al. (1995) demonstrated this empirically; advanced inbreds (F_8 generation) were found that exceeded F_1 hybrid performance for 12 traits including yield. Singh et al. (1983) demonstrated that a large part of heterosis in cotton is of a type which could be captured in elite inbreds (e.g., additive by additive epistasis). Therefore, hybrid performance as indicated by SCA effects might be a useful parameter in parent selection for trait improvement in cotton.

Baker (1978) addresses the relative merits of five methods of analyzing diallel data but notes that there is no inherent advantage or disadvantage to any of the methods. Griffing (1956) published formulae to determine mean squares to test GCA and SCA significance and to estimate GCA and SCA effects for each parent and parental combination. His formulae include calculations for both fixed effects (Model I) and random effects (Model II) and can be conducted with a calculator or spreadsheet program. In each case, the validity of testing GCA and SCA significance depends upon demonstrating significant differences among the genotypes (Griffing, 1956).

Software programs to analyze data according to Griffing's formulae also exist (Christie et al., 1988; Burow and Coors, 1994). However, these programs are limited to only a single year of data necessitating additional calculations to facilitate complete analysis of multiyear data. Zhang and Kang (1997) published a direct method of

analyzing diallel data from multiple years using SAS, presenting the basic SAS code along with instructions for modifying code to accommodate each of Griffing's methods. Output includes tests for significance of genotypic, GCA, and SCA effects, of their interactions with the environment (years or locations), estimates of GCA and SCA effects for each line and hybrid combination, and their significance.

Traits of Interest

Within-Boll Yield Components

Yield components are often interrelated so that improvements in some traits are accompanied by decreases in others. Therefore, the effect of changing individual components of yield on total yield and on other yield components is unpredictable. The inheritance of and interrelationships among yield components is of interest to cotton breeders (Coyle and Smith, 1997; Smith and Coyle, 1997), and the contribution to yield of various yield components is reviewed by Worley et al. (1976) and Heitholt (1999). Key factors include the number of bolls per plant and lint percentage. Simultaneous improvement in multiple yield components provides an opportunity to increase yield using straightforward selection parameters (Coyle and Smith, 1997).

Within bolls, yield can be dissected further. Cotton fibers are produced on the surface of seeds, so an increase in the number of seed should lead to an increase in fiber production. The number of seed produced in each boll, the amount of surface area on each seed, and the number of fibers produced per square centimeter of seed surface area all contribute to fiber production and therefore lint yield. Combining ability for within-boll yield components was evaluated by Coyle and Smith (1997), indicating that

genotypes with positive GCA effects for fiber quality had negative GCA effects for basic within-boll yield components such as seed number per boll (S/B). No study has yet determined the potential of exotic germplasm sources to improve within-boll seed yield components in elite cotton types.

Heat Tolerance

In addition to contributions to yield, seed number traits tend to be susceptible to environmental stresses (Stewart, 1986) so they might have potential as tools to screen genotypes in response to stress. Hall (2001) notes that improved efficiency in crop production will be necessary in the coming decades because of increases in population coupled with potential decreases in arable land and water availability. One strategy to improve production efficiency is to limit losses due to abiotic stresses such as drought and high temperatures. Heat tolerance is a desired trait in Texas crops, and heat stress may become a greater risk for crop production as some authorities predict temperatures to rise worldwide over the next several decades (Levitus et al., 2001; Zwier, 2002).

Heat tolerance has been studied in many species (Abrol and Ingram, 1996; Hall, 1992; Hall and Ziska, 2000; Klueva et al., 2001; Stone, 2001) including *Arabidopsis thaliana* (L.) Heynh. (Hong and Vierling, 2000; Murakami et al, 2000), cowpea [*Vigna unguiculata* L. (Walp.)] (Ismail and Hall, 1998; Ismail and Hall, 1999), maize (Klueva et al., 2001; Wilhelm et al., 1999), peanut [*Arachis hypogaea* L.] (Vara Prasad et al., 1999), soybean (addressed in Klueva et al., 2001), tobacco [*Nicotiana tabacum* L.] (Crafts-Brandner and Salvucci, 2000; Murakami et al., 2000; Salvucci et al., 2001), wheat [*Triticum aestivum* L.] (Burke et al., 1988; Law and Crafts-Brandner, 1999), and cotton

(Burke et al., 1985; Burke et al., 1988; Burke et al., 1990; Burke and O'Mahony, 2001; Crafts-Brandner and Salvucci, 2000; Hall, 1992; Law and Crafts-Brandner, 1999; McArthur, 1975; Radin, 1992; Radin et al., 1994; Reddy et al., 1991a; Reddy et al., 1991b; Reddy et al., 1992; Reddy et al., 2000; Rikin et al., 1993; Rodriguez-Garay and Barrow, 1988; Stewart, 1986; Yfoulis and Fasoulas, 1978)

Numerous physiological and biochemical components are sensitive to heat stress in crop plants. Biochemically sensitive components include enzyme activity in cotton, maize, tobacco, and wheat (Crafts-Brandner and Salvucci, 2000; Law and Crafts-Brandner, 1999; Wilhelm et al., 1999), enzyme kinetics in cotton and wheat (Burke et al., 1988; Burke et al., 1990), enzyme stability (Salvucci et al., 2001), and photosynthesis (Reddy et al. 1991a). Physiological components that are sensitive to high temperature stress include membrane properties in *Arabidopsis* and tobacco (Murakami et al., 2000), cowpea (Ismail and Hall, 1999), and cotton (Rikin et al., 1993), boll maturation period (Yfoulis and Fasoulas 1978), and reproductive components in peanut (Vara Prasad et al., 1999), cowpea (Ismail and Hall, 1999), and cotton (Reddy et al., 1991a; Reddy et al., 1991b; Reddy et al., 1992).

Biochemical approaches to improve heat tolerance include heat shock protein research (after Burke and O'Mahony, 2001) and incorporation of heat tolerant forms of enzymes (after Spreitzer and Salvucci, 2002) in crop plants. Physiological approaches to improve heat tolerance in plants include carbohydrate partitioning in cowpea (Ismail and Hall, 1998), membrane fatty acid composition in tobacco (Murakami et al., 2000),

stomatal conductance in pima cottons (Radin et al., 1994), and pollen viability in upland cotton (Rodriguez-Garay and Barrow, 1988).

Hall (2001) notes that under high temperature conditions, different limitations to yield occur in different species such as reproductive development in cotton versus photosynthesis in wheat. Upland cotton experiences decreases in reproductive growth at temperatures above 30^0C (Reddy et al. 1991a; Reddy et al., 1991b; Reddy et al., 1992). Damagingly high temperatures occur frequently in Texas and much of the Cotton Belt. The author knows of no specific breeding efforts for heat tolerance in upland cotton nor of any efforts to evaluate its quantitative genetics. Through impacts on pollen viability (Rodriguez-Garay and Barrow, 1988) and other reproductive components (Stewart, 1986) seed number traits are directly affected by reproductive heat stress. Therefore, evaluation of the sensitivity of individual within-boll seed yield components to high temperature stress might lead to development of screening tools for improvement of heat tolerance in cotton.

Heat tolerance is a relatively difficult trait to assess. There are no specific symptoms of heat stress, and heat stress usually occurs in conjunction with other environmental stresses such as drought and high light intensity in field situations. Therefore, appropriate phenotypic characterization of plant responses to heat stress is crucial to studies of heat tolerance. Field evaluation of cotton under high temperatures (35-45^0C) but with irrigation is a practical approach to evaluate heat responses. However, it is necessary also to confirm field data by performing experiments under controlled conditions (Hall, 2001). Growth chambers can be used to compare responses

under heat stress and non-stress while other conditions are held constant. Furthermore, they can reproduce climatic conditions which are necessary to test hypotheses but are impossible to achieve in the field.

Although growth chambers provide control over environmental variation, they are not necessarily representative of performance under field conditions (Hall, 2001). For example, soil volume in containers is typically small, affecting nutrient and moisture holding capacity, as well as buffering of the root zone from fluctuations in air temperature. Light intensity and quality also can differ from natural sunlight. Such limitations should be considered when interpreting data from controlled environment studies.

Timing of heat stress might affect the ability to screen for heat tolerance. It is clear that pollen can be sterilized in cotton (Rodriguez-Garay and Barrow, 1988), but Stewart (1986) notes that reproductive heat and drought sensitivity in cotton can also occur prior to flowering. Ehlig and LeMert (1973) reported a decrease in the number of flowers per meter of row three weeks after exposure to temperature stress of 42^0C. Second, plants have two distinct mechanisms for heat tolerance: inherent and acquired heat tolerance (Klueva et al., 2001). Inherent heat tolerance involves pre-existing characteristics that promote heat tolerance whereas acquired thermotolerance is a physiological response of plants to heat exposure. Klueva et al. (2001) note that variation within species for acquired heat tolerance exceeds that of inherent heat tolerance and suggest that acquired heat tolerance will be more useful for crop improvement. In screening for acquired heat tolerance, it seems that a gradual

imposition of heat stress over a period of days would suffice to trigger acquired heat tolerance responses.

Research to identify genetic variation for physiological traits in plants that are correlated with heat stress is being conducted, and at least one program is pursuing such traits in cotton (Burke, 2001). However, it also would be useful to identify a trait that correlates with heat tolerance which is inexpensive, simple, and quick to evaluate. Such a trait could be used to screen genotypes in the field. Ultimately, yield and quality under heat stress should be the criterion for selection but environmental variation limits this approach in field evaluation. A trait that can be used to screen genotypes in the absence of heat stress would be desired.

Objectives

The research in this dissertation had two primary objectives: 1) To determine the potential of within-boll seed yield components in screening for heat tolerance across three upland cotton genotypes; and 2) to determine the potential to improve within-boll seed yield components and fiber properties by a diallel analysis of eight upland cotton genotypes.

CHAPTER II

MATERIALS AND METHODS

Growth Chamber Phenotypic Evaluation of Heat Stress and Seed Number Traits

Heat Stress Screening Regime

A heat stress screening regime was developed for upland cotton based on hourly temperature and humidity fluctuations observed near College Station, Texas during the summer of 1998. Nine days exceeding 38^0C were selected, and the temperatures and relative humidity (RH) values for each hour over the nine days were averaged to devise growth chamber set points. (See Figure 1.) The conditions for a non-stress screening regime were as follows: 30^0C and 60% RH day, 20^0C and 80% RH night, 12 hour daylength. Environmental Growth Chambers (Chagrin Falls, OH) were employed to impose the regimes. Temperatures were verified independently with laboratory thermometers in shade in each chamber. Thermometer-determined temperatures tended to lie within one to two degrees celsius of set points.

Heat stress was imposed gradually to allow plants to acclimate by increasing temperatures over several days in the heat stress chamber following the emergence of the first true leaf and to simulate natural increases in temperature over a season. (See Figure 1.) Given the apparent lag in appearance of reproductive heat stress symptoms following the onset of high temperatures (addressed in Chapter I), flowers were removed until 21 days had passed following the final temperature change. Plants remained in the chambers for at least 20 days after pollination to allow all bolls to reach full size and were subsequently removed to a greenhouse until all bolls opened naturally.

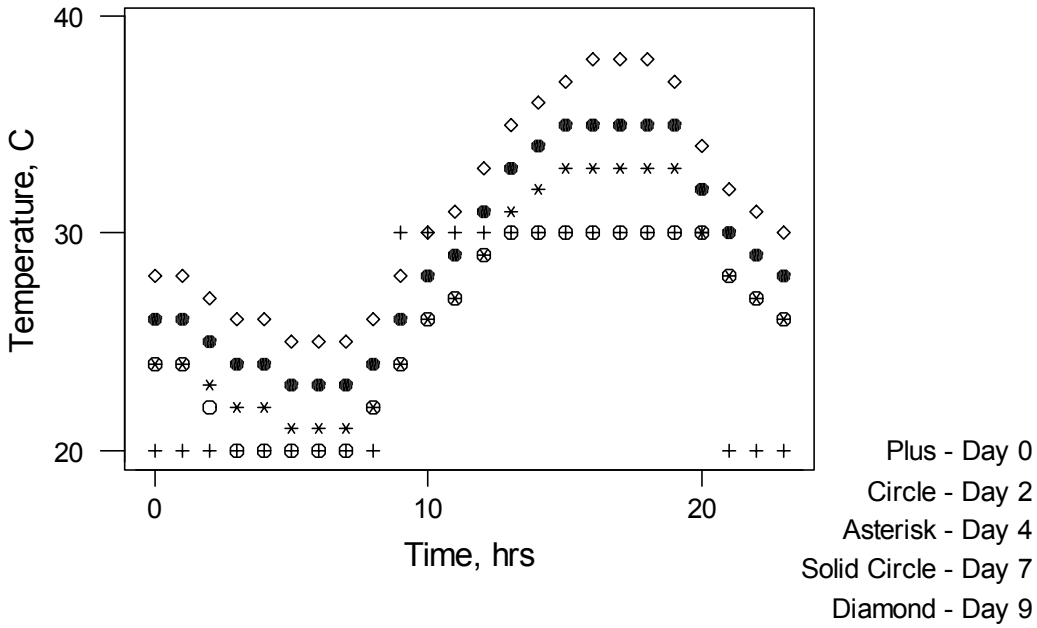

Fig. 1. Hourly temperatures for gradual imposition of heat stress by day of temperature change. Time 0 represents 12:00 am, Day 9 corresponds to final temperature regime.

Genotypes

Three genotypes were evaluated in this experiment, two CRS accessions and one elite breeding line, selected based on field and preliminary growth chamber observations of one within-boll seed yield component, seed setting efficiency, which is the proportion of ovules in a boll that develop into mature seed (data not shown). M-8844-0096 represents a high-SSE CRS accession, M-9044-0244 represents a low-SSE CRS accession, and TAM 94L-25 represents a commercial type with extremely low SSE. Seed for the experiment were produced by open-pollinating selected plants in a preliminary growth chamber evaluation. Cotton is primarily self-pollinated in the

absence of insect vectors (Oosterhuis and Jernstedt, 1999), so open-pollinated bolls can be considered self-pollinated under growth chamber conditions. CRS seed originated from aliquots of seed provided by the USDA-ARS U.S. Gossypium Collection (College Station, TX) in 1998. TAM 94L-25 seed originated from a TAMU Cotton Improvement Laboratory seed increase in Weslaco in 1998.

Experimental Design

Two plants each of the three genotypes (TAM 94L-25, CRS M-8844-0096, and CRS M-9044-0244) were grown in each of two temperature regimes (heat-stressed and non-stressed). The experiment was replicated twice by conducting successive trials from seeding to maturity. The five highest SSE bolls from each plant were selected for statistical tests.

Cultivation

Individual plants were cultivated in 19-liter pots. Growth medium for the experiment was Metromix 200 (Scotts, Marysville, OH). Two seed per pot were sown directly into moist soil and allowed to germinate under the following conditions: 30^0C day, 20^0C night at 60% RH with a 12-hour day length. Pots were thinned to one plant each after the emergence of the first true leaf. Plants were watered daily to field capacity, and water-holding pot bottoms were utilized in the heat stress chamber to ensure adequate moisture during the highest daily high temperatures.

Plants were randomized within each chamber and were rotated daily to minimize effects of local variation in light intensity, humidity, and temperature. Any open flowers that were sprayed by fertilizer, insecticide, or humidifiers were removed since moisture

sprayed into the chamber can wet open flowers, impairing pollen viability and reducing SSE (after Burke et al., 2001).

Peters Professional Season Long time-release fertilizer (15-13-13; Scotts, Marysville, OH) was added to the pots after emergence of the first true leaf at a rate of approximately 208 kg ha^{-1} for nitrogen and phosphorus and 180 kg ha^{-1} for potassium. Plants were also fertilized with 100 ppm of aqueous Peters Professional Peat Lite Special to runoff (20-10-20; Scotts, Marysville, OH) at six-day intervals during flowering. This corresponds to a rate of approximately 189 kg ha^{-1} for nitrogen and potassium and 95 kg ha^{-1} for phosphorus. During flowering, plants developing interveinal chlorosis on new growth, consistent with sulfur deficiency, were treated with 11.4 kg ha^{-1} of ammonium sulfate applied with the 20-10-20 aqueous fertilizer. When any leaves yellowed, plants were misted with aqueous ammonium sulfate at a rate of 5.7 kg ha^{-1} to ensure rapid recovery. Plants were treated for insect pressure as needed according to standard growth chamber treatment practices. Thrips pressure was heavy during seedling growth in the second replication.

Seed Number Trait Determination

Seeds per boll (S/B), motes per boll (M/B), total ovules per boll (O/B), and seed setting efficiency (SSE) were determined for each boll on every plant. A seed was defined as a full size seed which resisted crushing. Motes are failed reproductive structures that do not contribute to lint yield (Rea, 1929a; Rea, 1929b). Motes range from small unfertilized ovules (approximately one mm in diameter) to nearly full-sized seed. The total number of ovules is determined by summing seed and motes. Seed

setting efficiency is determined by dividing the number of seed in the boll by the number of ovules in the boll. The five bolls for each plant with the highest SSE values were selected for statistical analyses. Such bolls correspond to phenotypically normal, full-sized bolls. It should be noted that seed which can be crushed easily (pops) were also counted as motes, but it is unclear if they produce spinnable fibers and contribute to lint yield. Full-sized motes were rare in this population (personal observation), so it seems that any biases attributable to inclusion of pops in this study should be minimal.

Statistical Tests

Genotypic, environmental, and interaction effects were tested with PROC GLM in SAS (SAS, 2000) using the following model: $Trait_{ijkl} = G_i + T_j + R_k(Tj) + G\times T_{ij} + G\times R(T)_{ijk} + e_{ijkl}$ where G represents the effect of genotype i, T represents the effect of temperature j, R represents the effect of replication k within temperature j, G×T represents the effect of the genotype by temperature interaction for genotype i in temperature j, $G\times R(T)_{ijk}$ represents the effect of the similar genotype by replication within temperature interaction, and e_{ijkl} represents variation associated with the lth observation (i.e., individual plants) of genotype i in the kth replication within temperature j. In this crossed-nested model (Neter et al., 1996), temperature tests over R(T), genotype and the G×T interaction test over G×R(T), and R(T) and the G×R(T) interaction test over the residual error term. The R(T) and G×R(T) terms are of limited interest, serving primarily as methods of controlling error variation.

Diallel Analysis of Seed Number Traits and Fiber Properties Under Field Conditions

Genotypes

Converted Race Stock accessions were selected for the diallel study to represent extremes of SSE based on preliminary results obtained from field studies conducted near College Station in 1998 (Nasirci and Smith, 1999). Accessions M-8844-0096 and M-9044-0162 have putatively high SSE, M-9044-0237 and M-9044-0244 have putatively low SSE (Nasirci and Smith, unpublished data, 1999).

Two cultivars and two public germplasm lines were included in the diallel study to represent diverse production areas of Texas, the mid-south, and the east coast. TAM 94L-25 is a recent germplasm release of the Texas Agricultural Experiment Station (Smith, 2003). This strain has apparent drought tolerance, competitive yield and excellent fiber properties, large seed with relatively few seed per boll, and low SSE. Tamcot CAMD-E is a near obsolete ultra short season Texas type cultivar released in 1979 by the Texas Agricultural Experiment Station (Bird, 1979). It has short fibers, poor fiber strength, low micronaire, and unknown SSE (Coyle and Smith, 1997; unpublished data). Deltapine Acala 90 is a mid-South type cultivar released in 1981 by the Delta and Pine Land Company. It has small seed, and unknown SSE (Coyle and Smith, 1997; unpublished data). PD 6186 is a germplasm line made available in 1984 by the USDA-ARS in South Carolina (unreleased breeding line). It has excellent fiber quality, large seed, and unknown SSE (unpublished data). Seed for the experiment were taken from Texas A&M breeding stocks.

Mating Design

The eight genotypes were mated in a diallel crossing scheme (Griffing ,1956). Method 2, which includes parents and F_1 progeny without reciprocals, was employed. The genotypes in the experiment were considered to be non-random for two reasons: 1) They represent a small sample (fewer than 10 lines); and 2) they were selected based on preliminary data. A non-random population requires diallel analysis to be conducted by Griffing's Model I (Griffing, 1956) and precludes estimating genetic variance components and heritability (Chapter I).

The diallel population for the first year of evaluation (2000) was produced by hand crossing in the summer of 1999 and for the second year of evaluation (2001) by hand crossing in the summer of 2000. Additional parental seed were produced by self-pollination. Not enough seed for all combinations could be produced in the summer, so individual plants were removed from the field and taken to a greenhouse in the winter to produce additional seed. Seed produced in the off-season were treated with hot water to break dormancy (Smith, personal communication, 2001). Seed were immersed in water at 71^0C for 60 s then cooled with tap water (approximately 20^0C) for about five minutes.

As addressed in Chapter I, CRS have two serious limitations in genetic studies. To overcome donor parent contamination, individuals were selected within each CRS accession to serve as parents. Selection was conducted before flowering and was based on the presence of more primitive traits including plant height, multiple branches per node, and stem and leaf pubescence. Such individuals should harbor relatively more of the exotic parent genome than individuals with a more commercial phenotype. To

overcome heterogeneity within accessions, plant-to-plant crosses were conducted to facilitate post-harvest selection based on expected SSE. Individual plant-to-plant combinations for which one or the other parent had aberrant SSE were discarded (data not shown). Reciprocal effects were ignored in this experiment because all CRS lines contain the same commercial cytoplasm type (McCarty and Jenkins, 1993). Among CRS parents, both sets of reciprocal F_1 crosses were conducted to generate enough seed for field evaluation when reciprocals were pooled. Among the four commercial types, crosses were made in either direction as was practical.

Experimental Design

Genotypes were grown in single plant culture, 0.3 by 2.0 m, to minimize inter- and intra-plot competition. The eight parental genotypes and their 28 F_1 progeny were evaluated in four replications of five plants per replication. Standard agronomic and pest control practices were employed throughout the growing season and plots were irrigated to prevent confounding drought effects. Field experiments were conducted at the Texas Agricultural Experiment Station near College Station Texas. Plots were evaluated in Belk Clay, a fine, mixed, thermic Entic Hapludert in both years. Seed were planted on May 11-12 in 2000 and on May 24 in 2001.

Seed Number Traits and Fiber Properties Determination

At least two phenotypically normal, full-sized bolls were harvested from each plant bearing fruit. Seed number traits (S/B, M/B, O/B, and SSE) were determined on a whole plot basis. Bolls were ginned on laboratory saw gins, fiber weight was determined, and lint was analyzed by High Volume Instrument (HVI) at the Cotton

Incorporated Textile Services Laboratory (Cary, NC). Data for upper half mean fiber length in mm (UHM), fiber bundle strength in grams per tex (Str.), fineness in micronaire units (Mic.), percent fiber uniformity index (UI) defined as the ratio of the average length of all fibers to the average length of the longest 50% of fibers in the sample, elongation before break (Elo.), and percent short fiber content in percent (SFC) were generated.

Test for Genotypic Effects

Estimating genetic parameters from diallel data requires identifying differences among genotypes in the population. Tests for genotypic effects were conducted using DIALLEL-SAS (Zhang and Kang, 1997). (See Appendix for source code.) Genotypes in the diallel population were tested as: $Trait_{ijkl} = Y_i + R_j(Y_i) + G_k + G\times Y_{ik} + e_{ijk}$, where Y represents year i, $R_j(Y_i)$ represents replication j within year i, G represents genotype k, G×Y represents the interaction of genotype k with year i, and e represents residual error variation including the interaction of genotypes with replications within years. In this model (Zhang and Kang, 1997), years tests over R(Y), genotypes test over G×Y, and G×Y tests over the residual error term. Zhang and Kang (1997) employ an orthogonal partitioning of the genotype sum of squares to test GCA and SCA effects. Similar partitioning of the genotype by year interaction sum of squares is used to test GCA by year and SCA by year interactions.

The data were unbalanced due to missing plots. A full data set with two bolls plant, five plants per plot, 36 genotypes, and four replications would comprise 1440 bolls per year. However, only 1220 phenotypically normal, full-sized bolls could be

harvested in 2000 and 1151 in 2001. Data were pooled on a plot basis to overcome most missing observations. To accommodate the remaining unbalanced data, PROC GLM in SAS (SAS, 2000) was employed to analyze the data and to estimate genotypic means.

Comparison of Parental Lines

Parental genotypes were analyzed separately to determine and compare means. Genotypic effects were tested as described for diallel data and means were separated using the least-squares means procedure in SAS with Tukey's control adjustment for multiple comparisons (SAS, 2000). Mean comparisons were conducted using the Type III sum of squares which corrects for all terms in the model. For traits with a significant genotype by year interaction (G×Y), mean comparisons were conducted using G×Y as the error term. For traits without a significant G×Y, a reduced model was employed ($Trait_{ijk} = Y_i + R_j(Y_i) + G_k + e_{ijk}$). This model tests genotypes and conducts mean separations using the residual error term. Simultaneous confidence intervals for all pairwise comparisons among parental genotypes were generated using an experiment-wide error rate of 0.05.

Estimation of Genetic Parameters

Estimates and standard errors for GCA and SCA effects were generated using DIALLEL-SAS (Zhang and Kang, 1997) which accounts for unbalanced data. Representative GCA and SCA effects estimates from DIALLEL-SAS were equivalent to values generated by DIALLEL software (Burow and Coors, 1994) and to manual calculations (data not shown). Tests of significance ($P = 0.05$) were conducted for each estimate using two-sided t-tests (without experiment-wide error control).

CHAPTER III

RESULTS AND DISCUSSION

Growth Chamber Phenotypic Evaluation of Heat Stress

Motes per boll and SSE did not vary ($P = 0.05$) across the three genotypes and two growth chamber environments (Table 1). However, heat stress under growth chamber conditions reduced S/B from 29 to 26 ($P \leq 0.05$), when averaged across genotypes. While the combined ANOVA for S/B indicated no genotype by temperature interaction, an ANOVA of temperature stress for each genotype indicated that S/B was lower under stress conditions for TAM 94L-25 ($P = 0.06$) and M-8844-0096 ($P = 0.13$) but M-9044-0244 was unchanged across the two temperature regimes studied (Table 2). When S/B and M/B were combined to determine O/B, the same trend was observed for two of the genotypes, suggesting that heat stress can impact not only the fertilization process as generally assumed, but the actual number of potential seed, i.e., ovules, within an ovary in some genotypes.

However, neither S/B nor O/B allowed discrimination among genotypes under heat stress, which reflects adversely on the ability of these traits to be used to screen genotypes for heat tolerance. Initially, variation for SSE among CRS accessions observed under extremely hot conditions near College Station, TX in 1998 were thought to reflect differing susceptibilities of CRS accessions to heat stress, potentially providing a source of heat tolerance to incorporate into elite cotton germplasm. The growth chamber experiments served two purposes. First, they remove extraneous environmental variation, allowing a test of the hypothesis that SSE observations in the field are

attributable to differences in heat susceptibility. Second, they allow reproduction of environmental conditions (e.g., extreme heat conditions as observed near College Station in 1998) that cannot be achieved in the field. These two characteristics afforded an opportunity to determine the relative genetic and temperature control of seed number traits under controlled conditions. It seems clear that heat stress reduces seed number per boll. The lack of a significant G×E interaction suggests that improvement could be made for S/B in the stress regime evaluated in this study by selection under the non-stress regime, in which genotypic differences can be detected.

Table 1. Analysis of variance for seed number traits under heat stress and non-stress conditions in growth chambers over two replications.

		Mean Squares			
Sources	**df**	**S/B‡**	**M/B**	**O/B**	**SSE**
Temperature (T)	**1**	**96.8** *	**43.2** *	**10.7** ns	**0.048** *
Reps(T)	**2**	**1.9**	**1.8**	**7.5**	**0.001**
Genotypes	**2**	**69.7** *	**30.7** †	**166.7** ***	**0.014** *
G × T	**2**	**22.6** ns	**0.5** ns	**25.1** *	**0.000** ns
G × Rep(T)	**4**	**8.8**	**5.1**	**2.5**	**0.004** ns
Error	**12**	**9.9**	**4.8**	**10.7**	**0.004** ns
R^2		**0.73**	**0.69**	**0.77**	**0.68**
%CV		**11.28**	**50.03**	**10.18**	**7.02**

‡ **S/B = seeds per boll; M/B = motes per boll; O/B = ovules per boll; SSE = seed setting efficiency.**

†, *, ***: ***P* = 0.10, *P* = 0.05, *P* = 0.01, and *P* = 0.001, respectively.**

Table 2. Mean performance of genotypes for seed and ovule number per boll under heat stress and non-stress conditions in growth chambers over two replications.

Genotype	S/B*		O/B		SSE	
	----- No. -----		----- No. -----		----- ratio -----	
	Non-Stress	Heat Stress	Non-Stress	Heat Stress	Non-Stress	Heat Stress
TAM 94L-25	33.2 a† A‡	26.7 a B	38.3 a A	34.8 a A	0.87 a A	0.77 a A
M-8844-0096	31.8 ab A	26.5 a B	34.2 ab A	31.0 a A	0.93 a A	0.86 a A
M-9044-0244	24.6 bc A	24.4 a A	26.1 bc B	28.8 a A	0.94 a A	0.85 a B

* S/B = seeds per boll; O/B = ovules per boll; SSE = seed setting efficiency.

† Values within columns followed by the same letter are not different at $P \leq 0.05$.

‡ Values within rows followed by the same capital letter are not different for a given trait at $P \leq 0.06$.

Diallel Analysis of Seed Parameters and Fiber Properties Under Field Conditions

Comparison of Parental Lines

Parents differed ($P \leq 0.05$) for every seed parameter (Table 3) and fiber trait measured (Table 4) with the exception of O/B. Except for O/B and elongation, all genotype by year interactions were not significant, allowing years to be combined for comparison of genotypic means (Table 5). These data support, in general, the reasoning for choosing this set of parents for this study. M-9044-0162 exhibited higher S/B and SSE than M-9044-0237 and M-9044-0244 while M-8844-0096 was intermediate. However, when viewed with the growth chamber data in Table 2, M-8844-0096 clearly tends to exhibit higher S/B and SSE than M-9044-0237 and M-9044-0244. There were no differences ($P = 0.05$) in S/B and SSE across the commercial-type checks in 2000 and

2001 which is a little surprising because previous experience would suggest that TAM 94L-25 would have lower S/B and SSE (Nasirci and Smith, 1999; unpublished data).

TAM 94L-25 was included because it produces exceptionally long fibers with high fiber bundle strength. Deltapine 90 and PD 6186 were known to possess exceptional fiber bundle strength and average UHM length, while Tamcot CAMD-E was known to have short and weak fibers. All of the three expected parameters were verified in 2000 and 2001 (Table 5). We were not cognizant of the relationship among the parents for other seed and fiber parameters or they did not enter into the parental decision equation. However, M-9044-0162 had the fewest M/B (Table 5), a necessity for having the highest SSE, and all other parents did not differ for M/B. The CRS tended to have higher micronaire (coarser fibers), lower strength, and higher elongation before break. There appears to be little or no trend in SFC and UI between the commercial-type parents and the CRS.

Diallel Analysis of Variance

Analysis of variance indicated an effect of years, genotypes, and an interaction of genotypes by years for all seed parameters and fiber properties measured on the 36 hybrids produced from eight parents. Significant differences for genotype indicates that it is valid to test for GCA and SCA effects for each trait according to Griffing (1956). Analyses of variance including tests for GCA and SCA effects are presented for all seed number traits (Table 6) and fiber properties (Table 7).

Table 3. Analysis of variance of parental genotypes for seed number traits evaluated near College Station, TX, in 2000 and 2001 with four replications in each year.

		Mean Squares			
Sources	df	S/B	M/B	O/B	SSE
Years	1	0.0 ^{ns}	2.8 ^{ns}	3.3 ^{ns}	0.002 ^{ns}
Reps(Y)	6	3.3	4.2	5.0	0.003
Genotypes	7	35.0 ***	12.6 *	11.3 ^{ns}	0.011 **
G × Y	7	12.6 ^{ns}	3.5 ^{ns}	12.0 **	0.003 ^{ns}
Error	42	6.8	3.5	2.9	0.003
R^2		0.55	0.49	0.62	0.49
%CV		8.90	29.40	4.77	6.61

† S/B = seeds per boll; M/B = motes per boll; O/B = ovules per boll; SSE = seed setting efficiency.

*, **, ***: $P = 0.05$, $P = 0.01$, and $P = 0.001$, respectively.

Table 4. Analysis of variance of parental genotypes for fiber properties evaluated near College Station, TX, in 2000 and 2001 with four replications in each year.

		Mean Squares					
Sources	df	Mic.†	UHM	UI	Str.	Elo.	SFC
Years	1	3.66 **	0.04 *	7.17 *	5.66 ^{ns}	7.79 *	12.70 ^{ns}
Reps(Y)	6	0.18	0.01	0.74	2.26	0.90	2.46
Genotypes	7	1.11 ***	0.06 ***	13.20 ***	221.00 ***	12.00 **	12.80 ***
G × Y	7	0.34 ^{ns}	0.00 ^{ns}	0.93 ^{ns}	4.94 ^{ns}	1.21 **	0.83 ^{ns}
Error	41	0.16	0.00	1.39	4.46	0.31	1.54
R^2		0.69	0.89	0.66	0.90	0.89	0.66
%CV		7.73	3.62	1.42	6.61	16.40	12.90

† Mic. = micronaire; UHM = upper half mean fiber length; UI = uniformity index; Str. = HVI fiber bundle strength; Elo. = elongation index; SFC = short fiber content.

*, **, ***: $P = 0.05$, $P = 0.01$, and $P = 0.001$, respectively.

Table 5. Mean performance of diallel population parental genotypes for seed number traits and fiber properties evaluated near College Station, TX, in 2000 and 2001 with four replications in each year.

Genotype	S/B[†]	M/B	SSE	Mic.	UHM	UI	Elo. '00	Elo. '01	Str.
	No.	No.	ratio	units	mm	ratio	ratio	ratio	g/tex
M-8844-0096	31.5 ab[‡]	5.2 ab	0.86 ab	5.5 a	25.9 de	83.0 bc	3.5 bc	4.1 bc	30.6 cde
M-9044-0162	33.3 a	4.2 b	0.89 a	5.5 a	24.6 ef	81.0 d	4.6 a	6.2 a	27.6 de
M-9044-0237	27.2 b	7.5 a	0.78 b	5.4 b	25.2 de	83.0 bc	3.8 b	5.8 ab	27.0 e
M-9044-0244	28.1 b	7.5 a	0.79 b	5.0 bc	25.2 de	84.0 ab	2.9 cd	4.1 c	30.8 cd
TAM 94L-25	28.0 b	6.5 ab	0.81 ab	4.8 c	30.5 a	83.0 bc	1.8 e	1.9 e	34.5 b
DP 90	28.6 ab	7.8 a	0.79 b	5.4 b	28.2 bc	83.0 bc	2.2 de	2.1 de	33.2 bc
PD 6186	28.1 b	6.0 ab	0.82 ab	4.9 bc	29.0 b	85.0 a	2.9 cd	2.8 cde	43.2 a
Tamcot CAMD-E	30.0 ab	6.1 ab	0.83 ab	4.6 c	26.7 cd	83.0 bc	2.9 cd	3.2 cde	28.5 de

[†] **S/B = seeds per boll; M/B = motes per boll; O/B = ovules per boll; SSE = seed setting efficiency; Mic. = micronaire; UHM = upper half mean fiber length; UI = uniformity index; Str. = HVI fiber bundle strength; Elo. = elongation index; SFC = short fiber content.**

[‡] **Values within columns followed by the same letter are not different at $P \leq 0.05$.**

Table 6. Diallel analysis of variance for seed number traits evaluated near College Station, TX, in 2000 and 2001 with four replications in each year.

		Mean Squares			
Sources	**df**	**S/B**[‡]	**M/B**	**O/B**	**SSE**
Years	**1**	**29.61** **	**37.05** *	**132.91** **	**0.0153** *
Reps(Y)	**6**	**1.81**	**3.66**	**6.44**	**0.0021**
Genotypes	**35**	**29.00** ***	**13.04** *	**10.89** **	**0.0108** *
GCA[§]	**7**	**58.88** ***	**17.36** ***	**24.45** ***	**0.0156** ***
SCA	**28**	**22.28** ***	**12.32** ***	**7.54** ***	**0.0100** ***
G × Y	**35**	**8.83** **	**6.94** ***	**4.62** *	**0.0050** ***
GCA × Y	**7**	**16.67** **	**7.61** *	**9.81** **	**0.0060** *
SCA × Y	**28**	**7.37** †	**7.36** ***	**3.32** ^{ns}	**0.0052** ***
Error	**207**	**4.89**	**3.08**	**132.91**	**0.0023**
R^2		**0.56**	**0.52**	**0.56**	**0.52**
%CV		**7.21**	**31.51**	**4.55**	**5.69**

[‡] S/B = seeds per boll; M/B = motes per boll; O/B = ovules per boll; SSE = seed setting efficiency.

†, *, **, ***: $P = 0.056$, $P = 0.05$, $P = 0.01$, and $P = 0.001$, respectively.

[§] GCA – general combining ability; SCA – specific combining ability.

Table 7. Diallel analysis of variance for fiber properties evaluated near College Station, TX, in 2000 and 2001 with four replications in each year.

		Mean Squares					
Sources	**df**	**Mic.‡**	**UHM**	**UI**	**Str.**	**Elo.**	**SFC**
Years	**1**	**4.84 *****	**0.15 *****	**20.60 ****	**85.13 ***	**18.50 ****	**73.20 *****
Reps(Y)	**6**	**0.09**	**0.00**	**1.43**	**6.46**	**1.01**	**1.39 ns**
Genotypes	**35**	**0.63 *****	**0.03 *****	**5.20 ****	**76.01 *****	**5.31 *****	**6.59**
GCA§	**7**	**2.32 *****	**0.13 *****	**12.80 *****	**317.70 *****	**22.30 *****	**21.90 *****
SCA	**28**	**0.20 ***	**0.01 *****	**3.25 *****	**14.83 *****	**1.00 *****	**2.72 ****
G × Y	**35**	**0.18 ***	**0.00 *****	**1.88 ****	**6.74 ****	**0.81 *****	**2.19 †**
GCA × Y	**7**	**0.18 ns**	**0.01 *****	**2.97 ****	**11.88 ****	**2.67 *****	**3.62 ***
SCA × Y	**28**	**0.18 ***	**0.00 *****	**1.61 ***	**5.62 ***	**0.35 ****	**1.79 ns**
Error	**205**	**0.11**	**0.00**	**0.95**	**3.38**	**0.19**	**1.49**
R^2		**0.59**	**0.87**	**0.59**	**0.81**	**0.86**	**0.56**
%CV		**6.61**	**3.00**	**1.17**	**5.82**	**14.10**	**13.30**

‡ Mic. = micronaire; UHM = upper half mean fiber length; UI = uniformity index; Str. = HVI fiber bundle strength; Elo. = elongation index; SFC = short fiber content.

†, *, **, ***: $P = 0.10$, $P = 0.05$, $P = 0.01$, and $P = 0.001$, respectively.

§ GCA – general combining ability; SCA – specific combining ability.

General Combining Ability Effects

General combining ability effects represent the average performance of parents in hybrid combinations. These estimates provide an indication of which parents will combine best across all of the parents in the diallel study. Good general combiners should have the greatest impact on trait performance.

Results of the analyses of variance revealed interactions of GCA by year for S/B, M/B, SSE, upper half mean fiber length, uniformity index, strength, elongation, and SFC, necessitating calculation of GCA effects for each year separately. GCA effects for micronaire was determined from means pooled over years. These interactions could pose difficulty in selection for adaptation across wide geographic areas. The rate of trait improvement could also be slowed because different genotypes could have the best performance in different years necessitating multi-year screening to identify the best types.

Converted Race Stock M-9044-0162, which exhibited a high S/B and low M/B (Table 5), produced F_1 hybrids with the other seven parents in this study with an average increase of 0.9 and 1.8 S/B, an average decrease in M/B of 0.8 and 1.2, and an increase in SSE of 0.02 and 0.04 in 2000 and 2001, respectively (Table 8). No other CRS nor commercial-type genotype was consistent in improving all three seed traits in both years. M-9044-0244, as expected, combined with the other seven parents to reduce S/B by 0.9 and 1.4 in 2000 and 2001, respectively. However, it increased M/B and decreased SSE only in 2001.

General combining ability effects for fiber properties were as expected (Table 9). None of the CRS combine with the other seven parents consistently to improve any of these parameters except that M-9044-0162 and M-9044-0237 combined to improve elongation in both 2000 and 2001, which may be an improvement in overall fiber spinning quality. All CRS consistently combined for shorter UHM and M-9044-0162 and M-9044-0237 consistently produced progeny with weaker fibers. Among the commercial-type genotypes, PD 6186 combined well for longer UHM, more uniform fiber length, stronger fibers, and lower SFC. Other parents exhibited significant GCA effects for specific fiber properties in the desired direction, e.g., UHM length, but none were so desirable as a parent as PD 6186. The observed values of fiber bundle strength for PD 6186 seem uncharacteristically high (Coyle and Smith, 1997), but were verified upon inspection of the raw data.

Specific Combining Ability Effects

Specific combining ability effects represent the deviation of hybrid performance from that expected from the GCA effects of each parent. Good specific combiners can be used to develop superior hybrids or to identify populations harboring complementary alleles from which to select superior inbreds. It should be noted that good SCA effects do not necessarily indicate superior trait performance. Two lines with poor overall trait performance can combine better than expected with one another, but their hybrid progeny could still have poor trait performance. Of particular interest are combinations of lines with good to superior trait mean performance and beneficial GCA effects that also have beneficial SCA effects. Such combinations tend to be rare, as observed for

Table 8. General combining ability effects for seed number traits evaluated near College Station, TX, in 2000 and 2001 with four replications in each year.

Parent	S/B‡		M/B		O/B		SSE	
	2000	2001	2000	2001	2000	2001	2000	2001
	----- No. -----		----- No. -----		----- No. -----		----- ratio -----	
M-8844-0096	0.82 **	-0.26 ^{ns}	-0.68 **	0.58 †	0.14 ^{ns}	0.32 ^{ns}	0.0196 **	-0.0160 †
M-9044-0162	0.91 **	1.84 ***	-0.76 **	-1.25 ***	0.15 ^{ns}	0.59 *	0.0219 ***	0.0367 ***
M-9044-0237	0.04 ^{ns}	-0.75 *	0.46 *	0.21 ^{ns}	0.50 *	-0.54 *	-0.0110 ^{ns}	-0.0080 ^{ns}
M-9044-0244	-0.88 **	-1.36 ***	0.31 ^{ns}	0.76 *	-0.57 *	-0.59 *	-0.0110 ^{ns}	-0.0230 **
TAM 94L-25	-1.04 ***	-0.61 ^{ns}	0.44 †	-0.33 ^{ns}	-0.60 **	-0.94 ***	-0.0160 *	0.0049 ^{ns}
DP 90	-0.15 ^{ns}	0.01 ^{ns}	0.27 ^{ns}	0.35 ^{ns}	0.12 ^{ns}	0.37 ^{ns}	-0.0070 ^{ns}	-0.0080 ^{ns}
PD 6186	0.05 ^{ns}	-0.67 ^{ns}	-0.09 ^{ns}	-0.06 ^{ns}	-0.03 ^{ns}	-0.72 *	0.0024 ^{ns}	-0.0020 ^{ns}
Tamcot CAMD-E	0.26 ^{ns}	1.80 ***	0.04 ^{ns}	-0.28 ^{ns}	0.30 ^{ns}	1.52 **	0.0003 ^{ns}	0.0140 ^{ns}

‡S/B = Seeds per boll; M/B = motes per boll; O/B = ovules per boll; SSE = seed setting efficiency.

†, *, **, ***: $P = 0.10$, $P = 0.05$, $P = 0.01$, and $P = 0.001$, respectively.

Table 9. General combining ability effects for fiber properties evaluated near College Station, TX, in 2000 and 2001 with four replications in each year.

Parent	Mic.‡	UHM		UI		Str.		Elo.		SFC	
	Combined	2000	2001	2000	2001	2000	2001	2000	2001	2000	2001
	units	----- mm -----		----- ratio -----		----- g/tex -----		----- ratio -----		----- % -----	
M-8844-0096	0.17***	-0.55***	-0.46**	0.50***	0.15^{ns}	-0.65**	-0.20^{ns}	0.26***	0.12^{ns}	-0.30*	-0.14^{ns}
M-9044-0162	0.23***	-1.32***	-1.49***	-0.57***	-0.55**	-1.88***	-1.82***	0.65***	1.21***	0.50***	0.40†
M-9044-0237	0.05^{ns}	-0.64***	-0.74***	-0.14^{ns}	0.36*	-1.63***	-1.62***	0.19***	0.67***	0.34**	-0.16^{ns}
M-9044-0244	-0.08*	-0.26*	-0.75***	-0.07^{ns}	0.36*	-0.75***	-0.17^{ns}	-0.10†	-0.02^{ns}	0.17^{ns}	0.13^{ns}
TAM 94L-25	-0.15***	1.44***	1.52***	0.16^{ns}	-0.22^{ns}	1.72***	1.16***	-0.55***	-0.78***	-0.59***	-0.30^{ns}
DP 90	0.15***	0.65***	0.81***	-0.12^{ns}	-0.27^{ns}	1.01***	0.63†	-0.46***	-0.72***	0.04^{ns}	0.07^{ns}
PD 6186	-0.12***	0.75***	1.72***	0.47***	0.86***	3.33***	4.53***	-0.05^{ns}	-0.55***	-0.60***	-1.18***
Tamcot CAMD-E	-0.23***	-0.07^{ns}	-0.60***	-0.25*	-0.69***	-1.15***	-2.51***	0.04^{ns}	0.05^{ns}	0.44***	1.19***

‡Mic. = micronaire; UHM = upper half mean fiber length; UI = uniformity index; Str. = HVI fiber bundle strength.

†, *, **, ***: $P = 0.05$, $P = 0.01$, and $P = 0.001$, respectively.

this population. More common are cases in which SCA effects are beneficial but mean performance and GCA are not. Given the definition of SCA effects as deviations from expectations based on GCA effects, this is not surprising. Of interest are SCA effects for combinations of CRS with commercial types. For every trait evaluated, very few specific combinations demonstrated beneficial SCA effects whereas many had significant adverse effects (Tables 10-19).

Crosses among commercial types are also of considerable interest because they demonstrate which combinations of agronomically acceptable types should lead to trait improvement. Of particular interest is the cross of TAM 94L-25 with PD 6186 which combine well both for UHM (Table 15) and fiber bundle strength (Table 17) because both lines have good to superior performance for each trait. This cross appears to provide the opportunity to improve both fiber length and fiber bundle strength potential in upland cotton.

Table 10. Specific combining ability effects for seeds per boll (No.) evaluated near College Station, TX, in 2000 and 2001 with four replications in each year.

	1		2		3		4		5		6		7		8	
	M-8844-0096		M-9044-0162		M-9044-0237		M-9044-0244		TAM 94L-25		DP 90		PD 6186		Tamcot CAMD-E	
1	1.0 ^{ns}	-0.3 ^{ns}	1.2 ^{ns}	2.1 †	-0.9 ^{ns}	2.0 †	-1.8 *	-9.9 ***	-1.4 ^{ns}	0.0 ^{ns}	0.1 ^{ns}	2.3 †	-1.3 ^{ns}	1.9 †	2.1 *	2.1 †
2			0.3 ^{ns}	-0.5 ^{ns}	2.1 *	0.5 ^{ns}	0.0 ^{ns}	0.5 ^{ns}	-1.9 *	-0.6 ^{ns}	-0.7 ^{ns}	-1.0 ^{ns}	-0.8 ^{ns}	0.4 ^{ns}	-0.5 ^{ns}	-0.9 ^{ns}
3					-1.7 *	-3.7 ***	0.5 ^{ns}	2.1 †	0.8 ^{ns}	0.5 ^{ns}	0.4 ^{ns}	1.3 ^{ns}	-0.1 ^{ns}	0.8 ^{ns}	0.5 ^{ns}	0.2 ^{ns}
4							-1.3 †	0.7 ^{ns}	2.0 *	2.1 †	1.1 ^{ns}	2.0 †	0.2 ^{ns}	0.7 ^{ns}	0.5 ^{ns}	1.0 ^{ns}
5									-0.9 ^{ns}	-1.1 ^{ns}	1.2 ^{ns}	0.1 ^{ns}	0.7 ^{ns}	-1.5 ^{ns}	0.3 ^{ns}	1.4 ^{ns}
6											-1.1 ^{ns}	-2.6 *	0.7 ^{ns}	0.9 ^{ns}	-0.7 ^{ns}	-0.5 ^{ns}
7													-1.3 †	-2.5 *	3.2 ***	1.8 ^{ns}
8															-2.8 ***	-2.6 *

†, *, **, ***: $P = 0.05$, $P = 0.01$, and $P = 0.001$, respectively.

Table 11. Specific combining ability effects for motes per boll (No.) evaluated near College Station, TX, in 2000 and 2001 with four replications in each year.

	1		2		3		4		5		6		7		8	
	M-8844-0096		M-9044-0162		M-9044-0237		M-9044-0244		TAM 94L-25		DP 90		PD 6186		Tamcot CAMD-E	
1	0.2 ^{ns}	-0.9 ^{ns}	-1.6 *	-1.4 ^{ns}	0.0 ^{ns}	-0.9 ^{ns}	1.0 ^{ns}	9.4 ***	0.8 ^{ns}	0.0 ^{ns}	-0.7 ^{ns}	-1.6 †	-0.2 ^{ns}	-2.3 *	0.3 ^{ns}	-1.2 ^{ns}
2			0.5 ^{ns}	0.7 ^{ns}	-1.3 †	0.9 ^{ns}	-0.1 ^{ns}	-1.0 ^{ns}	1.7 *	-0.2 ^{ns}	0.9 ^{ns}	0.2 ^{ns}	0.3 ^{ns}	0.0 ^{ns}	-0.9 ^{ns}	0.1 ^{ns}
3					1.4 *	1.0 ^{ns}	-0.8 ^{ns}	-2.8 **	-0.6 ^{ns}	0.9 ^{ns}	-0.6 ^{ns}	0.8 ^{ns}	0.4 ^{ns}	-1.4 ^{ns}	0.3 ^{ns}	0.4 ^{ns}
4							2.4 ***	-0.8 ^{ns}	-2.0 **	-1.6 †	-1.8 *	-2.1 *	-0.5 ^{ns}	0.4 ^{ns}	-0.7 ^{ns}	-0.6 ^{ns}
5									0.9 ^{ns}	0.6 ^{ns}	-1.4 †	-0.3 ^{ns}	-0.6 ^{ns}	1.6 †	0.3 ^{ns}	-1.5 †
6											1.4 *	1.7 *	0.0 ^{ns}	-0.2 ^{ns}	0.6 ^{ns}	-0.3 ^{ns}
7													0.3 ^{ns}	0.8 ^{ns}	0.1 ^{ns}	0.3 ^{ns}
8															-0.1 ^{ns}	1.4 †

†, *, **, ***: $P = 0.05$, $P = 0.01$, and $P = 0.001$, respectively.

Table 12. Specific combining ability effects for ovules per boll (No.) evaluated near College Station, TX, in 2000 and 2001 with four replications in each year.

	1		2		3		4		5		6		7		8	
	M-8844-0096		M-9044-0162		M-9044-0237		M-9044-0244		TAM 94L-25		DP 90		PD 6186		Tamcot CAMD-E	
1	1.3 ^{ns}	-1.2 *	-0.4 ^{ns}	0.6 ^{ns}	-0.9 †	1.1 ^{ns}	-0.9 †	-0.5 ^{ns}	-0.6 ^{ns}	0.0 ^{ns}	-0.6 ^{ns}	0.7 ^{ns}	-1.5 *	-0.4 ^{ns}	2.4 ^{ns}	0.9 ^{ns}
2			0.8 ^{ns}	0.2 ^{ns}	0.7 ^{ns}	1.4 ^{ns}	-0.1 ^{ns}	-0.5 ^{ns}	-0.2 ^{ns}	-0.8 ^{ns}	0.3 ^{ns}	-0.7 ^{ns}	-0.5 ^{ns}	0.4 ^{ns}	-1.4 *	-0.8 ^{ns}
3					-0.3 ^{ns}	-2.7 ***	-0.3 ^{ns}	-0.7 ^{ns}	0.2 ^{ns}	1.4 ^{ns}	-0.2 ^{ns}	2.2 ^{ns}	0.3 ^{ns}	-0.6 ^{ns}	0.9 ^{ns}	0.6 ^{ns}
4							1.1 ^{ns}	-0.1 ^{ns}	0.1 ^{ns}	0.5 ^{ns}	-0.7 ^{ns}	-0.1 ^{ns}	-0.3 ^{ns}	1.0 ^{ns}	-0.2 ^{ns}	0.4 ^{ns}
5									0.0 ^{ns}	-0.5 ^{ns}	-0.1 ^{ns}	-0.3 ^{ns}	0.1 ^{ns}	0.1 ^{ns}	0.7 ^{ns}	-0.1 ^{ns}
6											0.3 ^{ns}	-0.9 ^{ns}	0.8 ^{ns}	0.8 ^{ns}	0.0 ^{ns}	-0.7 ^{ns}
7													-1.1 *	-1.7 *	3.3 ^{ns}	2.0 ^{ns}
8															-2.8 ***	-1.2 *

†, *, **, ***: $P = 0.05$, $P = 0.01$, and $P = 0.001$, respectively.

Table 13. Specific combining ability effects for seed setting efficiency (%) evaluated near College Station, TX, in 2000 and 2001 with four replications in each year.

	1		2		3		4		5		6		7		8	
	M-8844-0096		M-9044-0162		M-9044-0237		M-9044-0244		TAM 94L-25		DP 90		PD 6186		Tamcot CAMD-E	
1	-0.3 ^{ns}	2.0 ^{ns}	4.4 *	4.1 †	-0.3 ^{ns}	3.0 ^{ns}	-3.1 ^{ns}	-25.7 ***	-2.3 ^{ns}	0.1 ^{ns}	1.7 ^{ns}	4.6 †	0.2 ^{ns}	6.4 *	0.1 ^{ns}	3.7 ^{ns}
2			-1.1 ^{ns}	-1.9 ^{ns}	3.9 †	-1.9 ^{ns}	0.4 ^{ns}	2.8 ^{ns}	-4.9 *	0.4 ^{ns}	-2.6 ^{ns}	-1.0 ^{ns}	-1.1 ^{ns}	0.2 ^{ns}	2.1 ^{ns}	-0.8 ^{ns}
3					-3.9 *	-4.4 *	2.2 ^{ns}	7.6 **	1.9 ^{ns}	-1.9 ^{ns}	1.5 ^{ns}	-1.2 ^{ns}	-0.9 ^{ns}	3.9 ^{ns}	-0.4 ^{ns}	-0.7 ^{ns}
4							-6.6 ***	1.9 ^{ns}	5.7 **	4.6 †	4.9 *	5.8 *	1.2 ^{ns}	-0.5 ^{ns}	1.8 ^{ns}	1.7 ^{ns}
5									-2.6 ^{ns}	-1.8 ^{ns}	3.8 †	0.8 ^{ns}	1.8 ^{ns}	-4.5 †	-0.7 ^{ns}	4.0 †
6											-3.9 *	-5.1 *	0.2 ^{ns}	0.8 ^{ns}	-1.8 ^{ns}	0.3 ^{ns}
7													-1.2 ^{ns}	-3.2 ^{ns}	1.0 ^{ns}	0.2 ^{ns}
8															-1.0 ^{ns}	-4.2 †

†, *, **, ***: $P = 0.05$, $P = 0.01$, and $P = 0.001$, respectively.

Table 14. Specific combining ability effects for micronaire (units) evaluated near College Station, TX, in 2000 and 2001 with four replications in each year.

	1		2		3		4		5		6		7		8	
	M-8844-0096		M-9044-0162		M-9044-0237		M-9044-0244		TAM 94L-25		DP 90		PD 6186		Tamcot CAMD-E	
1	0.0 ns	0.1 ns	0.1 ns	0.1 ns	0.1 ns	0.0 ns	0.1 ns	-0.4 ns	-0.1 ns	0.0 ns	-0.2 ns	-0.1 ns	0.0 ns	0.0 ns	0.0 ns	0.1 ns
2			-0.2 ns	0.1 ns	-0.1 ns	0.0 ns	0.1 ns	-0.3 ns	0.1 ns	-0.1 ns	-0.1 ns	0.0 ns	-0.1 ns	0.1 ns	0.2 ns	0.0 ns
3					0.0 ns	0.3 †	0.1 ns	-0.3 ns	0.0 ns	-0.1 ns	-0.1 ns	0.0 ns	-0.3 †	0.1 ns	0.1 ns	-0.2 ns
4							-0.4 **	0.4 *	0.3 *	0.4 *	0.2 ns	0.4 *	-0.1 ns	-0.7 ***	0.1 ns	0.0 ns
5									0.1 ns	0.0 ns	0.0 ns	-0.1 ns	0.1 ns	-0.2 ns	-0.4 **	0.0 ns
6											0.0 ns	0.0 ns	0.1 ns	0.2 ns	0.0 ns	-0.3 †
7													0.0 ns	0.1 ns	0.3 *	0.3 †
8															-0.2 ns	0.0 ns

†, *, **, ***: $P = 0.05$, $P = 0.01$, and $P = 0.001$, respectively.

Table 15. Specific combining ability effects for upper half mean fiber length (mm) evaluated near College Station, TX, in 2000 and 2001 with four replications in each year.

	1		2		3		4		5		6		7		8	
	M-8844-0096		M-9044-0162		M-9044-0237		M-9044-0244		TAM 94L-25		DP 90		PD 6186		Tamcot CAMD-E	
1	-0.3 ^{ns}	-1.2 **	-1.6 ***	-0.2 ^{ns}	0.1 ^{ns}	0.6 ^{ns}	0.4 ^{ns}	1.8 *	-0.3 ^{ns}	-0.5 ^{ns}	-0.1 ^{ns}	0.5 ^{ns}	1.7 ***	0.5 ^{ns}	0.3 ^{ns}	-0.3 ^{ns}
2			0.0 ^{ns}	-0.4 ^{ns}	0.7 †	-1.3 *	0.1 ^{ns}	2.1 ***	0.4 ^{ns}	-0.5 ^{ns}	1.3 ***	0.9 *	-0.9 *	0.5 ^{ns}	-0.2 ^{ns}	-0.8 †
3					-1.4 ***	-1.0 *	0.5 ^{ns}	1.3 **	-0.1 ^{ns}	-0.1 ^{ns}	1.0 **	0.3 ^{ns}	0.6 ^{ns}	0.4 ^{ns}	-0.1 ^{ns}	0.8 †
4							-0.9 *	-1.5 ***	-0.6 ^{ns}	-0.8 †	-0.2 ^{ns}	-0.4 ^{ns}	-0.3 ^{ns}	-0.5 ^{ns}	1.8 ***	-0.5 ^{ns}
5									-0.2 ^{ns}	0.3 ^{ns}	0.7 †	-0.4 ^{ns}	0.3 ^{ns}	1.6 ***	0.0 ^{ns}	0.2 ^{ns}
6											-1.0 **	-0.9 *	-0.2 ^{ns}	0.5 ^{ns}	-0.6 ^{ns}	0.3 ^{ns}
7													-0.9 **	-1.5 ***	0.6 †	-0.1 ^{ns}
8															-0.9 **	0.2 ^{ns}

†, *, **, ***: $P = 0.05$, $P = 0.01$, and $P = 0.001$, respectively.

Table 16. Specific combining ability effects for uniformity index (ratio) evaluated near College Station, TX, in 2000 and 2001 with four replications in each year.

	1		2		3		4		5		6		7		8	
	M-8844-0096		M-9044-0162		M-9044-0237		M-9044-0244		TAM 94L-25		DP 90		PD 6186		Tamcot CAMD-E	
1	-0.8 *	0.0 ^{ns}	0.1 ^{ns}	0.0 ^{ns}	0.9 *	0.0 ^{ns}	-0.3 ^{ns}	0.1 ^{ns}	-0.1 ^{ns}	0.0 ^{ns}	0.0 ^{ns}	0.0 ^{ns}	0.2 ^{ns}	0.0 ^{ns}	0.9 *	0.0 ^{ns}
2			-1.4 ***	0.0 ^{ns}	0.0 ^{ns}	-0.1 ^{ns}	0.1 ^{ns}	0.1 ^{ns}	1.3 **	0.0 ^{ns}	1.2 **	0.0 ^{ns}	-0.1 ^{ns}	0.0 ^{ns}	0.3 ^{ns}	0.0 ^{ns}
3					0.6 †	0.0 ^{ns}	-0.5 ^{ns}	0.1 ^{ns}	-0.5 ^{ns}	0.0 ^{ns}	-0.1 ^{ns}	0.0 ^{ns}	-1.3 **	0.0 ^{ns}	0.5 ^{ns}	0.0 ^{ns}
4							0.2 ^{ns}	-0.1 ^{ns}	0.3 ^{ns}	0.0 ^{ns}	0.5 ^{ns}	0.0 ^{ns}	0.1 ^{ns}	0.0 ^{ns}	-0.6 ^{ns}	0.0 ^{ns}
5									-0.5 ^{ns}	0.0 ^{ns}	-0.6 ^{ns}	0.0 ^{ns}	0.2 ^{ns}	0.1 ^{ns}	0.2 ^{ns}	0.0 ^{ns}
6											-0.7 *	0.0 ^{ns}	0.7 †	0.0 ^{ns}	-0.3 ^{ns}	0.0 ^{ns}
7													0.4 ^{ns}	-0.1 ^{ns}	-0.5 ^{ns}	0.0 ^{ns}
8															-0.2 ^{ns}	0.0 ^{ns}

†, *, **, ***: $P = 0.05$, $P = 0.01$, and $P = 0.001$, respectively.

Table 17. Specific combining ability effects for fiber bundle strength (g/tex) evaluated near College Station, TX, in 2000 and 2001 with four replications in each year.

	1		2		3		4		5		6		7		8	
	M-8844-0096		M-9044-0162		M-9044-0237		M-9044-0244		TAM 94L-25		DP 90		PD 6186		Tamcot CAMD-E	
1	-0.5 ^{ns}	0.1 ^{ns}	0.5 ^{ns}	-0.6 ^{ns}	2.5 ***	1.3 ^{ns}	0.3 ^{ns}	2.3 ^{ns}	-1.3 *	-0.9 ^{ns}	-1.6 **	0.1 ^{ns}	-0.7 ^{ns}	-1.6 ^{ns}	1.3 *	-0.9 ^{ns}
2			-0.3 ^{ns}	-0.4 ^{ns}	0.2 ^{ns}	0.0 ^{ns}	0.6 ^{ns}	1.0 ^{ns}	1.1 †	-0.9 ^{ns}	0.9 ^{ns}	1.6 ^{ns}	-2.3 ***	-1.2 ^{ns}	-0.4 ^{ns}	0.9 ^{ns}
3					-0.6 ^{ns}	-2.1 *	0.3 ^{ns}	-0.1 ^{ns}	-0.2 ^{ns}	0.3 ^{ns}	0.5 ^{ns}	0.5 ^{ns}	-1.9 **	0.8 ^{ns}	-0.3 ^{ns}	1.4 ^{ns}
4							-1.0 †	0.8 ^{ns}	0.0 ^{ns}	-0.5 ^{ns}	0.9 ^{ns}	0.9 ^{ns}	-3.0 ***	-4.1 ***	2.9 ***	-1.1 ^{ns}
5									-0.2 ^{ns}	0.1 ^{ns}	0.4 ^{ns}	-1.3 ^{ns}	0.1 ^{ns}	2.7 *	0.4 ^{ns}	0.2 ^{ns}
6											-0.4 ^{ns}	0.3 ^{ns}	1.4 *	-1.4 ^{ns}	-1.6 *	-1.1 ^{ns}
7													3.7 ***	3.7 ***	-1.3 *	-2.6 *
8															-0.5 ^{ns}	1.6 †

†, *, **, ***: $P = 0.05$, $P = 0.01$, and $P = 0.001$, respectively.

Table 18. Specific combining ability effects for elongation (ratio) evaluated near College Station, TX, in 2000 and 2001 with four replications in each year.

	1		2		3		4		5		6		7		8	
	M-8844-0096		M-9044-0162		M-9044-0237		M-9044-0244		TAM 94L-25		DP 90		PD 6186		Tamcot CAMD-E	
1	0.2 ^{ns}	0.5 *	0.0 ^{ns}	-0.1 ^{ns}	-0.3 †	-0.6 *	-0.1 ^{ns}	-0.5 ^{ns}	0.3 †	0.2 ^{ns}	0.0 ^{ns}	-0.1 ^{ns}	-0.2 ^{ns}	-0.3 ^{ns}	0.0 ^{ns}	0.3 ^{ns}
2			0.5 ***	0.4 †	0.0 ^{ns}	0.9 ***	-0.1 ^{ns}	-0.6 *	-0.5 **	-0.1 ^{ns}	-0.4 *	-0.9 ***	0.2 ^{ns}	-0.3 ^{ns}	-0.1 ^{ns}	0.2 ^{ns}
3					0.6 ***	1.1 ***	-0.2 ^{ns}	-0.9 ***	-0.1 ^{ns}	-0.4 †	-0.2 ^{ns}	-0.4 †	-0.5 **	-0.5 *	0.2 ^{ns}	-0.3 ^{ns}
4							0.2 ^{ns}	0.8 **	0.3 †	0.0 ^{ns}	0.0 ^{ns}	0.0 ^{ns}	0.2 ^{ns}	0.2 ^{ns}	-0.5 **	0.2 ^{ns}
5									0.1 ^{ns}	0.1 ^{ns}	-0.2 ^{ns}	0.5 *	-0.1 ^{ns}	-0.3 ^{ns}	0.2 ^{ns}	-0.1 ^{ns}
6											0.3 †	0.2 ^{ns}	0.0 ^{ns}	0.2 ^{ns}	0.2 ^{ns}	0.2 ^{ns}
7													0.1 ^{ns}	0.6 **	0.1 ^{ns}	-0.1 ^{ns}
8															-0.1 ^{ns}	-0.2 ^{ns}

†, *, **, ***: $P = 0.05$, $P = 0.01$, and $P = 0.001$, respectively.

Table 19. Specific combining ability effects for short fiber content (%) evaluated near College Station, TX, in 2000 and 2001 with four replications in each year.

	1		2		3		4		5		6		7		8	
	M-8844-0096		M-9044-0162		M-9044-0237		M-9044-0244		TAM 94L-25		DP 90		PD 6186		Tamcot CAMD-E	
1	0.9 *	1.1 †	0.0 ns	-0.3 ns	-0.5 ns	-1.1 ns	0.3 ns	-1.6 ns	0.0 ns	1.3 †	0.1 ns	-0.6 ns	-0.8 *	-0.7 ns	-0.8 †	0.7 ns
2			0.7 *	0.9 ns	-0.4 ns	0.0 ns	-0.2 ns	-1.4 †	-0.4 ns	0.3 ns	-0.9 *	-0.4 ns	0.7 †	0.1 ns	-0.2 ns	0.0 ns
3					-0.1 ns	1.3 *	0.6 ns	0.1 ns	0.6 ns	-0.4 ns	-0.5 ns	-0.4 ns	0.9 *	-0.4 ns	-0.4 ns	-0.4 ns
4							0.2 ns	0.1 ns	-0.1 ns	0.1 ns	-0.5 ns	-0.4 ns	0.1 ns	2.1 **	-0.6 ns	0.9 ns
5									0.5 ns	0.0 ns	-0.1 ns	0.9 ns	-0.4 ns	-1.1 ns	-0.5 ns	-1.1 ns
6											1.0 **	0.3 ns	-0.5 ns	0.2 ns	0.4 ns	0.2 ns
7													-0.2 ns	-0.4 ns	0.4 ns	0.8 ns
8															0.8 *	-0.6 ns

†, *, **, ***: $P = 0.05$, $P = 0.01$, and $P = 0.001$, respectively.

CHAPTER IV

CONCLUSIONS

It was clear that significant genotypic variation for within-boll seed yield components can be detected in the field. Moreover, the diallel analysis demonstrated that there was sufficient genetic variation in these traits to facilitate trait improvement through selection. Such interactions indicate that multiple years and environments will be necessary to breed for improvements in these traits. The parent with greatest potential to improve within-boll seed yield components in this population was CRS accession M-9044-0162.

The growth chamber experiments confirmed that S/B, M/B, and SSE respond to heat stress, which supports their use as putative heat tolerance screening traits. Although genotypic differences could not be detected under the heat stress screening regime, it appears these traits have utility in heat tolerance screening for two reasons. First, the continual exposure to high temperatures throughout the growing season in growth chambers represents an unnatural extreme for heat stress. It is my understanding that such continual high temperatures during reproductive growth are observed in the southwestern US but generally not in the remainder of the Cotton Belt. This hypothesis could be tested with a growth chamber evaluation involving periodic rather than continual heat stress. Until then, it seems reasonable to classify the best genotype for within-boll seed yield components, M-9044-0162, as putatively heat tolerant.

Second, S/B, M/B, and SSE lacked genotype by temperature interactions, suggesting that selection of superior genotypes under any condition should improve

yield. Results from the field trials clearly demonstrated that genotypic differences can be detected and used for selection decisions. On a practical basis, determining S/B requires less time and effort than determining M/B and therefore SSE so it seems that S/B would be more time efficient in a breeding scheme for improving yield and putative heat tolerance.

As expected, the CRS accessions reduce fiber quality parameters in addition to known impairment of other agronomic traits. As is common for trait introgression from exotic sources, a backcross breeding approach will probably be necessary to introgress improved within-boll seed yield components into elite lines. Liu et al. (2000) suggest that marker-assisted selection (MAS) should be conducted to maximize the probability of recovering exotic alleles in a backcross scheme. To ensure capturing of exotic alleles for within-boll seed yield components and to maintain the integrity of the commercial recurrent parent for agronomic traits, simultaneous selection could be conducted for within-boll seed yield components and highly heritable morphological traits. This simple phenotypic screening for traits to be introgressed (e.g., S/B), coupled with morphological selection for recurrent parent traits, should accomplish the same goal as MAS at considerably less cost. To maximize recovery of exotic alleles and to reduce linkage drag associated with donor parent traits (e.g., S/B), it seems that a large population should be screened for within-boll seed yield components and morphological traits at each backcross stage.

Finally, an unexpectedly good combination of two superior commercial genotypes for fiber length and for fiber strength was observed for the combination of

TAM 94L-25 with PD 6186. This finding suggests that a population resulting from this cross might have potential for simultaneous improvement of fiber length and fiber bundle strength.

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APPENDIX

DIALLEL-SAS SOURCE CODE

```
/* SAS Code to Analyze an Eight Parent Diallel with
    Griffing's Model I, Method 2) */

OPTIONS PS=56 LS=78;
DATA METHOD2;TITLE 'GRIFFING METHOD 2';
INPUT I     J     Rep   HYBRID      BollNum     SeedPer     MotPer
      OvPer SSE   MIC   UHM   UI    STR   ELO   Rd    b     AREA  SFC
      ENV;
DROP N NI NJ P;
P=8; *NUMBER OF PARENTAL LINES;
ARRAY GCA(N) G1 G2 G3 G4 G5 G6 G7;
 DO N=1 TO (P-1);
  GCA = ((I=N)-(I=P)) + ((J=N)-(J=P));
 END;
ARRAY SCA(N) S11 S12 S13 S14 S15 S16 S17 S22 S23 S24 S25 S26 S27 S33
S34 S35 S36 S37 S44 S45 S46 S47 S55 S56 S57 S66 S67 S77;
N=0;
 DO NI=1 TO (P-1);
  DO NJ=NI TO (P-1);
  N+1;
  IF NI=NJ THEN DO;
  SCA=(I=NI)*((J=NJ)-(J=P)*2) + (I=P)*(J=P);
  END;
  ELSE DO;
   SCA=(I=NI)*(J=NJ)-(J=P)*((I=NI)+(I=NJ)-(I=P));
   END;
  END;
 END;
CARDS; /* After this statement enter data */

;
PROC SORT; BY ENV REP I J;
/* ANOVA of the data */ TITLE 'ANOVA';
PROC SORT; BY REP ENV I J HYBRID;
PROC GLM;
 CLASS I    J     Rep   HYBRID      ENV;
  MODEL SeedPer   MotPer      SSE   MIC   UHM   UI    STR   ELO   Rd
      SFC = ENV REP(ENV) HYBRID ENV*HYBRID;
  TEST H=HYBRID E=ENV*HYBRID;
  TEST H=ENV E=REP(ENV);
  LSMEANS HYBRID; RUN;
  /* SAS program based on Kang's */ TITLE 'DIALLEL-SAS 1';
PROC GLM;
 CLASS I    J     Rep   HYBRID      ENV;
 MODEL  SeedPer   MotPer      SSE   MIC   UHM   UI    STR   ELO   Rd
      SFC    = ENV REP(ENV) G1 G2 G3 G4 G5 G6 G7 S11 S12 S13 S14 S15
S16 S17 S22 S23 S24 S25 S26 S27 S33 S34 S35 S36 S37 S44 S45 S46 S47 S55
S56 S57 S66 S67 S77 G1*ENV G2*ENV G3*ENV G4*ENV G5*ENV G6*ENV G7*ENV
S11*ENV S12*ENV S13*ENV S14*ENV S15*ENV S16*ENV
```

```
S17*ENV S22*ENV S23*ENV S24*ENV S25*ENV S26*ENV S27*ENV S33*ENV S34*ENV
S35*ENV S36*ENV S37*ENV S44*ENV S45*ENV S46*ENV S47*ENV S55*ENV S56*ENV
S57*ENV S66*ENV S67*ENV S77*ENV;
/* Change model if number of parental lines changes */
%MACRO GCASCA;
CONTRAST 'GCA'G1 1,G2 1,G3 1,G4 1,G5 1, G6 1, G7 1;
/* Contrast Statement changes according to the GCA ARRAY statement */
CONTRAST 'SCA'S11 1,S12 1,S13 1,S14 1,S15 1,S16 1,S17 1,S22 1,S23 1,S24
1,S25 1,S26 1,S27 1,S33 1,S34 1,S35 1,S36 1,S37 1,S44 1,S45 1,S46 1,S47
1,S55 1,S56 1,S57 1,S66 1,S67 1,S77 1;
/* Contrast Statement changes according to the SCA ARRAY Statement */

ESTIMATE 'G1' G1 1; ESTIMATE 'G2' G2 1; ESTIMATE 'G3' G3 1; ESTIMATE
'G4' G4 1; ESTIMATE 'G5' G5 1; ESTIMATE 'G6' G6 1; ESTIMATE 'G7' G7 1;
/* Change estimate Statements based on PROC GLM */
/* model and descriptions in the text */
ESTIMATE 'G8' G1 -1 G2 -1 G3 -1 G4 -1 G5 -1 G6 -1 G7 -1;
/* See SCA Calulation File */
ESTIMATE 'S11' S11 1;
ESTIMATE 'S12' S12 1;
ESTIMATE 'S13' S13 1;
ESTIMATE 'S14' S14 1;
ESTIMATE 'S15' S15 1;
ESTIMATE 'S16' S16 1;
ESTIMATE 'S17' S17 1;
ESTIMATE 'S18' S11 - 1 S12 - 1 S13 - 1 S14 - 1 S15 - 1 S16 - 1 S17 - 1;
ESTIMATE 'S22' S22 1;
ESTIMATE 'S23' S23 1;
ESTIMATE 'S24' S24 1;
ESTIMATE 'S25' S25 1;
ESTIMATE 'S26' S26 1;
ESTIMATE 'S27' S27 1;
ESTIMATE 'S28' S12 - 1 S22 - 1 S23 - 1 S24 - 1 S25 - 1 S26 - 1 S27 - 1;
ESTIMATE 'S33' S33 1;
ESTIMATE 'S34' S34 1;
ESTIMATE 'S35' S35 1;
ESTIMATE 'S36' S36 1;
ESTIMATE 'S37' S37 1;
ESTIMATE 'S38' S13 - 1 S23 - 1 S33 - 1 S34 - 1 S35 - 1 S36 - 1 S37 - 1
;
ESTIMATE 'S44' S44 1;
ESTIMATE 'S45' S45 1;
ESTIMATE 'S46' S46 1;
ESTIMATE 'S47' S47 1;
ESTIMATE 'S48' S14 - 1 S24 - 1 S34 - 1 S44 - 1 S45 - 1 S46 - 1 S47 - 1;
ESTIMATE 'S55' S55 1;
ESTIMATE 'S56' S56 1;
ESTIMATE 'S57' S57 1;
ESTIMATE 'S58' S15 - 1 S25 - 1 S35 - 1 S45 - 1 S55 - 1 S56 - 1 S57 - 1;
ESTIMATE 'S66' S66 1;
ESTIMATE 'S67' S67 1;
ESTIMATE 'S68' S16 - 1 S26 - 1 S36 - 1 S46 - 1 S56 - 1 S66 - 1 S67 - 1;
ESTIMATE 'S77' S77 1;
ESTIMATE 'S78' S17 - 1 S27 - 1 S37 - 1 S47 - 1 S57 - 1 S67 - 1 S77 - 1;
```

```
/*ESTIMATE 'S88' S11 -1 S12 -1 S13 -1 S14 -1 S15 -1 S16 -1 S17 -1 S22 -
1 S23 -1 S24 -1 S25 -1 S26 -1 S27 -1 S33 -1 S34 -1 S35 -1 S36 -1 S37 -1
S44 -1 S45 -1 S46 -1 S47 -1 S55 -1 S56 -1 S57 -1 S66 -1 S67 -1 S77 -
1;*/
Estimate 'S88'
S11 - 1
S12 - 2  S13 - 2  S14 - 2  S15 - 2  S16 - 2  S17 - 2
S22 - 1
S23 - 2 S24 - 2 S25 - 2 S26 - 2 S27 - 2
S33 - 1
S34 - 2 S35 - 2 S36 - 2 S37 - 2
S44 - 1
S45 - 2 S46 - 2 S47 - 2
S55 - 1
S56 - 2 S57 - 2
S66 - 1
S67 - 2
S77 - 1;
%MEND GCASCA;
%GCASCA
%MACRO INTERACT;
CONTRAST 'GCA*ENV' G1*ENV 1 -1,G2*ENV 1 -1,G3*ENV 1 -1,G4*ENV 1 -
1,G5*ENV 1 -1,G6*ENV 1 -1,G7*ENV 1 -1;
CONTRAST 'SCA*ENV' S11*ENV 1 -1,S12*ENV 1 -1,S13*ENV 1 -1,S14*ENV 1 -
1,S15*ENV 1 -1,S16*ENV 1 -1,S17*ENV 1 -1,S22*ENV 1 -1,S23*ENV 1 -
1,S24*ENV 1 -1,S25*ENV 1 -1,S26*ENV 1 -1,S27*ENV 1 -1,S33*ENV 1 -
1,S34*ENV 1 -1,S35*ENV 1 -1,S36*ENV 1 -1,S37*ENV 1
-1,S44*ENV 1 -1,S45*ENV 1 -1,S46*ENV 1 -1,S47*ENV 1 -1,S55*ENV 1 -
1,S56*ENV 1 -1,S57*ENV 1 -1,S66*ENV 1 -1,S67*ENV 1 -1,S77*ENV 1 -1;
%MEND INTERACT;
%INTERACT
RUN;
```

VITA

Paul Irwin Ragsdale
306 Suffolk Avenue
College Station, TX 77840-3020

Education

Doctor of Philosophy, Genetics, Texas A&M University, August, 2003
Bachelor of Science, *summa cum laude,* Agronomic Systems, Louisiana State University, May, 1997
Bachelor of Science, *summa cum laude*, Biochemistry, Louisiana State University, May, 1997

Professional Memberships

American Association for the Advancement of Science
American Society of Agronomy
Crop Science Society of America

Graduate Funding

Tom Slick Graduate Research Fellowship, 2002-2003
C. Everette Salyer Fellowship in Cotton Research, 2000-2002
USDA National Needs Fellowship in Plant Biotechnology, 1997-2000

Graduate Awards

First Place Tie, Graduate Student Speakers Competition, Beltwide Cotton Improvement Conference, 2003
First Place, Graduate Student Speakers Competition, Beltwide Cotton Improvement Conference, 2000

Publications

Ragsdale, P.I., and C.W. Smith. 2003. Diallel analysis of seed-set efficiency in upland cotton. p. 820 *In* Proc. Beltwide Cotton Conf., 2003. National Cotton Council, Memphis, TN.
Ragsdale, P.I., C.W. Smith, and R. Creelman. 2000. Survey of vitamin E concentration in upland cotton. p. 520 *In* Proc. Beltwide Cotton Conf., 2000. Vol. 1. National Cotton Council, Memphis, TN.

Teaching Experience

Teaching assistant for laboratory section of Agronomy 301 (Introductory Soil Science), Department of Soil and Crop Sciences, Texas A&M University, Fall, 2001
Teaching assistant for laboratory section of Agronomy 304 (Plant Breeding), Department of Soil and Crop Sciences, Texas A&M University, Spring, 2000