ABSTRACT

COLE, CLAY BRADY. Impact of Heterozygosity and Heterogeneity on Cotton Lint Yield Stability. (Under the direction of Daryl T. Bowman).

Adequate stability of cotton (*Gossypium hirsutum* L.) lint yield is an integral criterion for cultivar release; however, the magnitude of lint yield variation today is close to six times greater than variation observed in the 1920's. Yield stability has often been associated with genetic diversity. Observing cotton lint yield in diverse population types containing various levels and kinds of genetic diversity over many environments could reveal information about stability and how it relates to diversity. An 18-environment field study was undertaken to observe lint yield stability in four population types of cotton. These populations were pure lines grown in pure stands (homozygous/homogeneous), pure lines grown in blended stands (homozygous/ heterogeneous), hybrids grown in pure stands (heterozygous/homogeneous), and hybrids grown in blended stands (heterozygous/heterogeneous). Lint yield components were also observed to determine the contribution each had towards lint yield stability.

Differences were determined by observing the coefficient of variation (CV) for mean yield and yield components of population types and over environments. We found the heterozygous populations to be more stable than the homozygous populations. This was attributed to the hybrids and blends of hybrids out-yielding the parents and blends of parents in the low-yielding environments. This advantage was not observed in the high-yielding environments and, in effect, reduced the amount of variation observed over all environments. The number of bolls/hectare was the only yield component that showed definitive differences for stability between population types with the heterozygous populations having significantly higher stability than the homozygous populations. The superior stability of the heterozygous

populations was attributed to an increased lint production in the lower yielding environments stemming from an increased number of bolls/hectare.

Impact of Heterozygosity and Heterogeneity on Cotton Lint Yield Stability

by

Clay Brady Cole

A dissertation submitted to the Graduate Faculty of
North Carolina State University
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

Crop Science

Raleigh, NC

2007

Approved by:

Dr. Daryl T. Bowman
Chair of Advisory Committee

Dr. James B. Holland

Dr. Christina Cowger

Dr. Thomas G. Isleib

Biography

Clay Brady Cole was born in Cleveland, MS in 1977 to Roy and Gail Cole. He and his older sister, Robin, were raised on a family farm spread over a small part of the Mississippi Delta. After graduating from Bayou Academy in 1996, Clay enrolled in Mississippi State University where he earned a Bachelor of Science degree in 2000 and a Master of Science degree in 2003, both in Agronomy. He was admitted to North Carolina State University in 2003 to pursue a Doctor of Philosophy degree in Crop Science. In 2007, Clay accepted a position with Syngenta Seeds as a soybean breeder.

ACKNOWLEDGEMENTS

I would like to thank my major advisor, Dr. Daryl Bowman, for his tremendous generosity and expert advice. It was an honor to study under such a well-known and respected scholar and cotton breeder. Special thanks go to Dr. Christina Cowger, Dr. Jim Holland, and Dr. Tom Isleib for serving on my committee.

Thanks to Dr. Todd Campbell, Dr. Dawn Fraser, Dr. David Weaver, Rachael Badger, David Caldwell, Jim Hayes, and Dr. Fred Bourland for their help in progressing this project. Thanks also to Cissy Alexander for her help and for beginning this project and setting it in the right direction.

I am grateful for the support and encouragement that I received from my parents, Roy and Gail Cole. Thanks to my sister, Robin, for instilling in me a healthy sense of friendly competition and personal improvement.

I would also like to thank my fiends and colleagues, Dwight Parrish, Johnny Denton, and Phil Johnson, for their help, advice, and instruction over the years. Finally, I would like to thank Cotton Incorporated. Without their support, this project would not have been possible.

TABLE OF CONTENTS

LIST OF TABLES	v
LIST OF FIGURES	vii
CHAPTER I	
General Introduction	1
Literature Cited	17
CHAPTER II	
Impact of Heterozygosity and Heterogeneity on Cotton (<i>Gossypium hirsutum</i> L.)	
Lint Yield Stability	20
Abstract	20
Introduction	21
Materials and Methods	25
Results and Discussion	27
Literature Cited	36
CHAPTER III	
Impact of Heterozygosity and Heterogeneity on Cotton (<i>Gossypium hirsutum</i> L.)	
Lint Yield Stability: II. Lint Yield Components	51
Abstract	51
Introduction	52
Materials and Methods	53
Results and Discussion	55
Literature Cited	63
APPENDIX	75

LIST OF TABLES

CHAPTER II

Table 1. Environments used in the stability study and the mean lint yield performance of all entries at each environment	40
Table 2. Source, degrees of freedom, mean square, and significance for main effects and interactions for lint yield.....	41
Table 3. Mean lint yield, standard deviation, coefficient of variation, blend responses, heterotic responses, percent heterosis, and correlations coefficients for percent response and environmental index	43
Table 4. Mean lint yield, standard deviation, and coefficient of variation among population types	45
Table 5. Mean lint yield, standard deviation, and coefficient of variation between population components.....	46
Table 6. Percent heterosis of lint yield for each hybrid, average heterosis, and environmental means in low, moderate, and high-yielding environments	49
Table 7. Coefficient of parentage between parental genotypes	50

CHAPTER III

Table 1. Environments used in the stability study and the mean lint yield performance of all entries at each environment	66
Table 2. Coefficient of parentage between parental genotypes	67
Table 3. Mean yield components for each parent over environments	68
Table 4. Maturity group means of parents for yield components.....	69
Table 5. The coefficient of variation values among population types for measured yield components	70
Table 6. Mean values among population types for yield components.....	71
Table 7. Correlation for percent heterosis of yield components with environmental mean.....	72

Table 8. Correlations of yield components over genotypes.....	73
Table 9. Standard deviation among population types for yield components.....	74

APPENDIX

Table 1. Mean lint yield, regression coefficient, and residual values among population types	81
Table 2. Mean lint yield, regression coefficient, and residual values between population components	82
Table 3. Mean lint yield, regression coefficient, standard deviation, coefficient of variation, and squared residuals of all entries from the 2000, 2004, and 2005 growing seasons	83
Table 4. Mean lint yield, standard deviation, and coefficient of variation of all entries from the 2005 growing season	84
Table 5. Mean lint yield, coefficient of variation, and standard deviation between population types for the 2005 growing season	85
Table 6. Mean lint yield, coefficient of variation, and standard deviation between population components for the 2005 growing season	86

LIST OF FIGURES

CHAPTER I

Figure I. Possible population types created using intra- and inter-genetic diversity.....	9
---	---

CHAPTER II

Figure 1. Linear trends for lint yield of each population type regressed on the overall mean lint yield of 18 environments	42
Figure 2. The mean lint yield of the four population types in each of 18 environments	47
Figure 3. Change in heterosis from high heterosis in low-yielding environments to low heterosis in high-yielding environments	48

CHAPTER III

Figure 1. Ontogenetic lint yield model	65
--	----

CHAPTER I

General Introduction

One goal of plant breeding involves developing high-yielding genotypes that will produce stable yields across a broad range of environments. This however, does not address the problem of cultivar failure during abnormal or deviant years. Abnormal environmental conditions that impact stability can be due to biotic or abiotic stresses. Addressing what can affect and possibly improve yield stability could benefit growers by the identification and release of genotypes that are more tolerant to broad swings in environmental conditions.

Lewis et al. (2000) linked fluctuations in recent U.S. cotton (*Gossypium hirsutum* L.) yields to changes in within-boll yield components of recent cotton cultivars. They compared obsolete and modern cultivars and found that the yields of modern cultivars were generated by an increased number of seeds/acre when compared to the obsolete cultivars. They speculated that a cultivar that relies on a high number of seeds to produce lint must fix more carbon/kg of lint/hectare than a cultivar that relies on heavy fiber weight or more fibers/seed for lint yield. Thus, a modern cotton plant must use more inputs to produce the same amount of lint, making it more sensitive to changes in the environment.

Several papers have attempted to classify stability in cotton based on lint yield and other characteristics. These papers, detailed below, compare homozygous and heterozygous populations for differences in stability over environments.

Kohel and White (1963) compared the phenotypic stability of parental lines and the hybrid offspring for several traits in cotton. They measured differences on an individual plant basis as well as a whole plot basis. Measurements on individual plants were made for days to first flower, first fruiting node, plant height, relative fruitfulness, and fruiting index.

Whole plot measurements were made for maturity, total yield, boll weight, seed index, and lint index. The hybrids were the most stable population when observing fruiting index and the parental lines were the most stable population with respect to lint index. Kohel and White, nevertheless, tentatively concluded that the parental entries were more stable than their hybrid counterparts. In reality, there were no clear-cut patterns and, therefore, no decisive answers about cotton stability.

Later, Kohel (1969) measured the height, maturity, seed index, lint percent, and lint yield for nine homozygous lines of cotton and all possible F_1 's developed from a complete diallel crossing system. The parental material consisted of eight doubled haploid (DH) plants and one line that was self-pollinated for 17 generations. Kohel theorized that using completely homozygous parents would maximize the difference between stability values of parents and F_1 's. The results agreed with previous findings (Kohel and White, 1963) where there was no clear-cut advantage for either parents or F_1 's with respect to the stability of numerous traits. Their results indicated the parents were more stable for lint yield and hybrids were more stable for lint percent. Kohel concluded that the lack of differences between a homozygous and heterozygous population could be due to the allotetraploid nature of cotton. The A and D genomes could cause a near-steady heterozygous state between homeologous chromosomes, thus delaying the development of a truly homozygous state.

Quisenberry and Kohel (1971) evaluated three species of *Gossypium* - *G. arboreum*, *G. hirsutum*, and *G. barbadense*. They measured pistil length, ovule number, boll weight, leaf dimension ratio, lint yield, boll number, days to first flower, and mean maturity date. There was no pattern for stability regardless of the species. Parents were more stable in some environments and hybrids more stable in others. Comparing the diploid *G. arboreum* to the

tetraploid species resulted in no discernable difference with respect to stability. This indicated that the continuous heterozygous state found in allotetraploids could not account for the absence of any relationship between stability and diversity in a self-pollinated species.

The experiments above attempted to discern differences in stability as it pertained to genetic variation and concluded that heterozygosity did not increase stability in cotton. It is important to note that: 1) some traits measured were on single plant basis; 2) whole plot data were collected from a minimal number of plants putting greater weight on single plant productivity; 3) some variability was eliminated by germinating all entries in the greenhouse before transplanting to the field; 4) all entries were tested in a minimal number of environments. These factors could reduce the level of variation found between population types, making it difficult to observe differences. When measuring stability, it is important to sample a large number of environments (Kang, 1990) that are within the range of adaptation for all entries, while including diverse environmental conditions that encourage variation between entries or population types.

Several other authors have tested cotton genotypes for stability using different statistics with varying results. Some measured differences between homozygous and heterozygous populations while others tested differences in local popular cultivars. These additional articles are summarized below and offer a brief overview of yield stability studied in cotton.

Myers and Bordelon (1997) used Shukla's stability variance (Shukla, 1972) to estimate the stability of cotton lint yield for cultivars grown within the major cotton producing areas of the United States. This stability measure can be described as an individual cultivar's overall contribution towards genotype-by-environment (GxE)

interaction. Data from the 1993 to 1995 state-run Official Variety Trials were collected, categorized into regional data sets, and labeled North (Missouri and Tennessee), Texas, Southeast (Alabama, Georgia, North Carolina, South Carolina), and Mid South (Arkansas, Louisiana, Mississippi). Only varieties grown in all three years found in all areas that make up a region were included in the reduced data sets. There was no significant GxE interaction for any genotype in the North region. Other regions had two or three genotypes with interactions that were significantly different from zero. Conclusions pertaining to the best genotype were based on the stability and yield of each variety grown in two or more regions; the genotypes that followed these criteria were ‘ST LA887’, ‘ST 132’, ‘DP 51’, and ‘DP 5690’. This type of conclusion would be unreliable when selecting a stable genotype considering the diverse environmental range of the entire cotton belt. When reporting stability based on GxE interactions, conclusions should be drawn from regional data of entries that are widely grown in that area.

Opondo and Ombakho (1997) used the deviations from regression (Eberhart and Russell, 1966) and the coefficient of determination (R^2) values to measure yield stability and the regression coefficient (Yates and Cochran, 1938; Finlay and Wilkinson, 1963) to measure adaptability of nine cotton varieties and strains in 21 environments in western Kenya. The entries included two introduced cultivars (HARNA(73)44 and REBA B50), one obsolete commercial cultivar (BPA68), two commercial cultivars (UKA59/240 and BPA75), three strains (KSA20, KSA123, and KSA112), and one blend of eight strains (KSA81M). All strains were developed by pedigree selection from a base population of ‘UKA59/240’ collected from the four major cotton producing regions in Kenya. The strains were selected for high lint percent. Strains KSA20 and KSA112 had deviations from regression that were

significantly different from zero, indicating instability. The blend KSA81M was stable (non-significant deviation from regression) and showed good adaptation to all environments (regression coefficient not different from 1.0). R^2 values for all entries were significantly different from zero, indicating good predictability. The authors concluded that the use of blended cultivars would be advantageous to cotton growers due to their stability and adaptability.

McPherson and Gwathmey (1996) tested 19 *G. hirsutum* genotypes in three west Tennessee locations over three years. Shukla's stability variance (Shukla, 1972) was used as the measure of stability. Results showed six genotypes had interaction terms that were not significantly different from zero but ranged from 3,505 to 20,826. Significant interactions ranged from 21,903 to 107,664. Further analysis revealed a positive correlation (0.49, $p=0.03$) between yield and variance. The authors determined that, on average, a high-yielding genotype would have a low level of stability. They concluded that varietal selection should be balanced between high yield and high stability, such that the chosen variety should include a moderate level of stability even if it is associated with a slight reduction in yield.

Hernandez-Jasso (1988) grew seven Mexican lines and one commercial cultivar in eight locations for three years to observe stability parameters for yield, lint percent, boll weight, and seed index. The coefficient of regression (Yates and Cochran, 1938; Finlay and Wilkinson, 1963) and deviations from regression (Eberhart and Russell, 1966) were used as measures of stability. There were no differences for stability between entries for any of the traits observed as measured by deviations from regression. All entries had similar regression coefficients for all traits measured and were not significantly different from 1.0. The authors

concluded that the yield response of the tested entries was predictable over a broad range of environments.

Mahill et al. (1984) developed 15 *G. hirsutum* DH cotton lines using semigamy. These lines were tested at three locations in 1980 and one location in 1981. Observations were made on 15 DH lines, four parental strains, and two commercial checks. Stability was measured by regression (Yates and Cochran, 1938; Finlay and Wilkinson, 1963) and R^2 . The authors determined that the DH were generally not different from the parents with respect to yield stability and any observed differences did not show a specific trend for stability pertaining to parents or DH.

Bilbro and Ray (1976) observed the adaptation and stability of several *G. hirsutum* entries over three periods spanning 1960-1962 (12 entries), 1963-1965 (10 entries), and 1966-1968 (12 entries). Each location and year combination was treated as an environment totaling 66 environments. Four genotypes spanned all periods and three were used as a standard where the mean of the three genotypes at each environment was used as the environmental index. The fourth genotype was measured against the environmental index to gauge the performance of the standard. The coefficient of regression (Yates and Cochran, 1938; Finlay and Wilkinson, 1963) of each entry on the environmental index was a measure of adaptation and the R^2 was a measure of stability. A cultivar was thought to be adapted to all environments if the regression coefficient was not significantly different from 1.0. If the regression coefficient was greater than 1.0, the cultivar was adapted to high-yielding environments. Having a regression coefficient less than 1.0 indicated the cultivar was adapted to low-yielding environments. A cultivar was stable if its R^2 value was not different from the highest R^2 value of the three standard cultivars. Results indicated most cultivars

were adapted to all environments because their b-values were not significantly different from 1.0. Only one cultivar was classified as unstable with an R^2 value of 0.887; it was found in the 1963-1965 period. The authors admitted to the bias associated with using cultivars to create an environmental index and testing those same cultivars against that very index. The magnitude of the bias depends on the number of cultivars used to create the index with a larger bias being found when fewer cultivars are used to create the index. The authors recommended using R^2 values as a measure of stability and b-values as a measure of adaptation when evaluating and characterizing advanced breeding material.

Feaster and Turcotte (1973) evaluated the yield stability of three Pima (*G. barbadense*) cotton varieties, their derived DH, and a blended population of the DH. They measured stability by observing the CV (Francis and Kannenberg, 1978), regression coefficient (Yates and Cochran, 1938; Finlay and Wilkinson, 1963) and the deviation from regression (Eberhart and Russell, 1966). There was similar variation for all entries when compared using the CV. There was no significant difference between the cultivars and their subsequent DH when compared using regression. Deviations from regression indicated no differences among cultivars or DH; however, differences were observed between two varieties and the DH composite, where the composite had a lower deviation from regression. The results were not conclusive but suggested that heterogeneity was important with respect to stability in this population.

Meredith et al. (1970) investigated the genotype-by-location interaction for parental varieties, DH, and F_1 and F_2 hybrids of *G. hirsutum*. Two groups of parents and crosses were used. The first group consisted of the three parents, the three F_1 's, and the three resulting F_2 's. The second group was made up of three DH derived from the parental lines, the three

F_1 's, and the resulting F_2 's. Initial comparisons between parents and DH showed significant differences for several traits measured, indicating the parents were not homozygous.

Comparisons between DH and parents for environmental interactions showed no significant difference or trends for all characteristics measured. The authors reported a trend in the data that indicated the F_1 and F_2 populations had a lower interaction mean square than the parents, meaning the hybrids may have been more stable over environments. They go on to say that the F_1 and F_2 populations had similar interaction mean squares, indicating that the stability of the F_2 population could be due to the heterozygosity within plants as well as the heterogeneity among plants. The authors refrained from commenting on the practical uses of genetic stability in cotton breeding, saying it may have been too early to generalize on the subject.

Cotton breeders for years have generally thought that heterozygosity contributed to stability (Bowman, D. T., 2006, personal communication). Bowman and Gutierrez (2003) reported that 25% of cotton cultivars released up through 2000 were reselections from existing, thought to be homozygous and homogeneous, cultivars. This brings the purity of earlier cultivar release into question and indicates these early-released open-pollinated cultivars have a heterogeneous nature as well as some level of heterozygosity. The combination of these two types of diversity could be advantageous with respect to yield and yield stability.

Several studies have evaluated yield stability of other crops in population types that differ for kinds and levels of diversity (Haussmann et al., 2000; Stelling et al., 1994; Leon, 1991; Schnell and Becker, 1986; and Reich and Atkins, 1970). The kinds of diversity are intra-genic (allelic variation at a single locus) and inter-genic diversity (genotypic variation

between entire plants). The levels of diversity pertain to single vs. multiple kinds of diversity included in one population. Using these kinds and levels of diversity, we can construct four population types as seen below.

Figure 1. Possible population types created using intra- and inter-genetic diversity.

Only environmental variation is found in pure lines grown in pure stands. Allelic variation is found in hybrids grown in pure stands. Genotypic variation is found in pure lines grown in blended stands. Allelic and genotypic variation is found in hybrids grown in blended stands. These population types capture all kinds of discrete intra- and inter-genetic variation.

Stelling et al. (1994) studied yield stability in faba bean (*Vicia faba* L.) by observing eight inbred lines grown in pure stands, four two-way line blends, four hybrids, and two hybrid blends. They measured stability by evaluating the regression coefficient (Yates and Cochran, 1938; Finlay and Wilkinson, 1963), the deviation from that regression (Eberhart and Russell, 1966), and the ecovalence (Wricke, 1962) of each population type. Inbred lines had the lowest levels of stability. Improvements in yield stability were observed using both heterogeneity and heterozygosity with heterogeneity improving stability slightly more. The authors suggested that both heterogeneity and heterozygosity could be combined in a hybrid blend to produce an additive effect. They observed a 28, 23, and 51% increase in stability

when comparing the parental lines to the parental blends, hybrid lines, and hybrid blends, respectively.

Leon (1991) selected four winter oil seed rape (*Brassica napus* L. var. *napus*) cultivars as a base population to measure yield stability. These cultivars were chosen to represent a wide range of genetically diverse genotypes. The parents, parental blends, hybrids, and hybrid blends were measured for stability using Wricke's ecovalence (Wricke, 1962). Parental blends, hybrids, and hybrid blends resulted in a 43, 34, and 56% increase in stability when compared to pure lines, respectively. The increase in stability due to heterogeneity was greater for pure lines than hybrids. The additional increase in stability associated with blending the hybrid entries (22%) was substantially less than the 43% increase observed in the blends of parents. This indicated heterozygosity and heterogeneity both contributed to stability, but not in an additive manner.

Schnell and Becker (1986) studied yield and yield stability in *Zea mays* L. using the four population types mentioned above. Stability was measured using ecovalence (Wricke, 1962), the regression coefficient (Yates and Cochran, 1938; Finlay and Wilkinson, 1963), and the deviation from regression (Eberhart and Russell, 1966). The parental lines and parental blends exhibited the highest regression coefficients, indicating they performed well in the most favorable environment. Using ecovalence as a measure of stability, heterogeneity increased stability dramatically, averaging a 64% increase when compared to the homogeneous lines. There was no increase in stability observed for heterozygosity using the values calculated for ecovalence. The deviations from regression showed an increase in stability for both the blended pure lines and the blended hybrids; however, the increase

observed with deviations from regression for blended pure lines was larger than the increase observed with ecovalence.

Schnell and Becker (1986) noted that ecovalence and deviations from regression pose a problem when used as stability measures. As means increase, the variance often increases. They countered this by using the CV (Francis and Kannenberg, 1978) for each population type, which, in effect, gave greater weight to the variance observed for the low-yielding inbred population and less weight to the high-yielding hybrid population. The CV for deviations from regression showed an increase in yield stability for both heterogeneity and heterozygosity. There was a 50, 73, and 74% increase in stability for parental blends, hybrids, and hybrid blends, respectively, when compared to the stability of the parents.

Reich and Atkins (1970) investigated yield stability in grain sorghum (*Sorghum bicolor* L.) by observing a combination of the regression coefficient (Finlay and Wilkinson, 1963) and the deviations from regression (Eberhart and Russell, 1966) for parents, hybrids, parental blends, and hybrid blends. A stable genotype was described as one with a coefficient of regression close to 1.0 and a deviation from regression approaching zero. No population type fit both parameters; however all population types had deviations from regression that were less than the parents grown in pure stands. The parental blends had the largest increase in stability (70%) and the only regression coefficient that was significantly larger than 1.0. The hybrid blends had the second largest increase in stability (51%) followed by the hybrids (10%). Heterozygosity increased stability when observed in the homogeneous populations but decreased stability when found in the heterogeneous populations. Increases in stability were found for both types of diversity but heterogeneity had the largest impact.

Haussmann et al. (2000) followed Reich and Atkins's (1970) experiment by investigating yield and yield stability in grain sorghum in a semi-arid area of Kenya using deviations from regression (Eberhart and Russell, 1966) as the stability measurement. Parental blends, hybrids, and hybrid blends showed an increase in stability (29, 48, and 37% respectively) when compared to parental lines; however, significant differences between population types were not tested but based on trends observed among population types. These results differ from those reported by Reich and Atkins (1970) (heterogeneity is most important with respect to stability) and indicated the hybrid population was the most stable.

The previous studies generate several different conclusions that depend on the organism observed, trait studied, mating design, stability statistic, number and diversity of environments, as well as the data being considered. Each study should have outlined the specific objectives for observing stability and included the assumptions that are imbedded within each measure of stability. Of the stability statistics used above (Wricke's ecovalence, regression coefficient, deviations from regression, CV, and Shukla's stability variance), deviation from regression was the most common; however, different information will be generated depending on the choice and application of each measure of stability.

Lin et al. (1986) classified several stability statistics and tried to discern which was best and found that they measured different things and gave information on different natural systems. The best statistic to use depends on what conclusions one would like to draw about the experimental units. They defined three classes or types of stability.

Type I or biological stability is based on the variation observed for each genotype over environments. This type only observes the variation produced by different environments and can be useful when making statements or recommendations about a

genotype's stability relative to the geographic range that encompass those environments.

This measurement should be fairly consistent when calculated over many environments but is less useful if several unrelated environments outside the area of adaptation are included in the data set. These statistics have a very practical use in detecting usable stability but have not been widely used because stable cultivars described in this method can have lower yields in high-yielding environments. High-yielding genotypes tend to have greater variance than lower yielding genotypes; therefore, comparisons of variances per se may not be sufficient. In biological systems, variances tend to increase as the mean increases. We need to standardize the variances to make valid conclusions. This can be performed with the CV.

When using the CV, measuring variation within or between environments can result in different conclusions. Kohel (1969), Kohel and White (1963), and Quisenberry and Kohel (1971) measured some or all traits by observing variation between plants in individual plots and calculating the CV based on plant to plant variation. The CV values were then compared statistically based on within-plot variation. Calculating the CV for each plot and averaging it across locations would reduce the actual amount of variation associated with the SD across environments. Conditions within environments should be similar due to a shared proximity between entries that encounter comparable levels of sunlight, rainfall, insect pressure, and other biotic and abiotic environmental conditions, resulting in variation that is biased downwards as compared to environmental variation. Calculating the CV for means over environments will reveal the true environmental variation and a more accurate estimate of stability.

Type II or agronomic stability is based on a genotype's response to each environment relative to all other genotypes tested. Statements about stability can only be made about each

genotype relative to the other tested genotypes. This measurement has been widely accepted but has its shortcomings. Genotypes with adaptive advantages like drought tolerance or ones that have a low variance across environments can have a higher GxE interaction and be labeled unstable. A genotype that was determined to be stable in one study may be unstable in a separate study using different genotypes and environments. Ecovalence (Wricke, 1962) and Shukla's stability variance (Shukla, 1972) are examples of this measurement. The regression coefficients (Yates and Cochran, 1938; Finlay and Wilkinson, 1963) can be considered Type I or II stability depending on how a stable genotype is defined. Stability based on a regression coefficient of 1.0 is classified as Type II stability and stability based on a regression coefficient of zero is classified as Type I stability.

Type III stability is based on the deviations from regression when the mean yield is regressed on the mean environmental yield or environmental index. This stability measurement was described as the least desirable of the three types or at least until the environmental index can be replaced by actual environmental factors. Eberhart and Russell's (1966) deviation from regression would be an example of this type of stability. This statistic observes the deviations from the fitted regression line as a measure of predictability in a retroactive fashion, such that conclusions about the reaction of a specific genotype in a specific environment can only occur after the environmental index is evaluated.

As mentioned above, stability statistics are classified by the information each reveal about the tested material; however, some statistics are virtually interchangeable relative to the information generated. Becker (1981) studied the relationship of several stability statistics including variance, ecovalence, regression coefficient, and deviations from regression and defined them according to the information they generate. The definitions

were similar to those of Lin et al. (1986), but gave more information on the relationship between statistics. The variance and coefficient of regression (Finlay and Wilkinson, 1963) produced similar results with an average correlation of 0.94 over 15 trials in three years for four different crops. Ecovalence (Wricke, 1962) and deviations from regression (Eberhart and Russell, 1966) were highly correlated with an average correlation of 0.94 over 15 trials in three years for four different crops. These correlations were calculated on stability rankings and not values because the stability statistics could not be assumed normally distributed. Correlations between variance and deviations from regression, variance and ecovalence, regression coefficient and deviations from regression, and regression coefficient and ecovalence were highly variable with most values being non-significant because the compared statistics generate different results and reveal different information relative to the tested entries.

For the purpose of this study, we wanted to measure the natural variation found in specific population types by observing how they react to the environment. Measuring the variation using the variance or SD can cause problems associated with the common phenomenon of increasing variability coupled with increasing means. Using the CV to standardize the measurement allows for a direct comparison of stability values across population types regardless of the magnitude of the mean. Francis and Kannenberg (1978) used the CV of each genotype to measure stability. This procedure takes into account the increased variance of high-yielding varieties by expressing the SD as a percentage of the mean.

In response to the demand for improved lint yield stability in modern cotton cultivars, a study was conducted to determine if genetic structure impacts stability. Thus, the objective

of this study was to determine the effects of four population types containing varying degrees of diversity on lint yield stability in cotton. Because lint yield is the combined result of several traits, yield components were also examined and correlated.

Literature Cited

- Becker, H. C. 1981. Correlations among some statistical measures of phenotypic stability. *Euphytica* 30:835-840.
- Bilbro, J. D., and L. L. Ray. 1976. Environmental stability and adaptation of several cotton cultivars. *Crop Sci.* 16:821-824.
- Bowman, D. T., and O. A. Gutiérrez. 2003. Sources of fiber strength in the U.S. upland cotton crop from 1980 to 2000. *J. Cotton Sci.* 7:164-169.
- Eberhart, S.A., and W.A. Russell. 1966. Stability parameters for comparing varieties. *Crop Sci.* 6:36-40.
- Feaster, C. V., and E. L. Turcotte. 1973. Yield stability in doubled haploids of American Pima cotton. *Crop Sci.* 13:232-233.
- Finlay, K. W., and G. N. Wilkinson. 1963. The analysis of adaptation in a plant-breeding programme. *Aust. J. Agric. Res.* 14:742-754.
- Francis, T. R., and L.W. Kannenberg. 1978. Yield stability studies in short-season maize. I. A descriptive method for grouping genotypes. *Can. J. Plant Sci.* 58:1029-1034.
- Hausmann, B. I. G., A. B. Obilana, P. O. Ayiecho, A. Blum, W. Schipprack, and H. H. Geiger. 2000. Yield and stability of four population types of grain sorghum in a semi-arid area of Kenya. *Crop Sci.* 40:319-329.
- Hernandez-Jasso, A. 1988. Stability analysis for cotton (*Gossypium hirsutum* L.) and their sites of testing. In J. M. Brown (ed.) *Proc Beltwide Cotton Conf.*, New Orleans, LA. 3-8 Jan. National Cotton Council of America, Memphis, TN.
- Kang, M. S. 1990. Understanding and utilization of genotype-by-environment interaction in plant breeding, pp. 52-68, In M. S. Kang (ed), *Genotype-By-Environment Interaction and Plant Breeding*. Louisiana State Univ., Baton Rouge.
- Kohel, R. J. 1969. Phenotypic stability of homozygous parents and their F₁ hybrids in upland cotton, *Gossypium hirsutum* L. *Crop Sci.* 9:85-88.
- Kohel, R. J., and T. G. White. 1963. An analysis of the variability of five parents and their F₁ progenies in *Gossypium hirsutum* L. *Crop Sci.* 3:359-361.
- Leon, J. 1991. Heterosis and mixing effects in winter oilseed rape. *Crop Sci.* 31:281-284.

- Lewis, H., L. May, and F. Bourland. 2000. Cotton yield components and yield stability. p.532-536. In P. A. Dagger and D. A. Richter (ed.) Proc. Beltwide Cotton Conf., San Antonio, TX. 4-8 Jan. 2000. National Cotton Council of America, Memphis, TN.
- Lin, C. S., M. R. Binns, and L. P. Lefkovitch. 1986. Stability analysis: where do we stand? Crop Sci. 26:894-900.
- Mahill, J. F., J. N. Jenkins, J. C. McCarty, Jr., and W. L. Parrott. 1984. Performance and stability of doubled haploid lines of upland cotton derived via semigamy. Crop Sci. 24:271-277.
- McPherson, R., and O. Gwathmey. 1996. Yield and stability of cotton cultivars at three west Tennessee locations. In P. Dugger and D. A. Richter (ed.) Proc. Beltwide Cotton Conf, Nashville, TN. 9-12 Jan. National Cotton Council of America, Memphis TN.
- Meredith, W. R., Jr., R. R. Bridge, and J. F. Chism. 1970. Relative performance fo F_1 and F_2 hybrids from doubled haploids and their parent varieties in upland cotton, *Gossypium hirsutum* L.
- Myers, G. O., and F. Bordelon. 1997. Stable statistics for cotton varieties grown in the midsouth, southeast, north and Texas from 1993-1995. In P. Dugger and D. A. Richter (ed.) Proc. Beltwide Cotton Conf, New Orleans, LA. 6-10 Jan. National Cotton Council of America, Memphis TN
- Opondo, R. M., and G. A. Ombakho. 1997. Yield evaluation and stability analysis in newly selected 'KSA' cotton cultivars in western Kenya. African Crop Sci. J. 5(2):119-125.
- Quisenberry, J. E., and R. J. Kohel. 1971. Phenotypic stability of cotton. Crop Sci. 11:827-829.
- Reich, V. H., and R. E. Atkins. 1970. Yield stability of four population types of grain sorghum, *Sorghum bicolor* (L.) Moench, in different environments. Crop Sci. 10:511-517.
- Schnell, F. W., and H. C. Becker. 1986. Yield and yield stability in a balanced system of widely differing population structures in *Zea mays* L. Plant Breeding 97:30-38.
- Shukla, G. K. 1972. Some statistical aspects of partitioning genotype –environmental components of variability. Heredity 29:237-245.
- Stelling, D., E. Ebmeyer, and W. Link. 1994. Yield stability in faba bean, *Vicia faba* L. 2. Effects of heterozygosity and heterogeneity. Plant Breeding 112:30-39.
- Wricke, G. 1962. Über eine Methode zur Erfassung der ökologischen Streubreite in Feldversuchen. Z. Pflanzenzuchtg 47:92-96.

Yates, F., and W.G. Cochran. 1938. The analysis of groups of experiments. *J. Agric. Sci. (Camb.)* 28:556-580.

CHAPTER II

Impact of Heterozygosity and Heterogeneity on Cotton (*Gossypium hirsutum* L.) Lint Yield Stability

Abstract

An 18-environment field study was undertaken to observe lint yield stability in four population types of cotton that included: pure lines grown in pure stands (homozygous/homogeneous), pure lines grown in blended stands (homozygous/heterogeneous), hybrids grown in pure stands (heterozygous/homogeneous), and hybrids grown in blended stands (heterozygous/heterogeneous). Cotton lint yield was measured on each plot. Population types were compared using trait means, standard deviation (SD), and the coefficients of variation (CV) calculated over environments. The heterozygous populations had a higher mean yield than the homozygous populations; this difference was attributed to heterosis but was not consistent over environments and diminished as environmental mean increased (correlation of -0.72). The heterozygous populations had a lower CV (were more stable) than the homozygous populations. This stability was attributed to the heterozygous populations having a reduced range in yields as compared to the homozygous populations, such that the hybrids and blends of hybrids out-yielded the parents and blends of parents in the low-yielding environments but had similar yields in the high-yielding environments.

Introduction

The standard deviation (SD) of recent U.S. cotton (*Gossypium hirsutum*) lint yield is approximately five times larger than the SD of lint yield during the 1920's (National Agricultural Statistical Service). This increase in variation is expected when considering large variances are often associated with increases in mean values. National cotton yields over the past six years are, on average, four times larger than they were during the 1920's (NASS). When comparing the relative variation of the 1920's and 2000's using the coefficient of variation (CV), there is little difference, indicating variation is not relatively increasing; however, large swings in variation can be detrimental to some growers and should be addressed.

Diversity has often been associated with stability. Allard and Bradshaw (1964) attempted to detail environmental variation (aptly categorized into predictable and unpredictable variation) and what might quell it. They determined diversity was the answer in the form of "buffering" capacity that can be separated into individual buffering and population buffering.

Individual buffering comes in the form of heterozygous genotypes that theoretically resist change to the environment through allelic variation that produces complex enzymes with various optimal operating conditions or result in biochemical versatility that allows divergent biochemical pathways under diverse environmental conditions (Lewis, 1954; Haldane, 1954). Several studies, using a variety of statistics, have outlined individual buffering ability in self-pollinated and cross-pollinated species and are outlined below.

Leon (1991) found hybrid winter oil seed rape (*Brassica napus* L. var. *napus*) cultivars were 34% more stable than their homozygous counterparts. Stelling et al. (1994)

observed a 23% improvement in yield stability for the hybrid population when compared to the pure-line population in faba bean (*Vicia faba* L.). Shank and Adams (1959), and Schnell and Becker (1986) observed increases in the stability of corn hybrids (*Zea mays* L.) over the parental population for several measured traits. Several studies have also tested stability between homozygous and heterozygous populations and found no differences (Reich and Atkins, 1970; Smith and Foote, 1970; Kohel, 1969; Kohel and White, 1963; Quisenberry and Kohel, 1971; Peterson et al., 1997).

Population buffering is a function of two or more genotypes that, when grown together, have morphological or agronomic qualities that compensate for inadequacies found in each (Marshall and Brown, 1973). This compensation effect should be visible when the blended (heterogeneous) population is grown in diverse environmental conditions (Marshall and Brown, 1973). A large number of studies have been devoted to observing this phenomenon.

Smithson and Lenne (1996) constructed an extensive review of varietal mixtures as they pertain to sustainable agriculture and found that, in 32 of 38 reviewed data sets, the blended entries were more stable than the blend components. Leon (1991) found blended rape seed cultivars were 43% more stable than pure lines. Stelling et al. (1994) reported a 28% increase in stability of faba bean cultivars grown in blends as compared to pure lines. Several authors have also observed an increase in stability of blended entries when compared to individual blend components (Allard, 1960; Funk and Anderson, 1964; Reich and Atkins, 1970; Schnell and Becker, 1986; Opondo and Ombakho, 1997; Haussmann et al., 2000); however, blended entries do not always result in an increase in stability (Clay and Allard, 1969; Rasmusson, 1968; Smithson and Leene, 1996).

Another aspect of population buffering is the blending of individually buffered genotypes or a heterozygous and heterogeneous population. A few authors have studied this level of diversity and found differing results depending on the material tested. Leon (1991) found the blended hybrid population of rape seed to be the most stable population (56% increase in stability). Stelling et al. (1994) observed similar results in faba bean (51% increase); however, the increase in stability could be directly partitioned into the stability due to heterogeneity in the homozygous population (28% increase) plus the stability due to heterozygosity in the homogeneous population (23% increase). Schnell and Becker (1986) observed a 74% increase in stability for the blends of hybrids in maize but concluded that it was not much different than the increase observed for the hybrids alone (73%). Reich and Atkins (1970), working with grain sorghum (*Sorghum bicolor* L.), reported that the hybrid blends were the second most stable population type following the parental blends, indicating heterozygosity decreased stability. Haussmann et al. (2000), also working with sorghum, found the hybrid blends to be the second most stable population type following the hybrids, indicating heterogeneity decreased stability.

Stability observed between population types differing for levels and kinds of diversity are dependent on the organism, trait studied, mating design, stability statistic chosen, and the number of environments the population types are tested in. The studies outlined above use a variety of stability statistics that include the regression coefficient (Yates and Cochran, 1938; Finlay and Wilkinson, 1963), ecovalence (Wricke, 1962), deviations from regression (Eberhart and Russell, 1966), and CV (Francis and Kannenberg, 1978). Different conclusions can be drawn relative to yield stability depending on which statistic is used and how it is used. Becker (1981), Lin et al. (1986), and Becker and Leon (1988) outlined the

relationship between many stability statistics and differentiated them based on the information they generate about yield stability.

Becker (1981) described two concepts of stability designated biological and agronomic stability. Biological stability can be described as no change in yield over environments or a genotype that has zero variance. An example of agronomic stability is a genotype that has a predictable performance in a specific environment and does not deviate from that prediction. Becker and Leon (1988) also observed these different concepts of stability and labeled them static and dynamic concepts. Static and dynamic stability correspond to biological and agronomic stability respectively. Lin et al. (1986) separated the observed stability statistics into three types. Type I stability corresponds to biological stability and is most often measured by observing the variance or CV (Francis and Kannenberg, 1978). This stability is rarely used because a Type I stable genotype is often one that has insufficient yields. Type II stability is the interaction observed between the genotype and environment and can be measured using the regression coefficient (Yates and Cochran, 1938; Finlay and Wilkinson, 1963), ecovalence (Wricke, 1962), and Shukla's stability variance (Shukla, 1972). Type III stability is the deviation from regression (Eberhart and Russell, 1966). Type II and III can be considered agronomic or dynamic stability.

Both concepts of stability have relevance, but as Becker and Leon (1988) point out, dynamic and agronomic stability outline the predictability of a genotype. This is true for Type II and III stability statistics as well. Being able to predict a genotype's response in a specific environment will only be useful if the environment conditions are known prior to planting. Type I stability, or biological stability, gives information on the response of

genotypes over all tested environments. Given enough environments are tested (Kang, 1990), this statistic will give information on the range of phenotypic response over environments and can be used as a general guide to genotypic performance without having prior knowledge of environmental conditions.

The objective of this experiment was to determine the impact of heterozygosity and heterogeneity on cotton lint yield stability of four population types grown over multiple environments.

Materials and Methods

Four commercial cultivars, ‘Delta Pine 51’ (DP 51), ‘Stoneville 474’ (ST 474), ‘Stoneville LA 887’ (LA 887), and ‘Fiber Max 989’ (FM 989), were chosen for this experiment based on perceived stability and maturity. DP 51, ST 474, and LA 887 were thought to be relatively stable over years and locations (Bowman, D. T., 2006, personal communication). FM 989 was known to be a high-yielding cultivar (Bowman, 1999). Maturity could influence final lint yield in differing environmental conditions. Parents were chosen to represent equal divisions of early (DP 51 and ST 474) and full-season (LA 887 and FM 989) maturity groups. The coefficient of parentage (CP) values of parental material was calculated after the entries were selected to determine diversity of parental material (Sneller, 1994). The CP is a measure of the relatedness between two individuals reported as the proportion of alleles that are identical by descent.

Parents were crossed in a diallel excluding self-pollinations in 1999, 2000, and 2004. Reciprocal crosses were bulked. Parental lines were obtained from commercially available seed stock. Entries included four parents, six hybrids, six parental blends, and the 15 hybrid blends. Entries were tested in 21 environments; however, two environments, one in

Mississippi in 2000 and one in Georgia in 2004 were lost, while one environment in South Carolina in 2005 was discarded due to extreme variability among entries. Each location-by-year combination was treated as a single environment totaling 18 environments (Table 1).

Four population types were used in this study to represent contrasting levels of intra- and inter-genetic diversity. The homozygous/homogeneous population included the four parental lines grown in pure stands and represented the absence of genetic diversity. The homozygous/heterogeneous population included the parental lines grown in two-component blends, resulting in six blended entries. The heterozygous/homogenous population encompassed the six possible hybrid combinations grown in pure stands. The heterozygous/heterogeneous population was a combination of the two types of diversity and consisted of the six hybrids grown in two-component blends, resulting in 15 blended entries. Blended entries were produced by combining exactly one-half of the total number of seeds needed for each plot from each blend component into a labeled envelope and manually mixing the seed prior to planting.

All entries were grown as two-row plots and were arranged in a randomized, complete block design with three replicates in 2000 and two replicates in 2004 and 2005. Plot length ranged from 8.5m to 13.7m and row spacing ranged from 91.4 cm to 101.6 cm. Planting dates ranged from April 28 to May 21 and harvest dates ranged from September 17 to October 28. Plots were grown under rain fed conditions and cultural practices were implemented as needed and consistent with farming practices standard for each location.

Plots were machine harvested and weighed for seed cotton yield. Blend response was calculated by subtracting the average of the two blend components (mid-component) from the observed value of each blended entry in each environment and averaging over

environments. Heterotic response for the hybrid entries was calculated in a similar manner where the average of the two hybrid components (mid-component) was subtracted from the value of the hybrid entry in each environment and averaged over environments. Heterotic response for the blended hybrid entries was calculated by subtracting the average of the four parental components (mid-component) that correspond to each blend from the observed value of each blended entry in each environment and averaging over environments. Percent blend response and percent heterosis were calculated by dividing the response of each measured entry by the mid-component and multiplying by 100. Percent blend response and percent heterosis were calculated in each environment and averaged over environments.

The SD and CV of lint yield were calculated for each entry over environments and replicates, resulting in one observation/entry. Standard deviation, CV, and lint yield values were subjected to ANOVA using the generalized linear model procedure of SAS version 9.1 to determine differences between population types. Population types and entries were considered fixed effects; environments were deemed random effects. The CV was calculated using the formula: $CV = (s/\mu) \times 100$ where s is the SD and μ is the overall mean. Mean separation was conducted using Fisher's protected least significant difference (LSD) at the 0.05 level of probability.

Results and Discussion

Environments

Yields for the 18 environments were significantly different, indicating they were sufficiently variable to measure yield stability (Table 1). Environments differed for planting and harvest dates, soil type, and weather conditions (data not shown). Diversity with respect to environments was important in order to produce sufficient variability to measure stability.

The environments included in this test encompassed a region suitable for production of the four parents, ‘i.e.’ the area of adaptation. The number of environments was also important. Maximizing the number of environments increases the precision with which stability is measured while increasing the probability of repeatable data.

There was a significant population x environment interaction with respect to yield (Table 2). The interaction mean square was 1.5 times larger than error but only 1.0 and 2.7% as large as the environment and population mean squares, respectively. Significant interactions are not unexpected when conducting experiments over several years and many environments and were deemed sufficiently small to report main effects. Further analysis indicated that the interaction is a product of the relationship between the hybrids and hybrid blends and their change in rank from low-yielding to high-yielding environments (Figure 1). This interaction becomes non-significant when the two highest yielding environments are removed from the analysis (data not shown).

Coefficient of Variation

Maturity group did not affect stability rating. DP51 and ST474, early to medium-maturity varieties, had different CV values (23.9 and 21.0 respectively) (Table 3). LA887 and FM989, medium to full-season varieties, also had dissimilar CV values (21.3 and 24.0 respectively). The hybrids and blends of the hybrids had a significantly lower CV values when compared to the parents and blends of parents (Table 4). Comparing individual population components revealed no difference between the homogeneous (parents and hybrids) and heterogeneous (blends of parents and blends of hybrids) populations with respect to CV; however, the heterozygous population (hybrids and blends of hybrids) had significantly lower CV values compared to the homozygous population (parents and blends

of parents) (Table 5). This indicated no association between blending genotypes and stability and an increase in stability associated with hybrid genotypes.

The lack of an increase in stability associated with blended entries could be due to a lack of complementary morphological or agronomic characteristics (Marshall and Brown, 1973) that could elicit a blend response in the correct environmental conditions. The most likely environments to observe a blend response would have been the low-yielding environments (Went, 1963). There was no association between environment and blend response, reinforcing the ineffectiveness of blending entries to increase stability (Table 3).

CV values within population types could not be tested using this method; however, values within population types differed considerably, indicating population structure could not singly account for differences in stability. The CV values also followed a relatively predictive model.

Rank Comparisons

The resulting rank of the CV values of the hybrid entries was generally comparable to the rank of the individual parental components (Table 3). Crossing the parents with the lowest CV, ST 474 and LA 887 (21.0 and 21.3 respectively), resulted in the hybrid (2x3) with the lowest CV (15.8). Combining the two parents with the highest CV, DP 51 and FM 989 (23.9 and 24.0 respectively), resulted in the hybrid (1x4) with the highest CV (20.7). Intermediate CV values for hybrid combinations did not follow the predicted pattern due to hybrids 1x2 and 1x3 having the same CV value. ST 474 (Entry 2) and LA 887 (Entry 3) had a 0.3 difference between CV values. When these parents were crossed with FM 989 (Entry 4), there was a 0.3 difference between the hybrids. Conclusions may be more definitive using parental genotypes with more diverse CV values.

No specific trend was observed when comparing each entry in the parental blends to the corresponding components that made up each blend. DP 51 + FM 989 (1+4) had the highest CV for all entries (26.0) and is a blend of the two parents with the highest CV for yield stability (Table 3). Blending the two parents with the lowest CV (ST 474 and LA 887) resulted in the fourth lowest CV for parental blends (21.9); however, the difference between the CV measures from rank 1 to 4 was 0.6, indicating observations made on a group of parents with more diverse CV values may result in more predictable rankings. Three parental blends resulted in a decrease in CV when compared to the parental mid-component (Entries 1+2, 1+3, and 2+4) and three parental blends resulted in an increase in CV (Entries 1+4, 2+3, and 3+4), indicating no blend effect on CV associated with parental blends.

No trend was observed for the blends of hybrids. Blending the hybrids with the lowest CV (ST 474 x LA 887 and DP 51 x LA 887) resulted in the seventh lowest CV among blends of hybrids (Entry 23). Blending the two hybrids with the highest CV (DP 51 x FM 989 and LA 887 x FM 989) produced the blend with the ninth highest CV (Entry 28). Hybrid blends had higher CV values than their collective components, indicating an increase in variation associated with blending; however, this increase was not large for most CV values, averaging 1.9 over all 15 genotypes (Table 3).

Impact on Yield

Maturity groups were significantly different for yield (1309 vs. 1248 kg/ha for early and full-season cultivars, respectively; $P>0.01$). Early-season varieties yielded more than the full-season varieties due to the large lint yield of ST474 relative to all other parental genotypes (Table 3). Yield for each population type over environments was significantly different with the two heterozygous populations having a significantly higher yield than both

homozygous populations (Table 4). There was no difference between hybrids and hybrid blends or between parents and parental blends. This can also be seen when the population components are separated and compared directly (Table 5). There was no significant difference for mean yield when comparing the homogeneous and heterogeneous populations but there was a significant difference for mean yield when comparing the homozygous and heterozygous populations. Yields improved with an increase in genetic diversity within individual plants but did not improve with an increase in genotypic diversity among plants.

There was no clear trend for yield response in either blends of parents or blends of hybrids. Responses for blends of parents ranged from 41 kg/ha to -10 kg/ha and averaged 6.4 kg/ha (Table 3). Responses ranged from a 53 kg/ha to -45 kg/ha and averaged 9.1 kg/ha for blends of hybrids. There was no difference between the heterogeneous and homogeneous populations with respect to lint yield, indicating there was no benefit in blending entries (Table 5).

The percent blend response for each entry in each environment was correlated with environmental yield. Significant negative correlations should indicate a positive blend response in an unfavorable environment, 'i.e.', as mean yields decrease, the response of blended genotypes increase. Correlations for blends of parents ranged from -0.23 to 0.17 and were non-significant (Table 3). Correlation coefficients for blends of hybrids ranged from -0.15 to 0.67. Hybrid blend 5+9 had a significantly positive correlation coefficient as well as the highest CV for yield when compared to all other hybrid blends. The combination of inconsistent blend responses and the non-association of blend response and environmental means indicated that blending entries was not advantageous with respect to lint yield.

Standard Deviation

Standard deviations were calculated for each entry (Table 3). As means increase, variation often increases; however, the SD of the hybrids was significantly less than all other groups (Table 4). This, in itself, indicated the hybrid population was the most stable population type, regardless of mean yield. There was no significant difference for SD between parents, blends of parents, and blends of hybrids. Comparing individual components of each population type, there was no significant difference between the homogeneous and heterogeneous populations, but the heterozygous populations had a significantly lower SD than the homozygous populations (Table 5). The difference can be attributed to heterosis and is discussed below.

Heterosis

Significant improvement in yield stability may stem from the ability of each heterozygous genotype to yield well in unfavorable environments (Figure 2). The range of values for hybrids was lower than that of the parents and blends of parents resulting in significantly decreased SD and increased mean, which, in turn, increased stability. Similar trends were observed for the blends of hybrids; however, the reduction in the SD was not significant.

The heterosis observed for the hybrids was significant and negatively correlated with mean environment yield, where mid-component heterosis was evident in unfavorable environments and negligible in high-yielding environments. Plotting the average heterosis for each hybrid over three types of environments that represent the low, moderate, and high-yielding areas revealed an obvious decline in heterosis as mean yields increase (Figure 3).

The low-yielding environments had a significantly higher heterosis than the moderate and high-yielding environments (Table 6).

DP 51 x FM 989 (1x4) had the lowest yield stability among all hybrid genotypes and the lowest heterosis observed for the low-yielding environments (Table 6). ST 474 x LA 887 (2x3) had the highest yield stability and the second highest heterosis, indicating heterosis cannot explain all of the variation observed in yield stability for the hybrid genotypes. These two parents were very closely related ($CP = 0.37$, Table 7) and yet had high heterosis. Degree of heterosis and relatedness were not correlated (Tables 3 and 7).

Miller and Lee (1964) found decreasing levels of lint yield heterosis with increasing environmental means. They attributed this to similar hybrid response over all environments where the relative percent heterosis declined as parental means increased. Hawkins et al. (1965) also found increasing heterosis associated with decreasing environmental mean. Heterotic response, however, was not consistent across environments resulting in 35.0, 16.6, and 9.2% high-parent heterosis for environments that had parental means of 573, 636, and 897 lbs lint/acre respectively. This illustrated that heterosis and heterotic response decreased with increasing environmental mean.

Hybrid mid-component heterosis for yield was calculated at each environment and correlated with environmental means. Hybrids 1x2, 1x3, 2x3, 2x4, and 3x4 had significant negative correlations (Table 3). Averaged over all hybrids, the correlation was -0.72. This negative correlation supported the finding of decreasing heterosis with increasing environmental means. Hybrid 1x4 was negatively correlated with mean yield, but not significantly due to a weak heterotic response in the lowest-yielding environmental class (Table 6) (Figure 3).

There was a strong association between heterosis and environment mean and the effect each had on stability. The exact interaction is difficult to interpret with these data. One can clearly see that heterosis decreased as environmental yields increased (Figure 3). This may be attributed to a physiological response for hybrids in all environments that becomes less advantageous with increasing environmental quality. For example, a faster growing hybrid population could take full advantage of favorable environmental conditions early in the season and be better prepared for unfavorable conditions (drought, insects) occurring later in the season. This could result in increased yields and stability relative to the parents. The opposite of this would occur under favorable environmental conditions where any advantage associated with increased rate of growth would be negated by parental genotypes exploiting a full-season of favorable conditions (Went, 1953). Wells et al. (1988) observed leaf area and plant photosynthesis in hybrid and parental genotypes and attributed increased leaf area index of the hybrids to increased growth during the seedling stage. Leaf area and photosynthesis measurements taken early in plant development were significantly correlated. The early development of hybrids resulted in faster growth and bigger plants due to better light interception, resulting in more photosynthate production. Wells and Meredith (1986) found hybrids produced more lint and matured earlier than parental genotypes. Final leaf area index and total dry weight for hybrids were also greater than the parents and were attributed to the hybrids having a faster growth rate during the seedling stage.

Conclusions

The heterozygous populations had significantly greater yield stability than the homozygous populations. This was attributed to the heterozygous populations having a higher yield in the lower-yielding environments as compared to the homozygous populations.

This decreased the range of mean yield values over all environments and resulted in increased mean yields and smaller SD. Assuming an efficient method for producing hybrid cotton cultivars was available, hybrid cultivars should be a viable option for commercial production to decrease observed losses in low-yielding environments. Several male-sterile crossing systems are currently available (Meyer, 1975; Jia, 1990; Stewart, 1992; Meshram et al, 1994; Yuan et al., 1996); however, hybrid cotton grown in India and China is mainly produced through hand emasculation and pollination (Phipps, B. J., 2000, personal communication; Dong et al., 2004).

Future work should be based on quantifying the cause of increased stability. Heterosis for lint yield was negatively correlated with environmental mean yield and should be studied to determine the source of the difference between parents and hybrids for this trait. Two possible studies are: 1) determine the total number of fruiting sites and number of bolls produced in each population type to establish if differences were due to boll retention or boll production; 2) monitor plant growth and development during emergence, pre-bloom, full-bloom, and boll development to determine differences in growth potential. It would be important to conduct these experiments over several environments that include diverse environmental conditions.

Literature Cited

- Allard, R. W. 1960. Relationship between genetic diversity and consistency of performance in different environments. *Crop Sci.* 1:127-133.
- Allard, R. W., and A. D. Bradshaw. 1964. Implications of genotypes-environmental interactions in applied plant breeding. *Crop Sci.* 4:503-508.
- Becker, H. C. 1981. Correlations among some statistical measures of phenotypic stability. *Euphytica* 30:835-840.
- Becker, H. C., and J. Leon. 1988. Stability analysis in plant breeding. *Plant Breeding* 101:1-23.
- Bowman, D. T. 1999. Measured crop performance – cotton. *Crop Sci. Res. Rep.* No. 182. N.C. State University.
- Clay, R. E., and R. W. Allard. 1969. A comparison of the performance of homogeneous and heterogeneous barley populations. *Crop Sci.* 9:407-412.
- Dong, H., W. Li, W. Tang, and D. Zhang. 2004. Development of hybrid Bt cotton in China – A successful integration of transgenic technology and conventional techniques. *Curr. Sci.* 86(6):778-782.
- Eberhart, S.A., and W.A. Russell. 1966. Stability parameters for comparing varieties. *Crop Sci.* 6:36-40.
- Finlay, K. W., and G. N. Wilkinson. 1963. The analysis of adaptation in a plant-breeding programme. *Aust. J. Agric. Res.* 14:742-754.
- Francis, T. R., and L.W. Kannenberg. 1978. Yield stability studies in short-season maize. I. A descriptive method for grouping genotypes. *Can. J. Plant Sci.* 58:1029-1034.
- Funk, C. R., and J. C. Anderson. 1964. Performance of mixtures of field corn (*Zea mays* L.) hybrids. *Crop Sci.* 4:353-356.
- Haldane, J. B. S. 1954. The biochemistry of genetics. The MacMillan Co. New York.
- Hausmann, B. I. G., A. B. Obilana, P. O. Ayiecho, A. Blum, W. Schipprack, and H. H. Geiger. 2000. Yield and stability of four population types of grain sorghum in a semi-arid area of Kenya. *Crop Sci.* 40:319-329.
- Hawkins, B. S., H. A. Peacock, and W. W. Ballard. 1965. Heterosis and combining ability in upland cotton—effects on yield. *Crop Sci.* 5:543-546.

- Jia, Z. C. 1990. The development of cytoplasmic male sterile line 104-7A and its three line. *Chin. Cottons* 17(6):11-12.
- Kang, M. S. 1990. Understanding and utilization of genotype-by-environment interaction in plant breeding, pp. 52-68, In M. S. Kang (ed), *Genotype-By-Environment Interaction and Plant Breeding*. Louisiana State Univ., Baton Rouge.
- Kohel, R. J. 1969. Phenotypic stability of homozygous parents and their F₁ hybrids in upland cotton, *Gossypium hirsutum* L. *Crop Sci.* 9:85-88.
- Kohel, R. J., and T. G. White. 1963. An analysis of the variability of five parents and their F₁ progenies in *Gossypium hirsutum* L. *Crop Sci.* 3:359-361.
- Leon, J. 1991. Heterosis and mixing effects in winter oilseed rape. *Crop Sci.* 31:281-284.
- Lewis, D. 1954. A relationship between dominance, heterosis, phenotypic stability and variability. *Heredity* 8:333-356.
- Lin, C. S., M. R. Binns, and L. P. Lefkovitch. 1986. Stability analysis: where do we stand? *Crop Sci.* 26:894-900.
- Marshall, D. R., and A. H. D. Brown. 1973. Stability of performance of mixtures and multilines. *Euphytica* 22:405-412.
- Meshram, L. D., R. A. Ghongade, and W. M. Marawar. 1994. Development of male sterile systems from various sources in cotton (*Gossypium* spp.). *P. K. V. Res. J.* 18(1):83-86.
- Meyer, V. G. 1975. Male sterility from *Gossypium harknessii*. *J. Heredity.* 66:23-27.
- Miller, P. A., and J. A. Lee. 1964. Heterosis and combining ability in varietal top crosses of upland cotton, *Gossypium hirsutum* L. *Crop Sci.* 4:646-649.
- Opondo, R. M., and G. A. Ombakho. 1997. Yield evaluation and stability analysis in newly selected 'KSA' cotton cultivars in western Kenya. *African Crop Science Journal* 5(2):119-125.
- Peterson, C. J., J. M. Moffatt, and J. R. Erickson. 1997. Yield stability of hybrid vs. pureline hard winter wheats in regional performance trials. *Crop Sci.* 37:116-120.
- Quisenberry, J. E., and R. J. Kohel. 1971. Phenotypic stability of cotton. *Crop Sci.* 11:827-829.
- Rasmusson, D. C. 1968. Yield and stability of barley populations. *Crop Sci.* 8:600-602.

- Reich, V. H., and R. E. Atkins. 1970. Yield stability of four population types of grain sorghum, *Sorghum bicolor* (L.) Moench, in deferent environments. *Crop Sci.* 10:511-517.
- Schnell, F. W., and H. C. Becker. 1986. Yield and yield stability in a balanced system of widely differing population structures in *Zea mays* L. *Plant Breeding* 97:30-38.
- Shank, D. B., and M. W. Adams. 1960. Environmental variability within inbred lines and single crosses of maize. *J. Genet.* 57:119-126.
- Shukla, G. K. 1972. Some statistical aspects of partitioning genotype –environmental components of variability. *Heredity* 29:237-245.
- Smith, G. A. and W. H. Foote. 1970. Effect of heterozygosity on phenotypic stability in spring barley. *Can. J. Plant Sci.* 50:97-101.
- Smithson, J. B, and J. M. Lenne. 1996. Varietal mixtures: a viable strategy for sustainable productivity in subsistence agriculture. *Ann. Appl. Biol.* 128:127-158.
- Sneller, C. H. 1994. SAS programs for calculating coefficient of parentage. *Crop Sci.* 34:1679-1680.
- Stelling, D., E. Ebmeyer, and W. Link. 1994. Yield stability in faba bean, *Vicia faba* L. 2. Effects of heterozygosity and heterogeneity. *Plant Breeding* 112:30-39.
- Stewart, J. McD. 1992. A new cytoplasmic male sterile and restorer for cotton. p. 610. In *Proc. Beltwide Cotton Conf.*, Nashville, TN 6-10 Jan. 1992. National Cotton Council of America, Memphis TN.
- Wells, R., and W. R. Meredith, Jr. 1986. Heterosis in upland cotton. I. Growth and leaf area partitioning. *Crop Sci.* 26:1119-1123.
- Wells, R., W. R. Meredith, Jr., and J. R. Williford. 1988. Heterosis in upland cotton. II. Relationship of leaf area to plant photosynthesis. *Crop Sci.* 28:522-525.
- Went, F. W. 1953. Gene action in relation to growth and development. I. Phenotypic variability. *Proceedings of the National Academy of Sciences of the United States of America* 39(8):839-848.
- Wricke, G. 1962. Uber eine Methode zur Erfassung der okologischen Streubreite in Feldversuchen. *Z. Pflanzenzuchtg.* 47:92-96.
- Yates, F. and W.G. Cochran. 1938. The analysis of groups of experiments. *J. Agric. Sci. (Camb.)* 28:556-580.

Yuan, J., A. Zhang, K. L. Liu, X. R. Hao, and H. F. Wang. 1996. The discovery and observation of sterility and nuclear cytoplasmic interactions in cotton variety. *Jin-A. Acta Agric. Boreali Sinica* 11(4):29-32.

Table 1. Environments used in the stability study and the mean lint yield performance of all entries at each environment.

Location	Year	State	Mean (kg/ha)	Soil Classification
Clayton	2004	NC	1784	Fine-Loamy, Kaolinitic, Thermic Typic Kandiudults
Clayton Late	2005	NC	1722	Fine-Loamy, Kaolinitic, Thermic Plinthic Paleudults
Clayton Early	2005	NC	1676	Fine-Loamy, Kaolinitic, Thermic Plinthic Paleudults
Hartsville	2004	SC	1624	Fine-Loamy, Kaolinitic, Thermic Typic Kandiudults
Rocky Mount	2004	NC	1496	Fine-Loamy, Siliceous, Subactive, Thermic Aquic Paleudults
Rocky Mount	2005	NC	1487	Fine-Loamy, Siliceous, Subactive, Thermic Aquic Paleudults
Rocky Mount	2000	NC	1474	Fine-Loamy, Siliceous, Semiactive, Thermic Aeris Paleaquults
Bossier City	2004	LA	1459	Very Fine, Smectitic, Thermic Oxyaquic Hapluderts
Bertie	2000	NC	1425	Fine-Loamy, Siliceous, Subactive, Thermic Aquic Paleudults/Fine-Loamy, Siliceous, Semiactive, Thermic Aeris Paleaquults
Scotland	2004	NC	1379	Fine, Kaolinitic, Thermic Typic Paleudults
Hartsville	2000	SC	1293	Fine-Loamy, Kaolinitic, Thermic Typic Kandiudults
Bertie	2004	NC	1286	Fine-Loamy, Kaolinitic, Thermic Typic Kandiudults
Bertie	2005	NC	1229	Fine-Loamy, Kaolinitic, Thermic Typic Kandiudults
Bossier City	2005	LA	1212	Coarse-Silty Over-Clayey, Mixed Over Smectitic, Superactive, Calcareous, Thermic Oxyaquic Udifluvents
Auburn	2005	AL	1108	Fine-Loamy, Siliceous, Semiactive, Thermic Typic Hapludults
Scotland	2005	NC	1013	Fine, Kaolinitic, Thermic Typic Paleudults
Pee Dee	2005	SC	982	Fine-Loamy, Siliceous, Subactive, Thermic Aquic Paleudults
Keiser	2005	AR	950	Very Fine, Smectitic, Thermic Chromic Epiaquert
LSD $\alpha=.05$			53	

Table 2. Source, degrees of freedom, mean square, and significance for main effects and interactions for lint yield.

Source	DF	Mean Squares	F value	P value
Environments	17	3195525	21.88	<.0001
Reps(Environments)	21	156727	8.53	<.0001
Populations	3	1229483	65.50	<.0001
Populations x Environments	51	33762	1.50	0.017
Entry(Population)	27	104729	5.58	<.0001
Entry(Population) x Environment	459	22516	1.20	0.019
Error	601	18770

Figure 1. Linear trends for lint yield of each population type regressed on the overall mean lint yield of 18 environments.

Table 3. Mean, standard deviation, coefficient of variation, blend response, heterotic response, percent heterosis, and correlation coefficients for percent response and environmental index.

Entry	Genotype or Genotypic Combination	Mean (kg/ha)	SD	CV	Blend Response (kg/ha)	Percent Blend Response	Correlation of Percent Blend Response with Environmental Index	Heterotic Response and (kg/ha)	Percent Heterosis	Correlation of Percent Heterosis with Environmental Index
1	DP 51	1196	286	23.9	.	.	.	.	.	.
2	ST 474	1422	299	21.0	.	.	.	.	.	.
3	LA 887	1210	258	21.3	.	.	.	.	.	.
4	FM 989	1286	308	24.0	.	.	.	.	.	.
5	1x2	1382	233	16.8	.	.	.	72†	7.6†	-0.45†
6	1x3	1341	225	16.8	.	.	.	138*	12.8*	-0.60*
7	1x4	1347	279	20.7	.	.	.	106*	9.7*	-0.33
8	2x3	1467	232	15.8	.	.	.	150*	12.9*	-0.64*
9	2x4	1485	255	17.2	.	.	.	131*	11.3*	-0.66*
10	3x4	1378	242	17.5	.	.	.	130*	12.6*	-0.44†
11	1+2	1307	278	21.3	-2	0.5	-0.15	.	.	.
12	1+3	1244	265	21.3	41	3.9	-0.06	.	.	.
13	1+4	1254	326	26.0	13	1.1	0.13	.	.	.
14	2+3	1320	289	21.9	3	0.9	-0.15	.	.	.
15	2+4	1356	290	21.4	2	0.6	-0.23	.	.	.
16	3+4	1238	305	24.6	-10	-0.6	0.17	.	.	.

†, * Significantly different from zero at the 0.1 and 0.05 level of probability respectively.

Table 3. Continued.

Entry	Genotype or Genotypic Combination	Mean (kg/ha)	SD	CV	Blend Response (kg/ha)	Percent Blend Response	Correlation of Percent Blend Response with Environmental Index	Heterotic Response (kg/ha)	Percent Heterosis	Correlation of Percent Heterosis with Environmental Index
17	5+6	1415	255	18.0	53	4.1	0.05	159*	14.1*	-0.50*
18	5+7	1388	304	21.9	24	1.4	0.42	113*	9.6*	-0.14
19	5+8	1409	266	18.9	-16	-1.4	0.32	96*	8.5*	-0.29
20	5+9	1394	327	23.5	-39	-3.7	0.67*	62†	4.7	0.14
21	5+10	1416	252	17.8	36	2.7	0.10	137*	12.2*	-0.48*
22	6+7	1388	278	20.0	45	3.5	0.14	166*	14.6*	-0.26
23	6+8	1359	253	18.6	-45	-3.3	0.24	99*	8.9*	-0.38
24	6+9	1425	258	18.1	12	1.1	0.09	147*	13.0*	-0.46†
25	6+10	1349	232	17.2	-10	-0.5	-0.15	123*	11.7*	-0.55*
26	7+8	1409	262	18.6	2	0.6	-0.03	130*	11.6*	-0.41
27	7+9	1409	274	19.5	-7	-0.5	0.14	111*	9.8*	-0.43
28	7+10	1389	271	19.5	27	2.3	0.05	144*	12.9*	-0.39
29	8+9	1451	274	18.9	-25	-1.9	0.40	116*	9.5*	-0.36
30	8+10	1457	289	19.8	34	2.0	0.38	174*	14.2*	-0.25
31	9+10	1476	298	20.2	45	2.9	0.37	175*	14.5*	-0.28

†, * Significantly different from zero at the 0.1 and 0.05 level of probability respectively.

Table 4. Mean lint yield, standard deviation, and coefficient of variation among population types.

Population	Mean (kg/ha)	SD	CV
Parents	1279	288	22.6
Hybrids	1400	244	17.5
Blends of Parents	1286	292	22.8
Blends of Hybrids	1408	273	19.4
LSD $\alpha=.05$	31	26	2.0

Table 5. Mean lint yield, standard deviation, and coefficient of variation between population components.

Variation	Population Components	Mean (kg/ha)	SD	CV
Inter-genic	Homogeneous	1351	261	19.5
	Heterogeneous	1374	278	20.3
	LSD $\alpha=.05$	43	18	1.4
Intra-genic	Homozygous	1283	290	22.7
	Heterozygous	1406	265	18.8
	LSD $\alpha=.05$	43	18	1.4

Figure 2. The mean lint yield of the four population types in each of 18 environments.

Figure 3. Change in heterosis from high heterosis in low-yielding environments to low heterosis in high-yielding environments.

Table 6. Percent heterosis of lint yield for each hybrid, average heterosis, and environmental means in low, moderate, and high-yielding environments.

Environmental classification	Hybrid						Average Heterosis	Environmental Mean (kg/ha)
	1x2	1x3	1x4	2x3	2x4	3x4		
Low	15.1	18.9	12.8	19.9	18.1	21.6	17.7	965
Moderate	8.7	13.1	10.4	10.6	12.6	6.1	10.2	1236
High	-1.0	6.5	5.8	8.4	3.3	10.1	5.5	1455
LSD $\alpha=.05$							6.0	45

Table 7. Coefficient of parentage
between parental genotypes.

	Parental Genotypes		
	DP51	ST474	LA887
ST474	0.15		
LA887	0.17	0.37	
FM989	0.08	0.03	0.10

CHAPTER III

Impact of Heterozygosity and Heterogeneity on Cotton (*Gossypium hirsutum* L.)

Lint Yield Stability: II. Lint Yield Components

Abstract

In order to determine which yield components may contribute to yield stability, an 18-environment field study was undertaken to observe the mean, standard deviation (SD), and coefficient of variation (CV) for lint yield components in population types that differed for lint yield stability. This difference resulted in the hybrids and blends of hybrids (heterozygous populations) being more stable than the parents and blends of parents (homozygous populations). No within-boll component showed convincing evidence of differences between population types with respect to CV values. The CV values observed for bolls/hectare followed the same trend as lint yield in which the heterozygous populations were more stable than homozygous populations. This trend was also observed for the mean number of bolls/hectare. Heterosis for boll production was not consistent across locations and declined with increasing environmental mean. Ultimately, the difference between population types, with respect to yield and stability, was attributed to the heterozygous entries producing more bolls in the low-yielding environments while producing numbers that were similar to the homozygous populations in the high-yielding environments. This reduced the range of lint yield, reduced the variation across locations, and resulted in increased lint yield stability.

Introduction

Cotton lint yield/boll is the multiplicative product of mean fiber length, weight/length, fibers/unit surface area, and seed surface area (Worley et al., 1976) (Figure 1). The combination of these components forms more complex yield structures that ultimately coalesce into lint/boll (Worley et al., 1976; Manner et al., 1971; Kerr, 1966). Total lint yield/unit of land area is made up of bolls/unit of land area and lint/boll. The number of bolls/unit of land area represents the number or volume of lint forming units and is not considered a within-boll yield component. Selection for specific yield components will cause a cascade of changes due to correlations between many traits that ultimately may work together to influence lint yield or counteract one another, causing no change in lint yield (Cole, 2003; Smith and Coyle, 1997; Green and Culp, 1990; Harrell and Culp, 1976; Worley et al., 1976; Culp and Harrell, 1975; Meredith and Bridge, 1973; Worley et al., 1974; Bridge et al., 1971; Miller and Rawlings, 1967; Kerr, 1966).

Lewis et al. (2000) studied yield components during 1970-1985 and 1985-1998 to address the decrease in the rate of yield improvement. The comparisons revealed the obsolete cultivars produced more fibers/seed and the modern cultivars produced more seeds/acre. The authors also noted that lint yield in the 1990's was four times as variable as yield in the 1970's and attributed this increase in variation to the importance the more recent cultivars placed on the number of seeds/acre produced with respect to lint yield. They concluded that selecting for an increased number of fibers/seed and a decreased number of seeds/acre should result in similar lint yields at a lower energy cost to the plant, translating into a more stable variety over environments.

We studied the impact of various levels of intra- and inter-genic diversity on lint yield stability using four population types that represented four different combinations of genetic variation that included: pure-line cultivars (homozygous/homogeneous), two-component blends of pure-line cultivars (homozygous/heterogeneous), hybrid combinations of the pure-line cultivars (heterozygous/homogeneous), and two-component blends of the hybrid combinations (heterozygous/heterogeneous). We found that the four population types differed significantly for yield and stability with the hybrids and blends of hybrids being more stable and having a higher yield than the parents and blends of parents. This difference in yield and stability was attributed to heterosis that diminished as the environmental yields increased. This negative correlation reduced the range of observed values for the heterozygous populations over environments, increasing the mean, and decreasing the SD.

The objective of this study was to determine the relative contribution of yield components to overall yield stability in population types that differ for intra-population genetic variability.

Materials and Methods

Four commercial cultivars, ‘Delta Pine 51’ (DP 51), ‘Stoneville 474’ (ST 474), ‘Stoneville LA 887’ (LA 887), and ‘Fiber Max 989’ (FM 989), were chosen for this experiment based on perceived stability and maturity. DP 51, ST 474, and LA 887 were thought to be relatively stable over years and locations (Bowman, D. T., 2006, personal communication). FM 989 was known to be a high-yielding cultivar (Bowman, 1999). Maturity could influence final lint yield in differing environmental conditions. Parents

were chosen to represent equal divisions of early (DP 51 and ST 474) and full-season (LA 887 and FM 989) maturity groups. The coefficient of parentage (CP) values of parental material was calculated after the entries were selected to determine diversity of parental material (Sneller, 1994). The CP is a measure of the relatedness between two individuals reported as the proportion of alleles that are identical by descent.

Parents were crossed in a diallel excluding self-pollinations in 1999, 2000, and 2004. Reciprocal crosses were bulked. Parental lines were obtained from commercially available seed stock. Entries included four parents, six hybrids, six parental blends, and the 15 hybrid blends. Entries were tested at 21 environments; however, two environments, one in Mississippi in 2000 and one in Georgia in 2004 were lost, while one environment in South Carolina in 2005 was discarded due to extreme variability among entries. Each location-by-year combination was treated as a single environment totaling 18 environments (Table 1).

All entries were grown as two-row plots and were arranged in a randomized, complete block design with three replicates in 2000 and two replicates in 2004 and 2005. Plot length ranged from 8.5m to 13.7m and row spacing ranged from 91.4 cm to 101.6 cm. Planting dates ranged from April 28 to May 21 and harvest dates ranged from September 17 to October 28. Plots were grown under rain fed conditions and cultural practices were implemented as needed and consistent with farming practices standard for each location.

Twenty-five well-developed first position bolls were collected from each plot. Plots were machine harvested and weighed for seed cotton yield. Samples were ginned

on a 10-saw laboratory gin. Seeds and lint were weighed to determine seed weight, lint weight, lint percent, and boll weight. The number of bolls/hectare was calculated by dividing seed cotton weight by boll weight. The number of seeds/boll was determined using an electronic seed counter. Seed index was the weight of 100 delinted seeds and was calculated by dividing the total seed weight by the number of seeds and multiplying by 100. Fibers/seed, lint cotton/seed, and weight/fiber were calculated using formulas described by Worley et al. (1976). Approximately 15g of lint from each sample were collected and sent to Cotton Inc. to measure micronaire and upper half mean (UHM) length. Mid-parent heterosis was calculated as the difference between a hybrid entry and the corresponding mid-parent, divided by the mid-parent, and multiplied by 100.

The SD and CV of lint yield components were calculated for each entry over environments and replicates, resulting in one observation/entry. Standard deviation, CV, and lint yield component values were subjected to ANOVA using the general linear model procedure of SAS version 9.1 to determine differences between population types. Population types and entries were considered fixed effects; locations were deemed random effects. The CV was calculated using the formula: $CV = (s/\mu) \times 100$ where s is the SD and μ is the overall mean. Mean separation was conducted using Fisher's protected least significant difference (LSD) at the 0.05 level of probability.

Results and Discussion

Parental Material

The CP values averaged 0.15 and ranged from 0.03 (ST 474 & FM 989) to 0.37 (ST 474 & LA 887) (Table 2), indicating a broad range of allelic variation among

parents. Parents were significantly different for all measured within-boll components (Table 3).

Maturity groups were significantly different for all traits measured, excluding lint percent (Table 4). Early-season varieties had higher values for bolls/hectare, micronaire, and weight/fiber than full-season varieties; however, full-season varieties had higher values for all other significantly different traits.

Coefficient of Variation

CV values were calculated for each entry over environments and then compared statistically between population types for the traits of interest. Significant differences were only found for bolls/hectare.

The number of bolls/hectare was more stable in the heterozygous populations than the homozygous populations (Table 5). The stability of the heterozygous populations for bolls/hectare was mirrored in total lint yield stability and was not a surprising result since bolls/hectare is the major component of total lint yield (Worley et al., 1974; Manner et al., 1971).

The lack of variation between population types for CV values of within-boll components that are known to affect lint yield is an indication that these traits did not contribute to an increase in lint yield stability. Observing the trends between groups does not yield any additional information relative to divisions between diversity groups. The CV is a ratio of the SD to the mean. These measurements could lend more information relative this result.

Yield Components

Boll weight differed significantly, with the hybrids and blends of hybrids having a higher weight than the parents and blends of parents (Table 6). This division was also observed for total lint yield and can be considered heterosis for boll weight.

Boll weight is the sum of seed weight/boll and lint weight/boll. Hybrids and blends of hybrids had a significantly higher seed weight/boll and lint weight/boll than parents and blends of parents; again, mirroring total lint yield and considered to be heterosis (Table 6).

Seed weight/boll is the product of weight/seed (seed index) and seeds/boll. Hybrids and hybrid blends had more seeds/boll than the parents and blends of parents (Table 6). For seed index, the hybrids had significantly heavier seed than the parents and blends of parents. The hybrid blends had a significantly heavier seed index than the blends of parents, but showed no difference when compared to the parents.

The hybrids and blends of hybrids had more lint weight/boll than the parents and blends of parents (Table 6). Lint weight/boll consists of seeds/boll and lint weight/seed. There was no difference between population types with respect to lint weight/seed. This trend was also observed for the components of lint weight/seed, which included fibers/seed and weight/fiber. There was significant variation among genotypes for fibers/seed; however, the differences did not fall between groups but were erratically dispersed throughout all entries (data not shown). For example, two parental genotypes, LA 887 and DP 51, had the highest and lowest number of fibers/seed respectively. Differences between population types for lint weight/boll may be associated with the

increased number of seeds/boll. This is also evident when considering that there was no variation detected among population types for lint percent. An increase in seeds/boll could increase the lint/boll without changing the number of fibers/seed or weight/fiber.

There were differences for UHM length between population types. The hybrids and blends of hybrids had significantly longer fibers than parents and blends of parents (Table 6). This separation was also evident for micronaire. The heterozygous populations had significantly lower micronaire values than the homozygous populations.

The hybrids and blends of hybrids had significantly higher numbers of bolls/hectare than the parents and blends of parents (Table 6). This, again, corresponded to the division observed for total lint yield.

On a total lint yield basis, the lack of variation among population types for fibers/seed and weight/fiber, coupled with an observed increase in the number of bolls/hectare and boll weight, revealed that yield was influenced by changes in individual plant yield potential with respect to boll production and boll weight and not by an increase in any within-boll fiber component. Meredith (1990), Meredith and Bridge (1972), Al-Rawi and Kohel (1969), Marani (1963), and Turner (1953) have documented an increase in lint yield due to heterosis for boll weight and number of bolls/measurement.

Correlations

Mid-parent heterosis for lint yield was observed in all environments; however, levels of heterosis declined as the environmental means increased (data not shown). This result was highlighted in the earlier paper and compared the relationship between lint

yield heterosis and environmental mean lint yield (correlation of -0.72). Following this outcome, we wanted to determine the relationship between within-boll components exhibiting significant heterosis and environmental mean yield. No within-boll component exhibited significant correlations between heterosis and mean environmental lint yield, indicating heterosis for within-boll components was consistent over environments (Table 7). The number of bolls/hectare was negatively correlated with environmental mean yield and mirrored the result of lint yield.

The non-association of environmental index and heterosis for within-boll components indicated that these traits did not contribute to the observed stability of the heterozygous populations; however, calculating the correlations among all measured traits could indicate intrinsic trends within all population types that lead to increases in stability.

Number of fibers/seed was highly correlated with lint weight/seed, seed index, lint percent, boll weight, and lint weight/boll (Table 8). Seed index is the weight of 100 seed and can be affected by seed density, or more likely, seed dimensions. Seed index was also highly correlated with lint weight/seed. As seed size increased, the number of fibers increased, resulting in more fibers and fiber weight. These correlations did not result in an increase in lint yield. There was no correlation between lint yield and any within-boll component associated with fiber or seed yield.

The number of bolls/hectare was negatively correlated with boll size, seed weight/boll, lint weight/boll, seed index, seeds/boll, and positively correlated with lint yield. This was the only yield component that was positively correlated with overall

yield and can help explain the similar observations between the two traits for several measured statistics.

Micronaire was negatively correlated with UHM but positively correlated with lint percent and weight/fiber (Table 8). Upper half mean was negatively correlated with lint percent and weight/fiber. Lint percent was positively correlated with lint yield while no other lint characteristic showed an association.

These correlations revealed a different trend than the mean results. Correlations indicated that fiber characteristics and lint yield were not improved concomitantly, while the mean data indicated simultaneous increases in classically negatively correlated traits. Mean data also suggest simultaneous increases in boll weight and bolls/hectare; however, the number of bolls/hectare was negatively correlated with boll weight and all the components that compose it. These are indications that increases observed in the heterozygous populations for many components of lint yield occurred independently and may be a byproduct of increased numbers of bolls/hectare.

Standard Deviation

Results above indicated differences in mean values for most traits between population types; however, this did not bring about differences in CV. Differences between population types for SD may explain the lack of differences observed for CV.

Parents and blends of parents had a lower SD for UHM than blends of hybrids but were not different from hybrids (Table 9). There was no difference between the blends of hybrids and hybrids. The increase in SD was accompanied by an increase in mean UHM length (Table 6).

The number of bolls/hectare showed a decisive difference between population types for SD, with the heterozygous populations having lower values than the homozygous populations (Table 9). This was the only trait that fully separated the heterozygous and homozygous populations, reinforcing the increase in stability observed for the heterozygous populations when using the CV as the measure of stability.

The significant differences between mean values for several within-boll yield components were not observed for SD values. There were no trends associated with SD that showed division among population types for most within-boll components. The lack of diversity or structure between population types for SD and the minimal, but significant, differences for mean values of within-boll yield components may help explain the lack of diversity with respect to CV values.

Conclusions

Variation among population types for boll weight, seed weight/boll, lint weight/boll, seed index, seeds/boll, UHM, and micronaire was an indication that intra- and inter-genetic diversity significantly affected mean productivity of these traits. The non-association of heterosis for these components with mean environmental lint yield indicated heterosis was consistent across environments. The lack of variation for CV values of measured components among population types that are known to differ for stability indicated these components did not contribute to lint yield stability.

Heterosis for bolls/hectare was strongly correlated with environmental lint yield, such that heterosis for bolls/hectare increased as environmental lint yield decreased. This followed the same division observed for total lint yield. The number of bolls/hectare

showed significant variation among population types for CV, mean, and SD, indicating the heterozygous populations had a higher number of bolls and were more stable over environments. This also followed the division observed for lint yield. Worley et al. (1974) found that bolls/m² accounted for 94% of the variation observed in lint yield. It would follow that differences observed among population types for bolls/hectare would be similar to differences found for lint yield.

The number of fibers/seed did not contribute to yield stability and showed no variation among population types, even with significant differences for mean number of fibers/seed observed among parents. Differences in lint yield stability among population types were attributed to differences in number of bolls/hectare. Our findings contradict the proposed theory of stabilizing cotton yields by producing fewer seeds/acre and more fibers/seed. This result is realized when taking into account that lint weight/seed accounts for only 2.5% of total lint yield (Worley et al., 1974). The ultimate goal is to maximize yields in favorable environments while minimizing losses incurred in less favorable environments. This goal was achieved in part using F₁ hybrids that out-yielded parental genotypes in lower yielding environments by producing more harvestable fiber stemming from more bolls.

Literature Cited

- Al-Rawi, K. M., and R. J. Kohel. 1969. Diallel analyses of yield and other agronomic characters in *Gossypium hirsutum* L. Crop Sci. 9:779-783.
- Bridge, R. R., W. R. Meredith, Jr., and J. F. Chism. 1971. Comparative performance of obsolete varieties and current varieties of upland cotton. Crop Sci. 11:29-32.
- Bowman, D. T. 1999. Measured crop performance – cotton. Crop Sci. Res. Rep. No. 182. N.C. State University.
- Cole, C. B. 2003. Within-boll components of six genotypes of cotton and their F₁ and F₂ progeny. M.S. thesis. Mississippi State Univ. Mississippi State.
- Culp, T. W., and D. C. Harrell. 1975. Influence of lint percentage, boll size, and seed size on lint yield of upland cotton with high fiber strength. Crop Sci. 15:741-746.
- Green, C. C., and T. W. Culp. 1990. Simultaneous improvement of yield, fiber quality, and yarn strength in upland cotton. Crop Sci. 1990. 30:66-69.
- Harrell, D. C., and T. W. Culp. 1976. Effects of yield components on lint yield of upland cotton with high fiber strength. Crop Sci. 16:205-208.
- Kerr, T. 1966. Yield components in cotton and their interrelationships with fiber quality. Proc. 18th Cotton Improvement Conference. National Cotton Council of America, Memphis, TN.
- Lewis, H., L. May, and F. Bourland. 2000. Cotton yield components and yield stability. p.532-536. In P. A. Dagger and D. A. Richter (ed.) Proc. Beltwide Cotton Conf., San Antonio, TX. 4-8 Jan. 2000. National Cotton Council of America, Memphis, TN.
- Manner, B. A., S. Worley, D. C. Harrell, and T. W. Culp. 1971. A geometrical approach to yield models in upland cotton *Gossypium hirsutum* L. Crop Sci. 11:904-906.
- Marani, A. 1963. Heterosis and combining ability for yield and components of yields in a diallel cross of two species of cotton. Crop Sci. 3:552-555
- Meredith, W. R., Jr. 1990. Yield and fiber-quality potential for second-generation cotton hybrids. Crop Sci. 30:1045-1048.
- Meredith, W. R., Jr., and R. R. Bridge. 1972. Heterosis and gene action in cotton, *Gossypium hirsutum* L. Crop Sci. 12:304-310.
- Meredith, W. R., Jr., and R. R. Bridge. 1973. Yield, yield component and fiber property variation of cotton. Crop Sci. 13:307-312.

Miller, P. A., and J. O. Rawlings. 1967. Selection for increased lint yield and correlated responses in upland cotton, *Gossypium hirsutum* L. Crop Sci. 7:637-640.

Smith, C. W., and G. G. Coyle. 1997. Association of fiber quality parameters and within-boll yield components in upland cotton. Crop Sci. 37:1775-1779.

Sneller, C. H. 1994. SAS programs for calculating coefficient of parentage. Crop Sci. 34:1679-1680.

Turner, J. H., Jr. 1953. A study of heterosis in upland cotton. I. Yield of hybrids compared with varieties. Agron. J. 45:484-486.

Worley, S., T. W. Culp, and D. C. Harrell. 1974. The relative contributions of yield components to lint yield of upland cotton, *Gossypium hirsutum* L. Euphytica 23:399-403.

Worley, S., Jr., H. H. Ramey, Jr., D. C. Harrell, and T. W. Culp. 1976. Ontogenetic model of cotton. Crop Sci. 16:30-34.

Figure 1. Ontogenetic lint yield model.

Table 1. Environments used in the stability study and the mean performance of all entries at each environment.

Location	Year	State	Mean (kg/ha)	Soil Classification
Clayton	2004	NC	1784	Fine-Loamy, Kaolinitic, Thermic Typic Kandiudults
Clayton Late	2005	NC	1722	Fine-Loamy, Kaolinitic, Thermic Plinthic Paleudults
Clayton Early	2005	NC	1676	Fine-Loamy, Kaolinitic, Thermic Plinthic Paleudults
Hartsville	2004	SC	1624	Fine-Loamy, Kaolinitic, Thermic Typic Kandiudults
Rocky Mount	2004	NC	1496	Fine-Loamy, Siliceous, Subactive, Thermic Aquic Paleudults
Rocky Mount	2005	NC	1487	Fine-Loamy, Siliceous, Subactive, Thermic Aquic Paleudults
Rocky Mount	2000	NC	1474	Fine-Loamy, Siliceous, Semiactive, Thermic Aeris Paleaquults
Bossier City	2004	LA	1459	Very Fine, Smectitic, Thermic Oxyaquic Hapluderts
Bertie	2000	NC	1425	Fine-Loamy, Siliceous, Subactive, Thermic Aquic Paleudults/Fine-Loamy, Siliceous, Semiactive, Thermic Aeris Paleaquults
Scotland	2004	NC	1379	Fine, Kaolinitic, Thermic Typic Paleudults
Hartsville	2000	SC	1293	Fine-Loamy, Kaolinitic, Thermic Typic Kandiudults
Bertie	2004	NC	1286	Fine-Loamy, Kaolinitic, Thermic Typic Kandiudults
Bertie	2005	NC	1229	Fine-Loamy, Kaolinitic, Thermic Typic Kandiudults
Bossier City	2005	LA	1212	Coarse-Silty Over-Clayey, Mixed Over Smectitic, Superactive, Calcareous, Thermic Oxyaquic Udifluvents
Auburn	2005	AL	1108	Fine-Loamy, Siliceous, Semiactive, Thermic Typic Hapludults
Scotland	2005	NC	1013	Fine, Kaolinitic, Thermic Typic Paleudults
Pee Dee	2005	SC	982	Fine-Loamy, Siliceous, Subactive, Thermic Aquic Paleudults
Keiser	2005	AR	950	Very Fine, Smectitic, Thermic Chromic Epiaquert
LSD $\alpha=.05$			53	

Table 2. Coefficient of parentage between parental genotypes.

	Parental Genotypes		
	DP51	ST474	LA887
ST474	0.15		
LA887	0.17	0.37	
FM989	0.08	0.03	0.10

Table 3. Mean yield components for each parent over environments.

Trait	Unit	Genotype				LSD $\alpha=.05$
		DP 51	ST 474	LA 887	FM 989	
Boll Weight	g	5.34	5.05	6.30	5.60	0.20
Seed Weight/Boll	g	2.7	2.4	3.1	2.9	0.1
Lint Weight/Boll	g	2.1	2.2	2.6	2.3	0.1
Seed Index	g	8.65	8.75	9.70	9.22	0.23
Seeds/Boll	no.	31.4	27.9	32.2	31.7	1.3
Lint Weight/Seed	mg	67	78	81	73	2
Fibers/Seed	no.	14031	16430	17522	16144	438
Weight/Fiber	μ g	4.80	4.73	4.64	4.51	0.14
Lint Percent	%	40	43	42	41	0.01
Upper Half Mean	mm	29.2	28.0	29.3	29.4	0.3
Micronaire	value	4.9	5.1	4.7	4.6	0.1
Bolls/Hectare	no.	565093	649292	459447	555967	40369

Table 4. Maturity group means of parents for yield components.

Trait	Unit	Early	Full	LSD $\alpha=.05$
Boll Weight	g	5.20	5.95	0.12
Seed Weight/Boll	g	2.58	3.02	0.08
Lint Weight/Boll	g	2.16	2.48	0.05
Seed Index	g	8.70	9.46	0.19
Seeds/Boll	no.	29.7	31.9	0.9
Lint Weight/Seed	mg	72.6	77.0	1.9
Fibers/Seed	no.	15231	16833	291
Weight/Fiber	μg	4.77	4.58	0.11
Lint Percent	%	41.5	41.4	0.4
Upper Half Mean	mm	28.56	29.37	0.23
Micronaire	value	4.98	4.64	0.1
Bolls/Hectare	no.	607192	507707	21212

Table 5. The coefficient of variation values among population types for measured yield components.

Trait	CV				
	Parents	Hybrids	Blends of		LSD $\alpha=.05$
			Parents	Hybrids	
Boll Weight	9.4	9.0	10.2	9.0	1.2
Seed Weight/Boll	9.5	8.7	10.0	9.3	1.6
Lint Weight/Boll	10.0	9.8	11.3	10.1	1.2
Seed Index	5.1	5.1	5.3	5.0	0.9
Seeds/Boll	7.5	6.2	7.9	6.7	1.7
Lint Weight/Seed	7.4	7.2	7.9	7.6	1.0
Fibers/Seed	6.1	6.3	6.4	6.6	1.0
Weight/Fiber	5.6	6.0	5.8	5.6	1.0
Lint Percent	2.5	3.0	2.9	3.0	0.4
Upper Half Mean	2.4	2.5	2.4	2.8	0.4
Micronaire	6.4	7.4	6.6	7.0	1.0
Bolls/Hectare	19.5	14.8	18.7	14.7	2.5

Table 6. Mean values among population types for yield components.

	Unit	Means				LSD $\alpha=.05$
		Parents	Hybrids	Blends of Parents	Blends of Hybrids	
Boll Weight	g	5.57	5.83	5.56	5.82	0.10
Seed Weight/Boll	g	2.8	2.96	2.79	2.92	0.06
Lint Weight/Boll	g	2.32	2.41	2.31	2.41	0.04
Seed Index	g	9.08	9.19	9.03	9.14	0.10
Seeds/Boll	no.	30.5	32.2	30.8	32.0	0.54
Lint Weight/Seed	mg	74.8	74.8	74.8	75.1	1.3
Fibers/Seed	no.	16031	16051	16049	16053	290
Weight/Fiber	μg	4.67	4.66	4.66	4.68	0.05
Lint Percent	%	41	41	41	41	0.31
Upper Half Mean	mm	29.0	29.7	29.0	29.7	0.2
Micronaire	value	4.81	4.69	4.79	4.70	0.06
Bolls/Hectare	no.	557450	584008	557472	584479	14621
Lint Yield	kg/ha	1279	1400	1286	1408	31

Table 7. Correlation for percent heterosis of yield components with environmental mean.

Trait	Correlation
Boll Weight	-0.05
Seed Weight/Boll	0.01
Lint Weight/Boll	-0.04
Seed Index	-0.26
Seeds/Boll	0.10
Lint Weight/Seed	-0.33
Fibers/Seed	-0.35
Weight/Fiber	0.03
Lint Percent	0.05
Upper Half Mean	-0.10
Micronaire	0.08
Bolls/Hectare	-0.63**

** Significantly different from zero at the 0.01 level of probability.

Table 8. Correlation of yield components over genotypes.

	Boll Size	Seed Weight/ Boll	Lint Weight/ Boll	Seed Index	Seeds/ Boll	Lint Weight/ Seed	Fibers/ Seed	Weight/ Fiber	Lint Percent	Upper Half Mean	Micronaire	Bolls/ Hectare
Seed Weight/Boll	0.94*											
Lint Weight/Boll	0.92*	0.76*										
Seed Index	0.86*	0.82*	0.89*									
Seeds/Boll	0.79*	0.92*	0.51*	0.53*								
Lint Weight/Seed	0.35	0.07	0.67*	0.55*	-0.28							
Fibers/Seed	0.42*	0.22	0.71*	0.68*	-0.15	0.93*						
Weight/Fiber	-0.25	-0.40*	-0.2	-0.42*	-0.31	0.05	-0.32					
Lint Percent	-0.25	-0.47*	0.16	0.03	-0.73*	0.79*	0.70*	0.14				
Upper Half Mean	0.60*	0.76*	0.34	0.43*	0.84*	-0.34	-0.15	-0.46*	-0.67*			
Micronaire	-0.52*	-0.71*	-0.33	-0.49*	-0.71*	0.24	-0.06	0.80*	0.51*	-0.89*		
Bolls/Hectare	-0.64*	-0.60*	-0.55*	-0.62*	-0.46*	-0.21	-0.29	0.23	0.26	-0.14	0.21	
Lint Yield	0.05	-0.03	0.21	0.05	-0.07	0.3	0.25	0.09	0.40*	0.17	-0.06	0.69*

* Significantly different at the 0.05 level of probability.

Table 9. Standard deviation among population types for yield components.

Trait	Unit	Population Types				LSD $\alpha=.05$
		Parents	Hybrids	Blends of		
				Parents	Hybrids	
Boll Weight	g	0.52	0.52	0.57	0.52	0.08
Seed Weight/Boll	g	0.27	0.26	0.28	0.27	0.05
Lint Weight/Boll	g	0.23	0.24	0.26	0.24	0.03
Seed Index	g	0.46	0.47	0.47	0.45	0.09
Seeds/Boll	no.	2.32	1.99	2.44	2.14	0.52
Lint Weight/Seed	mg	5.55	5.45	5.88	5.74	0.86
Fibers/Seed	no.	983	1,017	1,023	1,068	165
Fiber Weight/Fiber	μ g	0.26	0.28	0.27	0.26	0.04
Lint Percent	%	0.010	0.013	0.012	0.012	0.002
Upper Half Mean	mm	0.702	0.734	0.710	0.834	0.115
Micronaire	value	0.31	0.35	0.32	0.33	0.05
Bolls/Hectare	no.	108883	86564	104129	86376	16092

APPENDIX

Regression Methods and Comments

Regression analysis was performed using the Proc Reg procedure in SAS as well as through functions in Excel. Regression analysis can be used to indicate stability or adaptation depending on how the regression coefficient (b-value) is interpreted. Regressing the mean of a genotype at each environment on the environmental mean will reveal the change in yield over environments relative to all other genotypes tested. A b-value of 1.0 indicates good adaptation to both high-yielding and low-yielding environments and is considered a Type II stability measure (Lin et al., 1986). A b-value >1.0 is a result of a genotype being well adapted to high-yielding environments and less adapted to low-yielding environments. A b-value of <1.0 shows the opposite where a genotype is adapted to low-yielding environments and less adapted to high-yielding environments. This scenario does not take into account the possibility that the two regression lines may not intersect and the genotype with a b-value <1.0 may have a mean yield that is greater than the genotype with a b-value of 1.0 or greater. In this case, the entry with the lower b-value will be better adapted at all locations.

Regression coefficients can also be a measure of stability, such that a b-value of zero is the most stable; this is considered Type I stability (Lin et al., 1986). The statistic can be viewed as the difference in yield from the low-yielding environment to the high-yielding environment. That difference can be observed as the range or variation over environments and decreases as the b-value decreases.

Observing the b-values of the four population types included in this study may

indicate stability as defined by Type I.

Regression Attributes

Regressing entry means on environmental means revealed differences between population types for the b-values. The hybrid population had a significantly lower b-value than all other population types (Table 1). This indicated that, relative to the mean of all entries in each environment, the hybrid population experienced the least change over environments. There was no difference between parents, blends of parents, and blends of hybrids. The heterogeneous populations had a significantly higher b-value than the homogeneous populations (Table 2). This can be attributed to the non-significant difference observed between the blends of parents and blends of hybrids and the significantly lower hybrid b-value. The heterozygous populations had a lower b-value and can also be attributed to the hybrid population having a low b-value.

These results correspond to previously discussed coefficient of variation (CV) values and are significantly correlated (0.85). The CV is an indication of the variation relative to the mean, while b-values are more representative of the variation per se over environments. Comparisons of the b-values and standard deviation (SD) indicated a higher degree of similarity with a correlation of 0.96.

It must be noted that this measurement is relative stability, such that the stability of each group depends on the mean of all other entries observed. The independent variable, location mean, is dictated by which entries are included in the calculation. This can introduce a bias depending on the number of entries included in the test, which decreases as the number of entries increases. The results presented herein, corresponded with the

previously examined data due to an adequate number of entries being included in the data set. Becker (1981) reported a high positive correlation between the environmental variance and the regression coefficient (0.94) averaged over 15 trials in three years for four different crops. The regression coefficients, CV, and SD, of all entries are included in Table 3.

Residual Methods and Comments

Residual values were calculated using the formula: $R_{ij} = Y_{ij} + \mu_{..} - \mu_{.j} - \mu_{.i}$, where Y_{ij} is the plot value in the i th column and j th row, $\mu_{..}$ is the overall mean, $\mu_{.j}$ is the entry mean, and $\mu_{.i}$ is the environment mean. Residual values were squared and averaged over all environments. ANOVA was used to determine differences between population types.

Large residual values can be an indication of an interaction between genotypes and environments. Small residual values are found for a genotype when the observed values fall exactly along the mean of all genotypes. Minimal interactions do not necessarily indicate stability but suggest similarity to the mean. It is possible for a genotype to have the highest residual value as compared to a set of genotypes and have the lowest SD. Thus, the residual values should be considered a measure of genotypic interaction and not stability.

Residuals

There was no identifiable pattern to the residual values (Table 3) and no significant difference between population types (Table 1). The variation found over the 18 environments was too great to determine significant differences using this method. Residuals calculated for specific genotypes over similar environments might produce more definitive results.

Multi-Blends

In 2005, the number of entries was expanded to include a 3-way and a 4-way parental blend (Table 4). The subset of nine environments produced results similar to the larger data set of 18 environments. The hybrids and blends of hybrids had significantly higher yields than all other population types (Table 5 and 6). The hybrids had the lowest SD among population types. The blends of hybrids had a lower SD than the 4-way blend of parents, but showed no difference between the remaining population types. The hybrids and blends of hybrids had lower CV values than the parents, blends of parents, and 4-way blend of parents, but were not different from the 3-way blends of parents. The variation associated with blending entries did not show a specific trend. Compared to the parents, there was an increase in variation when blending two parental components, blending three components resulted in slightly lower variation, and blending four components resulted in the highest variation.

These results were not as precise as the results generated from the complete data set but indicated a similar trend pertaining to stability. There was no increase in stability associated with heterogeneity. Ultimately, stability was only influenced by heterozygosity.

Literature Cited

Becker, H. C. 1981. Correlations among some statistical measures of phenotypic stability. *Euphytica* 30:835-840.

Lin, C. S., M. R. Binns, and L. P. Lefkovitch. 1986. Stability analysis: where do we stand? *Crop Sci.* 26:894-900.

Table 1. Mean lint yield, regression coefficient, and residual values among population types.

Population	Mean (kg/ha)	Regression Coefficient	Squared Residuals
Parents	1279	1.05	12193
Hybrids	1400	0.88	11080
Blends of Parents	1286	1.10	10792
Blends of Hybrids	1408	1.00	10355
LSD $\alpha=.05$	31	0.11	3837

Table 2. Mean lint yield, regression coefficient, and residual values between population components.

Variation	Population Components	Mean (kg/ha)	Regression Coefficient	Squared Residuals
Inter-genic	Homogeneous	1351	0.95	11526
	Heterogeneous	1374	1.03	10480
	LSD $\alpha=.05$	43	0.07	2586
Intra-genic	Homozygous	1283	1.08	11353
	Heterozygous	1406	0.97	10562
	LSD $\alpha=.05$	43	0.07	2586

Table 3. Mean lint yield, regression coefficient, standard deviation, coefficient of variation, and squared residual of all entries from the 2000, 2004, and 2005 growing seasons.

Entry	Population	Mean (kg/ha)	Regression Coefficient	SD	CV	Squared Residuals
1	DP 51	1196	1.00	286	23.9	16592
2	ST 474	1422	1.13	299	21.0	8191
3	LA 887	1210	0.93	258	21.3	11399
4	FM 989	1286	1.14	308	24.0	12592
1x2	Hybrid	1382	0.85	233	16.8	9092
1x3	Hybrid	1341	0.78	225	16.8	13705
1x4	Hybrid	1347	1.01	279	20.7	11470
2x3	Hybrid	1467	0.86	232	15.8	6995
2x4	Hybrid	1485	0.88	255	17.2	15325
3x4	Hybrid	1378	0.88	242	17.5	9895
1+2	Blend of Parents	1307	1.03	278	21.3	9290
1+3	Blend of Parents	1244	1.10	265	21.3	3684
1+4	Blend of Parents	1254	1.18	326	26.0	17952
2+3	Blend of Parents	1320	1.01	289	21.9	17587
2+4	Blend of Parents	1356	1.10	290	21.4	6672
3+4	Blend of Parents	1238	1.15	305	24.6	9570
5+6	Blend of Hybrids	1415	0.90	255	18.0	13305
5+7	Blend of Hybrids	1388	1.15	304	21.9	9071
5+8	Blend of Hybrids	1409	0.97	266	18.9	9756
5+9	Blend of Hybrids	1394	1.22	327	23.5	14015
5+10	Blend of Hybrids	1416	0.92	252	17.8	9285
6+7	Blend of Hybrids	1388	1.03	278	20.0	8890
6+8	Blend of Hybrid	1359	0.92	253	18.6	9211
6+9	Blend of Hybrids	1425	0.93	258	18.1	11355
6+10	Blend of Hybrids	1349	0.84	232	17.2	9450
7+8	Blend of Hybrids	1409	0.96	262	18.6	9713
7+9	Blend of Hybrids	1409	1.00	274	19.5	11242
7+10	Blend of Hybrids	1389	0.99	271	19.5	10569
8+9	Blend of Hybrids	1451	1.02	274	18.9	7949
8+10	Blend of Hybrids	1457	1.06	289	19.8	11340
9+10	Blend of Hybrids	1476	1.11	298	20.2	10168

Table 4. Mean lint yield, standard deviation, and coefficient of variation of all entries from the 2005 growing season.

Entry	Population	Mean (kg/ha)	SD	CV
1	DP 51	996	300	30.1
2	ST 474	1165	308	26.5
3	LA 887	999	285	28.5
4	FM 989	1017	290	28.6
1x2	Hybrid	1161	255	22.0
1x3	Hybrid	1119	242	21.6
1x4	Hybrid	1083	275	25.4
2x3	Hybrid	1231	239	19.4
2x4	Hybrid	1193	217	18.2
3x4	Hybrid	1150	243	21.1
1+2	Blend of Parents	1077	271	25.2
1+3	Blend of Parents	1040	288	27.7
1+4	Blend of Parents	976	330	33.8
2+3	Blend of Parents	1123	309	27.5
2+4	Blend of Parents	1125	310	27.5
3+4	Blend of Parents	994	322	32.4
5+6	Blend of Hybrids	1212	278	22.9
5+7	Blend of Hybrids	1160	310	26.8
5+8	Blend of Hybrids	1164	276	23.7
5+9	Blend of Hybrids	1098	322	29.3
5+10	Blend of Hybrids	1173	250	21.3
6+7	Blend of Hybrids	1164	315	27.0
6+8	Blend of Hybrids	1129	266	23.5
6+9	Blend of Hybrids	1206	272	22.5
6+10	Blend of Hybrids	1129	254	22.5
7+8	Blend of Hybrids	1191	257	21.6
7+9	Blend of Hybrids	1140	272	23.9
7+10	Blend of Hybrids	1179	293	24.8
8+9	Blend of Hybrids	1167	259	22.2
8+10	Blend of Hybrids	1174	277	23.6
9+10	Blend of Hybrids	1229	309	25.2
1+2+3	3-Way Blend of Parents	1111	274	24.7
1+2+4	3-Way Blend of Parents	1091	317	29.1
1+3+4	3-Way Blend of Parents	1059	282	26.6
2+3+4	3-Way Blend of Parents	1084	304	28.1
1+2+3+4	4-Way Blend of parents	1067	315	29.5

Table 5. Mean lint yield, coefficient of variation, and standard deviation between population types for the 2005 growing season.

Population	Mean (kg/ha)	CV	SD
Parents	1171	28.0	296
Hybrids	1296	21.3	245
Blends of Parents	1183	29.0	305
Blends of Hybrids	1309	24.1	281
3-Way Blends of Parents	1218	27.1	294
4-Way Blend of Parents	1196	29.6	315
LSD $\alpha=.05$	28	3.9	25

Table 6. Mean lint yield, coefficient of variation, and standard deviation between population components for the 2005 growing season.

Variation	Population Components	Mean (kg/ha)	CV	SD
Inter-genic	Homogeneous	1246	24.1	265
	Heterogeneous	1262	25.9	290
	LSD $\alpha=.05$	75	NS	11
Intra-genic	Homozygous	1190	28.4	300
	Heterozygous	1305	23.3	271
	LSD $\alpha=.05$	68	1.2	10