Impact of Heterozygosity and Heterogeneity on Cotton Lint Yield Stability

C. B. Cole,* D. T. Bowman, F. M. Bourland, W. D. Caldwell, B. T. Campbell, D. E. Fraser, and D. B. Weaver

ABSTRACT

In the last 8 yr, cotton (*Gossypium hirsutum* L.) growers in North Carolina have experienced variations in the year-to-year lint yield averages that range from a 56% increase to a 49% decrease. This variability results in wild fluctuations in income and a desire for more stable yields. Genetic structure may contribute to stability. This study was conducted to determine the impact of heterozygosity and heterogeneity on lint yield stability. Lint yield was observed in 18 environments over 3 yr among four population types that included homozygous lines grown in pure stands, homozygous lines grown in blended stands, hybrids grown in pure stands, and hybrids grown in blended stands. Comparisons were made using trait means, standard deviations, and the coefficients of variation (CVs) calculated over environments. There was no significant difference between lines grown in pure stands and blended lines with respect to yield or stability. Hybrids had a lower CV (were more stable) than homozygous lines. This stability was attributed to the hybrids and blends of hybrids out-yielding the homozygous lines and blends of homozygous lines in the low-yielding environments, but having similar yields in the high-yielding environments. These results do not support growing blends to increase stability or yield; however, growing hybrid cultivars could result in increased yields while reducing variability compared with current production practices.

C.B. Cole and D.T. Bowman, North Carolina State Univ., 3709 Hillsborough St., Raleigh, NC 27607; F.M. Bourland, Univ. of Arkansas, P.O. Box 48, Keiser, AR 72351; W.D. Caldwell, Louisiana State Univ. Agricultural Center, P.O. Box 8550, Bossier City, LA 71113; B.T. Campbell, USDA-ARS, 2611 West Lucas St., Florence, SC 29501; D.E. Fraser, Delta and Pine Land Company, P.O. Box 1529, Hartsville, SC 29550; D.B. Weaver, Auburn Univ., 201 Funchess Hall, Auburn, AL 36849-5412. Received 1 Aug. 2008. *Corresponding author (clay.cole@syngenta.com).

Abbreviations: CP, coefficient of parentage; CV, coefficient of variation; DP 51, 'Delta Pine 51'; FM 989, 'Fiber Max 989'; LA 887, 'Stoneville LA 887'; SD, standard deviation; ST 474, 'Stoneville 474'.

The standard deviation (SD) of lint yield of recent U.S. cotton (*Gossypium hirsutum* L.) cultivars is approximately five times larger than the SD of lint yield during the 1920s (National Agricultural Statistical Service [NASS] 2007). 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 1920s (NASS 2007). When comparing the relative variation of yields during the 1920s vs. 2000s using the coefficient of variation (CV), there is little difference, indicating variation is not relatively increasing; however, the larger variation associated with current high-yielding cultivars can be detrimental to 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 reduce it. They determined diversity was the answer in the form of "buffering" capacity that can be separated into individual buffering and population buffering.

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677 S. Segoe Rd., Madison, WI 53711 USA

Individual buffering comes in the form of heterozygous genotypes that theoretically are able to adapt to varying environments through allelic variation that produces complex enzymes with various optimal operating conditions or results in biochemical versatility that allows divergent biochemical pathways under diverse environmental conditions (Haldane, 1954; Lewis, 1954). Several studies, using a variety of statistical methods, have outlined individual buffering ability in self-pollinated and cross-pollinated species and are described 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 with the pure-line population in faba bean (*Vicia faba* L.). Shank and Adams (1960) and Schnell and Becker (1986) observed increases in the stability of corn (*Zea mays* L.) hybrids over the inbred population for several measured traits. Several studies have also tested stability between homozygous and heterozygous populations and found no significant differences (Kohel and White, 1963; Kohel, 1969; Reich and Atkins, 1970; Smith and Foote, 1970; 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 with pure lines. Several authors have also observed an increase in stability of blended entries when compared with 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 (Rasmusson, 1968; Clay and Allard, 1969; Smithson and Lenne, 1996).

Another aspect of population buffering is the blending of individually buffered genotypes or a heterozygous and heterogeneous population. Studies of this level of diversity reported 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), where 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 blends of maize hybrids, but concluded that it was no different than the increase observed for the hybrids alone (73%). Reich and Atkins (1970) reported that blends of hybrid grain sorghum (*Sorghum bicolor* L.) were the second most stable population type following the inbred 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 types of diversity are dependent on the organism, trait studied, mating design, stability statistic used for analysis, and the number of environments tested for population types. The studies cited above used 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). Because statistical methodologies can influence conclusions, the relationships among stability statistics have been estimated for 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, which 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 low yield. 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, agronomic stability outlines the predictability of a genotype. This also is true for Type II and III stability statistics. The ability to predict a genotype's response in a specific environment will only be useful if the environmental conditions are known before planting. Type I stability, or biological stability, gives information on the response of genotypes over all tested environments. When enough environments are included in its calculation, this statistic will give information about the range of phenotypic responses over environments and can be used as a predictor of genotypic performance with no prior knowledge of environmental conditions (Kang, 1990).

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 to represent equal divisions of early- (DP 51 and ST 474) and full-season (LA 887 and FM 989) maturity groups (Bowman, 1999). The coefficient of parentage (CP) values of inbred material were calculated after the entries were selected to determine diversity of inbred 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.

Inbreds were crossed in a diallel (excluding self-pollinations) in 1999, 2000, and 2004, and reciprocal crosses were bulked. Inbred lines were obtained from commercially available seed stock. Entries included four inbreds, six hybrids, six inbred blends, and 15 hybrid blends. Entries were tested in 21 environments, including four in 2000, seven in 2004, and 10 in 2005; 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 and unaccounted for variability among entries. Each location × 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 intergenetic diversity. The homozygous–homogeneous population included the four inbred lines grown in pure stands and represented the absence of genetic diversity. The homozygous– heterogeneous population included the inbred lines grown in two-component blends, resulting in six blended entries. The heterozygous–homogenous population included 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 before planting.

All entries were grown as two-row plots and arranged in a randomized complete block design with three replicates in 2000 and two replicates in 2004 and 2005. Plot length ranged from 8.5 to 13.7 m and row spacing ranged from 91.4 to 101.6 cm. Planting dates ranged from 28 April to 21 May and harvest dates ranged from 17 September to 28 October. 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 (midcomponent) 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 (midcomponent) 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 (midcomponent) 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 midcomponent 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^{-1}. Standard deviation, CV, and lint yield values were subjected to ANOVA using the general linear model procedure of SAS version 9.1 (SAS Institute Inc., Cary, NC) to determine differences between population types. Population types and

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

Location	State	Year	Mean	Soil classification
			kg ha^{-1}	
Clayton	NC	2004	1784	Fine-loamy, kaolinitic, thermic Typic Kandiudults
Clayton Late	NC	2005	1722	Fine-loamy, kaolinitic, thermic Plinthic Paleudults
Clayton Early	NC	2005	1676	Fine-loamy, kaolinitic, thermic Plinthic Paleudults
Hartsville	SC	2004	1624	Fine-loamy, kaolinitic, thermic Typic Kandiudults
Rocky Mount	NC	2004	1496	Fine-loamy, siliceous, subactive, thermic Aquic Paleudults
Rocky Mount	NC	2005	1487	Fine-loamy, siliceous, subactive, thermic Aquic Paleudults
Rocky Mount	NC	2000	1474	Fine-loamy, siliceous, semiactive, thermic Aeric Paleaquults
Bossier City	LA	2004	1459	Very-fine, smectitic, thermic Oxyaquic Hapluderts
Bertie	NC	2000	1425	Fine-loamy, siliceous, subactive, thermic Aquic Paleudults/ Fine-loamy, siliceous, semiactive, thermic Aeric Paleaquults
Scotland	NC	2004	1379	Fine, kaolinitic, thermic Typic Paleudults
Hartsville	SC	2000	1293	Fine-loamy, kaolinitic, thermic Typic Kandiudults
Bertie	NC	2004	1286	Fine-loamy, kaolinitic, thermic Typic Kandiudults
Bertie	NC	2005	1229	Fine-loamy, kaolinitic, thermic Typic Kandiudults
Bossier City	LA	2005	1212	Coarse-silty over clayey, mixed over smectitic, superactive, calcareous, thermic Oxyaquic Udifluvents
Tallassee	AL	2005	1108	Fine-loamy, siliceous, semiactive, thermic Typic Hapludults
Scotland	NC	2005	1013	Fine, kaolinitic, thermic Typic Paleudults
Pee Dee	SC	2005	982	Fine-loamy, siliceous, subactive, thermic Aquic Paleudults
Keiser	AR	2005	950	Very-fine, smectitic, thermic Chromic Epiaquerts
LSD$_{0.05}$			53	

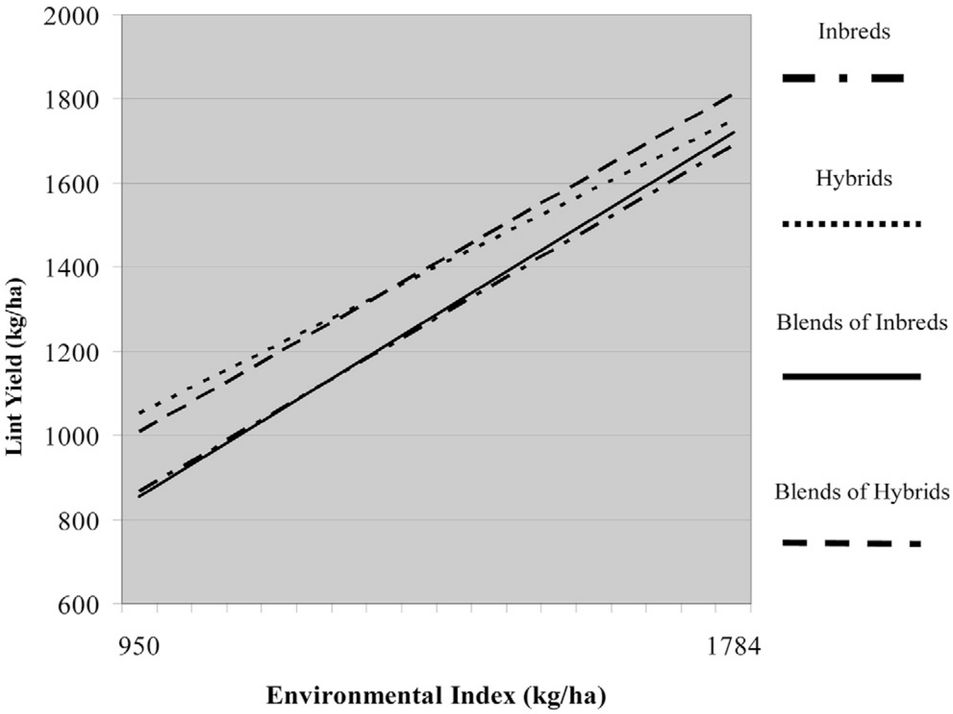

Figure 1. Linear trends for lint yield of each of four cotton population types regressed on the overall mean lint yield of 18 environments.

entries were considered fixed effects and environments were considered random effects. The CV was calculated using the formula CV = (s/μ) × 100, where s is the SD and μ is the overall mean. Mean separation was conducted using Fisher's protected 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 to produce sufficient variability to measure stability. The environments included in this test encompassed a region suitable for production of the four inbreds, that is, 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 × environment interaction with respect to yield. 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 (Fig. 1).

Coefficient of Variation

Maturity group did not affect stability rating. Delta Pine 51 and ST 474, early- to medium-maturity cultivars, had different CV values (23.9 and 21.0, respectively) (Table 2). Stoneville LA 887 and FM 989, medium- to full-season varieties, also had dissimilar CV values (21.3 and 24.0, respectively). The hybrids and blends of the hybrids had significantly lower CV values than the inbreds and blends of inbreds (Table 3). Comparing individual population components revealed no significant difference between the homogeneous (inbreds and hybrids) and heterogeneous (blends of inbreds and blends of hybrids) populations with respect to CV; however, the heterozygous population (hybrids and blends of hybrids) had significantly lower CV values than the homozygous population (inbreds and blends of inbreds) (Table 4). 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, 1953). There was no association between environment and blend response, reinforcing the ineffectiveness of blending entries to increase stability (Table 2).

The CV values within population types could not be tested using ANOVA; 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 2). Crossing the inbreds with the lowest CV, ST 474 and LA 887 (21.0 and 21.3, respectively), resulted in the hybrid (2×3) with the lowest CV (15.8). Combining the two inbreds with the highest CV, DP 51 and FM 989 (23.9 and 24.0, respectively), resulted in the hybrid (1×4) with the highest CV (20.7). Intermediate CV values for hybrid combinations did not follow the predicted pattern due to hybrids 1×2 and 1×3 having similar CV values. Stoneville 474 (Entry 2) and LA 887

Table 2. 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	SD	CV	Blend response	Percent blend response	Correlation of percent blend response with environmental index	Heterotic response	Percent heterosis	Correlation of percent heterosis with environmental index
		kg ha^{-1}			kg ha^{-1}			kg ha^{-1}		
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	1×2	1382	233	16.8	–			72†	7.6†	–0.45†
6	1×3	1341	225	16.8	–			138*	12.8*	–0.60*
7	1×4	1347	279	20.7	–			106*	9.7*	–0.33
8	2×3	1467	232	15.8	–			150*	12.9*	–0.64*
9	2×4	1485	255	17.2	–			131*	11.3*	–0.66*
10	3×4	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			
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

*Significant at the 0.05 probability level.

†Significant at the 0.1 probability level.

‡DP 51, 'Delta Pine 51'; FM 989, 'Fiber Max 989'; LA 887, 'Stoneville LA 887'; ST 474, 'Stoneville 474'.

(Entry 3) had a 0.3 difference between CV values. When these inbreds were crossed with FM 989 (Entry 4), there was also a 0.3 difference between the hybrids. Conclusions may have been more definitive using inbred genotypes with more diverse CV values.

No specific trend was observed when comparing each entry in the inbred blends with the corresponding components that made up each blend. Delta Pine 51 + FM 989 (1+4) had the highest CV for all entries (26.0) and is a blend of the two inbreds with the highest CV for yield stability (Table 2). Blending the two inbreds with the lowest CV (ST 474 and LA 887) resulted in the fourth lowest CV for inbred 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 inbreds with more diverse CV values may result in more predictable rankings. Three inbred blends resulted in a decrease in CV when compared with the parental midcomponent (Entries 1+2, 1+3, and 2+4) and three inbred blends resulted in an

Table 3. Mean lint yield, standard deviation, and coefficient of variation among four cotton population types.

Population	Mean	SD	CV
	kg ha–1		
Inbreds	1279	288	22.6
Hybrids	1400	244	17.5
Blends of inbreds	1286	292	22.8
Blends of hybrids	1408	273	19.4
LSD0.05	31	26	2.0

Table 4. Mean lint yield, standard deviation, and coefficient of variation between cotton population components.

Variation	Population components	Mean	SD	CV
		kg ha^{-1}		
Intergenic	Homogeneous	1351	261	19.5
	Heterogeneous	1374	278	20.3
	$LSD_{0.05}$	43	18	1.4
Intragenic	Homozygous	1283	290	22.7
	Heterozygous	1406	265	18.8
	$LSD_{0.05}$	43	18	1.4

increase in CV (Entries 1+4, 2+3, and 3+4), indicating no blend effect on CV associated with inbred blends.

No trend was observed for the blends of hybrids. Blending the hybrids with the lowest CV (ST 474 × LA 887 and DP 51 × LA 887) resulted in the seventh lowest CV among blends of hybrids (Entry 23). Blending the two hybrids with the highest CV (DP 51 × FM 989 and LA 887 × 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 2).

Diversity and Yield

Maturity groups were significantly different for yield (1309 vs. 1248 kg ha^{-1} 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 ST 474 relative to all other inbred genotypes (Table 2). 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 3). There was no significant difference between hybrids and hybrid blends or between inbreds and inbred blends. This was also observed when the population components were separated and compared directly (Table 4). 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 inbreds or blends of hybrids. Responses for blends of inbreds ranged from 41 to −10 kg ha^{-1} and averaged 6.4 kg ha^{-1} (Table 2). Responses ranged from 53 to −45 kg ha^{-1} and averaged 9.1 kg ha^{-1} for blends of hybrids.

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, that is, as mean yields decrease, the response of blended genotypes increase. Correlations for blends of inbreds ranged from −0.23 to 0.17 and were nonsignificant (Table 2). 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 with other hybrid blends. The combination of inconsistent blend responses and the nonassociation 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 2). As means increase, variation often increases; however, the SD of the hybrids was significantly less than all other groups (Table 3). This indicated the hybrid population was the most stable population type, regardless of mean yield. There was no significant difference for SD between inbreds, blends of inbreds, 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 4). 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 (Fig. 2). The range of values for hybrids was lower than that of the inbreds and blends of inbreds, resulting in significantly decreased SD and increased means, which, in turn, increased stability. Similar trends were observed for the blends of hybrids; however, the reduction in the SD was not significant.

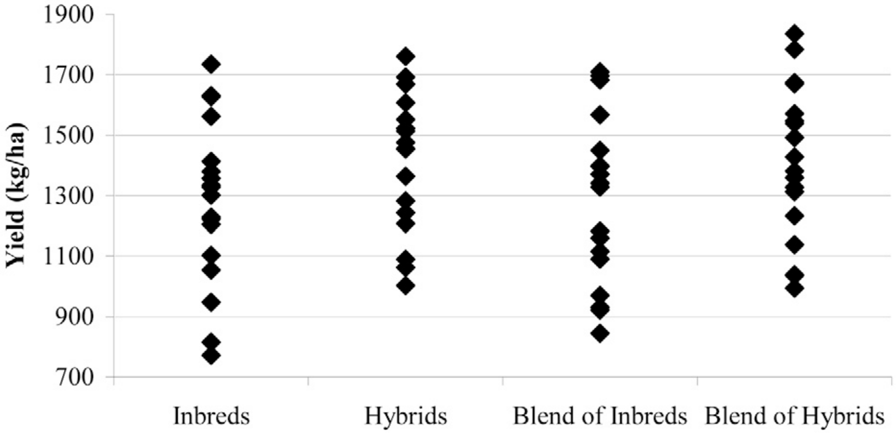

Figure 2. The mean lint yield of four cotton population types in each of 18 environments.

The heterosis observed for the hybrids was significant and negatively correlated with mean environment yield, where midcomponent heterosis was evident in unfavorable environments and negligible in high-yielding environments (Tables 2 and 5). 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 (Fig. 3).

Delta Pine 51 × FM 989 (1×4) had the lowest yield stability among all hybrid genotypes and the lowest heterosis observed for the low-yielding environments (Table 5). Stoneville 474 × LA 887 (2×3) 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 inbreds were very closely related (CP = 0.37; Table 5) and yet had high heterosis. Degree of heterosis and relatedness were not correlated (Tables 2 and 5).

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 inbred 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 means of 642, 712, and 1005 kg lint ha^{-1}, respectively. This illustrated that heterosis and heterotic response decreased with increasing environmental mean.

Hybrid midcomponent heterosis for yield was calculated at each environment and correlated with environmental means. Hybrids 1×2, 1×3, 2×3, 2×4, and 3×4 had significant negative correlations (Table 2). Averaged over all hybrids, the correlation was −0.72. This negative correlation supported the finding of decreasing heterosis with increasing environmental means. Hybrid 1×4 was negatively correlated with mean yield, but not significantly due to a weak heterotic response in the lowest yielding environmental class (Table 6 and Fig. 3).

There was a strong association between heterosis and environment mean and the effect each had on stability. The exact interaction is difficult to predict with these data. One can clearly see that heterosis decreased as environmental yields increased (Fig. 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 better tolerate unfavorable conditions (drought, insects) occurring later in the season. This could result in increased yields and stability relative to the inbreds. The opposite of this would occur under favorable environmental conditions where any advantage associated with increased rate of growth would be negated by inbred genotypes exploiting a full season of favorable conditions (Went, 1953). Wells et al. (1988) observed leaf area and plant photosynthesis in hybrid and inbred genotypes and attributed increased leaf

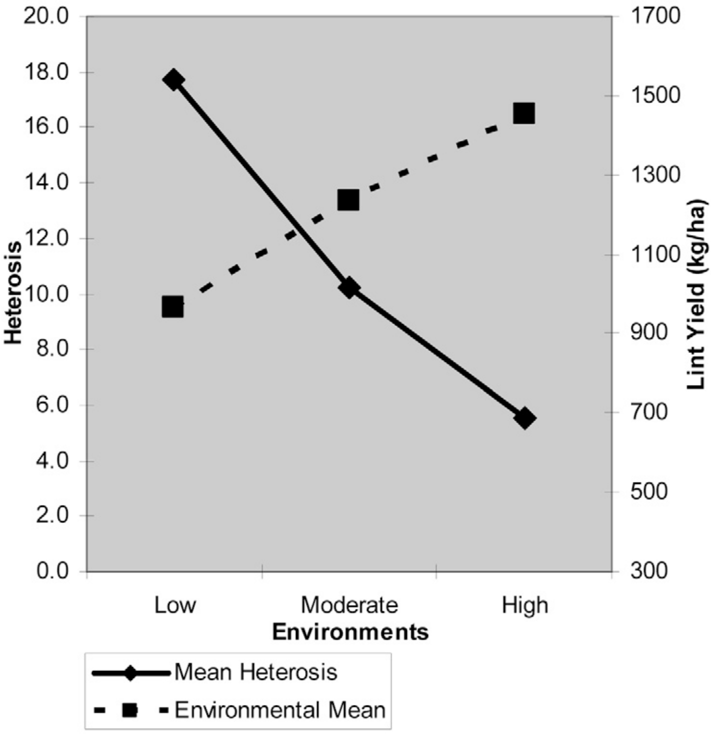

Figure 3. Change in heterosis in cotton from high heterosis in low-yielding environments to low heterosis in high-yielding environments. Change in lint yield from low-yielding environments to high-yielding environments.

Table 5. Coefficient of parentage between homozygous genotypes.[†]

	Homozygous genotypes		
	DP51	ST474	LA887
ST 474	0.15		
LA 887	0.17	0.37	
FM 989	0.08	0.03	0.10

[†] DP 51, 'Delta Pine 51'; FM 989, 'Fiber Max 989'; LA 887, 'Stoneville LA 887'; ST 474, 'Stoneville 474'.

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

Environmental classification	Hybrid						Average heterosis	Environmental mean
	1×2	1×3	1×4	2×3	2×4	3×4		
								kg ha^{-1}
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$_{0.05}$							6.0	45

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. During the early stages of development, hybrids had faster growth, bigger plants, and better light interception, resulting in more photosynthate production. Wells and Meredith (1986) found hybrids produced more lint and matured earlier than inbred genotypes. Final leaf area index and total dry weight for hybrids were also greater than the inbreds and were attributed to the hybrids having a faster growth rate during the seedling stage.

CONCLUSIONS

There were no differences with respect to yield and stability between the heterogeneous and homogeneous populations. 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 with the homozygous populations. This decreased the range of mean yield values over all environments and resulted in increased mean yields and smaller SD.

Using these parents in blended varieties is not recommended to increase yields or to decrease variability; however, these results indicate that growing hybrid cultivars could result in increased yields while reducing variability relative to homozygous lines. Growing hybrid cotton cultivars would allow farmers to utilize more diverse environments or to mitigate losses during environmentally stressful years. 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.

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 inbreds and hybrids for this trait. Two possible studies are (i) 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; and (ii) monitor plant growth and development during emergence, prebloom, 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.

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