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BREEDING AND GENETICS

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

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ABSTRACT

An 18-environment field study was undertaken to observe the mean and coefficient of variation (as a measure of stability) for cotton (*Gossypium hirsutum* L.) lint yield components in population types that differed for lint yield stability to determine which yield components contributed to yield stability. Hybrids and blends of hybrids (heterozygous populations) were more stable than the parents and blends of parents (homozygous populations) for lint yield. No within-boll yield component showed convincing evidence of differences between population types with respect to stability. Stability observed for bolls/hectare followed the same trend as lint yield in which the heterozygous populations were more stable than homozygous populations. 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. Manipulating within-boll components might not increase lint yield stability.

Cotton lint yield/boll is the product of mean fiber length, weight/length, fibers/unit surface area, and seed surface area (Worley et al., 1976). The combination of these components forms more complex yield structures that ultimately coalesce into lint/boll (Kerr, 1966; Manner et al., 1971; Worley et al., 1976). 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 can work together to influence lint yield or counteract one another, causing no change in lint yield (Bridge et al., 1971; Cole, 2003; Culp and Harrell, 1975; Green and Culp, 1990; Harrell and Culp, 1976; Kerr, 1966; Meredith and Bridge, 1973; Miller and Rawlings, 1967; Smith and Coyle, 1997; Worley et al., 1974, 1976).

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

In a previous study (Cole et al., 2009), we determined the impact of various levels of intra- and intergenic diversity on lint yield stability using four population types that represented four different combinations of genetic variation: pure-line cultivars (homozygous/homogeneous), two-component blends of pure-line cultivars (homozygous/heterogeneous), hybrid combinations of the pure-line cultivars

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(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 (Cole et al., 2009). 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 standard deviation (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 intrapopulation genetic variability.

MATERIALS AND METHODS

Four commercial cultivars of *Gossypium hirsutum* L., Deltapine 51 (DP 51), Stoneville 474 (ST 474), Stoneville LA 887 (LA 887), and FiberMax 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 (D.T. Bowman, personal communication, 2006). 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 were 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. Data are presented in Cole et al. (2009).

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 and one environment in South Carolina in 2005 was discarded due to extreme variability of the data. Each location-by-year combination was treated as a single environment totaling 18 environments (See Cole et al., 2009).

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 8.5 m to 13.7 m and row spacing ranged from 0.91 m to 1.02 m. 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.

Twenty-five well-developed 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 percentage, and boll weight (lint weight + seed weight/25). 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. Approximate numbers of fibers/seed, lint cotton/seed, and weight/fiber were calculated using formulas described by Worley et al. (1976). Approximately 15 g of lint from each sample were collected and sent to Cotton Incorporated to measure micronaire (Mic) 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 coefficient of variation (CV) of lint yield components was calculated for each entry over environments and replicates, resulting in one observation/entry. The CV was used as a stability measure and accounted for variance as a percentage of the mean (Francis and Kannenberg, 1978).

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 effect. Mean separation was conducted using Fisher's protected least significant difference (LSD) at the 0.05 level of probability. Table 1 describes the sources of variation and degrees of freedom.

Table 1. Source and degrees of freedom for main effects and interactions for analysis of variance

Source	Degrees of Freedom
Environment	17
Reps (environments)	21
Populations	3
Populations x Environments	51
Entry (Population)	27
Entry (Population) x Environment	459
Error	601

RESULTS AND DISCUSSION

Parental Material. The CP values averaged 0.15 and ranged from 0.03 (ST 474 and FM 989) to 0.37 (ST 474 and LA 887) indicating a broad range of allelic variation among parents (Cole et al., 2009). There were significant differences among parents for all measured within-boll components (Table 2).

Maturity groups were significantly different for all traits measured, excluding lint percentage (Table 3). Early-season cultivars had higher values for bolls/hectare, micronaire, and weight/fiber than full-season varieties; however, full-season cultivars 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.

Table 3. Maturity group means of parents for yield components over 18 environments

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 Percentage	%	41.5	41.4	0.4
Upper-Half Mean	mm	28.56	29.37	0.23
Micronaire (Mic)	value	4.98	4.64	0.1
Bolls/Hectare	no.	607192	507707	21212

The number of bolls/hectare was more stable (lower CV) in the heterozygous populations than the homozygous populations (Table 4). The stability of the heterozygous populations for bolls/hectare was mirrored in total lint yield stability and was not a surprising result because bolls/hectare is the major component of total lint yield (Manner et al., 1971; Worley et al., 1974).

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.

Table 2. Mean yield components for each parent over 18 environments

Trait	Unit	Genotype				LSD $\alpha = .05$
		DP 51[z]	ST 474[z]	LA 887[z]	FM 989[z]	
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	µg	4.80	4.73	4.64	4.51	0.14
Lint Percentage	%	39.68	43.51	41.87	41.31	0.01
Upper-Half Mean	mm	29.2	28.0	29.3	29.4	0.3
Micronaire (Mic)	value	4.9	5.1	4.7	4.6	0.1
Bolls/Hectare	no.	565093	649292	459447	555967	40369

[z] DP = DeltaPine, ST = Stoneville, LA = Louisiana , FM = FiberMax

Table 4. The coefficient of variation values among population types for measured yield components

Trait	CV				LSD α = .05
	Parents	Hybrids	Blends of Parents	Blends of 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 Percentage	2.5	3.0	2.9	3.0	0.4
Upper-Half Mean	2.4	2.5	2.4	2.8	0.4
Micronaire (Mic)	6.4	7.4	6.6	7.0	1.0
Bolls/Hectare	19.5	14.8	18.7	14.7	2.5

Table 5. Mean values among population types for yield components over 18 environments

	Unit	Parents	Means		Blends of Hybrids	LSD α = .05
			Hybrids	Blends of Parents		
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 Percentage	%	41.6	41.5	41.6	41.5	0.3
Upper-Half Mean	mm	29.0	29.7	29.0	29.7	0.2
Micronaire (Mic)	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

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 5). This division was also observed for total lint yield.

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 mirroring total lint yield and considered to be heterosis (Table 5).

Seed weight/boll is the product of seed index and seeds/boll. Hybrids and hybrid blends had more seeds/boll than the parents and blends of parents (Table 5). For seed index, the hybrids had significantly heavier seeds 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 5). 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 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 might 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 percentage. 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 5). 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 5). 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, suggested 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. Al-Rawi and Kohel (1969), Marani (1963), Meredith (1990), Meredith and Bridge (1972), 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 Cole et al. (2009) and compared the relationship between lint yield heterosis and environmental mean lint yield (correlation of -0.72). Following that result, 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 6). The number of bolls/hectare was negatively correlated with environmental mean yield and mirrored the result of lint yield.

Table 6. Correlation for percentage 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 Percentage	0.05
Upper Half Mean	-0.10
Micronaire(Mic)	0.08
Bolls/Hectare	-0.63[z]

[z] Significantly different from zero at the 0.01 level of probability.

The nonassociation 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 percentage, boll weight, and lint weight/boll (Table 7). Seed index is the weight of 100 seeds 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, and 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 percentage and weight/fiber (Table 7). Upper-half mean was negatively correlated with lint percentage and weight/fiber. Lint percentage was positively correlated with lint yield, whereas no other lint characteristic showed an association.

Table 7. Correlation of yield components over genotypes

	Boll Size	Seed Wt./ Boll	Lint Wt./ Boll	Seed Index	Seeds/ Boll	Lint Wt./ Seed	Fibers/ Seed	Wt./ Fiber	Lint Percentage	Upper-Half Mean	Mic	Bolls/ Ha
Seed Wt./Boll	0.94[z]											
Lint Wt./Boll	0.92[z]	0.76[z]										
Seed Index	0.86[z]	0.82[z]	0.89[z]									
Seeds/Boll	0.79[z]	0.92[z]	0.51[z]	0.53[z]								
Lint Wt./Seed	0.35	0.07	0.67[z]	0.55[z]	-0.28							
Fibers/Seed	0.42[z]	0.22	0.71[z]	0.68[z]	-0.15	0.93[z]						
Weight/Fiber	-0.25	-0.40[z]	-0.2	-0.42[z]	-0.31	0.05	-0.32					
Lint Percentage	-0.25	-0.47[z]	0.16	0.03	-0.73[z]	0.79[z]	0.70[z]	0.14				
UHM	0.60[z]	0.76[z]	0.34	0.43[z]	0.84[z]	-0.34	-0.15	-0.46[z]	-0.67[z]			
Micronaire	-0.52[z]	-0.71[z]	-0.33	-0.49[z]	-0.71[z]	0.24	-0.06	0.80[z]	0.51[z]	-0.89[z]		
Bolls/Hectare	-0.64[z]	-0.60[z]	-0.55*	-0.62[z]	-0.46[z]	-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[z]	0.17	-0.06	0.69[z]

[z] Significantly different at the 0.05 level of probability.

These correlations revealed a different trend than the mean results. Correlations indicated that fiber characteristics and lint yield were not improved concomitantly, whereas the mean data indicated simultaneous increases in classically negatively correlated traits. Mean data also suggested a simultaneous increase 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 could be a byproduct of increased numbers of bolls/hectare.

CONCLUSIONS

The lack of variation for CV values of measured lint yield components among population types that are known to differ for stability indicated these components did not contribute to lint yield stability.

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/m^2 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. These findings contradict the proposed theory of Lewis et al. (2000) that cotton yield stability could be increased by selecting for varieties that produce fewer seeds/hectare 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 F_1 hybrids that out yielded parental genotypes in lower yielding environments by producing more harvestable fiber stemming from more bolls. These results support the findings of Worley et al. (1974) that selection of increased number of bolls/unit land area, whether it be through the creation of hybrids or through homozygous lines, will lead to an increase in cotton lint yield.

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