Dissecting Genotype × Environment Interactions and Trait Correlations Present in the Pee Dee Cotton Germplasm Collection following Seventy Years of Plant Breeding

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ABSTRACT

Genotype × environment (G × E) interactions and trait correlations significantly impact efforts to develop high-yield, high-quality, and environmentally stable Upland cotton (*Gossypium hirsutum* L.) cultivars. Knowledge of both can and should be used to design optimal breeding programs and effective selection criteria. In this study, we examined the G × E interactions and trait correlations present in the 70-yr Pee Dee cotton germplasm enhancement program. Since beginning in 1935, the Pee Dee program has employed a variety of unique germplasm and breeding methods to release >80 improved germplasm lines and cultivars. Results suggest that significant G × E interactions exist for several agronomic and fiber quality performance traits that are mostly due to changes in magnitude. Negative genotypic correlations still persist between lint percent/lint yield and fiber length/fiber strength. However, apparently the breeding methods and selection criteria used over 70 yr have lessened the negative relationship between agronomic performance and fiber quality over time to some degree. The results provide cotton breeders a resource to select specific Pee Dee germplasm lines for increased environmental stability. Cotton breeders can also use the information herein to select specific Pee Dee germplasm lines that represent rare recombination events that combine high yield and fiber quality potential.

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Abbreviations: AFIS, Advanced Fiber Information System; G × E, genotype × environment; HVI, high-volume instrument.

Tʜᴇ ᴇꜰꜰᴇᴄᴛɪᴠᴇɴᴇss of plant breeding programs is often influenced by genotype × environment (G × E) interactions and correlations among traits for improved productivity and quality. Like many other globally important agricultural commodities, knowledge of G × E interactions and trait correlations in Upland cotton (*Gossypium hirsutum* L.) is paramount toward efforts to develop high-yield, high-quality, and environmentally stable cultivars. Today, cotton breeders most often attempt to develop cultivars with minimum G × E influence on agronomic and fiber quality performance traits, thereby directly or indirectly selecting for environmental stability across an array of production areas. Alternatively, attempts are made to target specific cultivars to specific production areas if knowledge of the G × E influence is available.

In addition to G × E, knowledge of the relationships among traits for improved productivity and quality is critical when designing trait selection criteria or indices in breeding programs. Without knowledge of such associations, unfavorably correlated traits present a difficult situation for breeders interested in selecting for the optimum value of both traits.

Information concerning the extent of G × E interactions is critically important for cotton breeding programs to recognize a given cultivar's likely area of adaptation (Campbell and Jones, 2005). Geng et al. (1987) listed genotype stability for agronomic performance and fiber quality as an important breeding objective. After lint yield potential, Bowman (2000) listed yield stability as the second most important criterion for selecting breeding parents. Previous research suggests that G × E interactions significantly impact lint yield performance (Bilbro and Ray, 1976; Geng et al., 1987, 1990; Meredith, 1984; Meredith and Bridge, 1984). Genotype × environment interactions also impact the selection of superior genotypes for fiber quality in cotton performance trials, but to a lesser degree than G × E interactions for lint yield (Geng et al., 1987; Paterson et al., 2003). Using data collected from South Carolina Official Variety Tests, Campbell and Jones (2005) found that G × E interactions explained 8% of the total variation for lint yield, 20% for lint percent, 8% for fiber length and strength, 24% for fiber uniformity, 9% for micronaire, and 3% for fiber elongation.

Genotypic correlations between agronomic performance and fiber quality traits were recognized in the 1950s and became a major breeding emphasis thereafter. Meredith (1984) suggested that if genotypic correlations between two or more traits were high, the selection of one trait would simultaneously result in changes of the correlated trait(s). Unfavorable genotypic correlations between traits of greatest breeding importance create a great challenge for cotton breeders. Early studies summarized by Meredith (1984) reported that lint yield was negatively correlated with fiber strength and fiber length, while positively correlated with fiber elongation and micronaire. A positive correlation between lint yield and micronaire is not desirable because high micronaire results in lower fiber quality. Subsequent studies were summarized by May (1999), who reported that length and strength were positively correlated. Correlations involving strength and length with other fiber quality traits (fineness, elongation, maturity) have not been conclusive, with reports of positive and negative correlations between specific pairs of fiber quality traits.

One of the longest standing public U.S. cotton germplasm enhancement programs is known as the Pee Dee program. After being initiated in 1935, the long-term objective of the Pee Dee germplasm program evolved into developing Upland cultivars with improved fiber strength and lint yield. During the 1940s, unique triple-hybrid strains (*G. arboreum* L. × *G. thurberi* Todaro × *G. hirsutum* L.) with improved fiber strength were developed and distributed to the Pee Dee program and

other breeding programs (Beasley, 1940; Kerr, 1960). Culp and Harrell (1973) described a complex intercrossing program (e.g., recurrent selection) involving two triple-hybrid strains (TH 108 and TH 171) and several Upland parents (Sealand, Earlistaple, and 'Hopi Acala') that gave rise to the Upland progenitor lines (designated F, J, A, and N) that form the basis of the current Pee Dee germplasm program. During this time, they reported the difficulty in simultaneously improving fiber quality and agronomic performance due to the negative relationship between fiber quality and agronomic performance. By 1979, Culp et al. (1979) reported a breaking of the negative relationship between fiber strength and lint yield by developing germplasm with both high strength and lint yield. In addition, they suggested linkage as the mechanism for a negative relationship between strength and lint yield.

Previously, Campbell et al. (2009, 2011) examined the genetic diversity and genetic trends associated with germplasm developed within eight primary breeding cycles of the Pee Dee germplasm program since 1935. It was found that genetic gain for lint percent and lint yield has increased 3% per breeding cycle while fiber quality properties have decreased <1% per cycle. Genotype × environment interactions were reported in Campbell et al. (2011), but they were not described in detail. Hence, the objectives of this research were: (i) to dissect G × E interactions associated with the agronomic and fiber quality performance of Pee Dee germplasm evaluated across southeastern U.S. environments, and (ii) determine the correlations among and within agronomic and fiber quality performance traits.

MATERIALS AND METHODS

Plant Materials and Trait Evaluations

Based upon both breeding cycle and pedigree, 82 officially released cotton germplasm lines and/or cultivars were selected to represent the history of the Pee Dee cotton germplasm enhancement program (see Campbell et al. [2011] for detailed germplasm information). For each field trial, a total of two to six check cultivars were selected for comparison purposes. Two of the checks were conventional cultivars 'Deltapine 491' (DP491, PVP 200100159) and 'FiberMax 958' (FM958, PVP 200100208) and the remaining four included transgenic, commercial cultivars widely grown in the southeastern United States. These included 'Deltapine 444BR' (DP444BR, PVP 200300134), 'Deltapine 555BR' (DP555BR, PVP 200200047), 'FiberMax 960BR' (FM960BR, PVP 200400224), and 'Stoneville 5599BR' (ST5599BR, PVP 200300279).

As described in Campbell et al. (2011), during 2004 to 2006, a total of 14 replicated field trials were conducted across North Carolina, South Carolina, Georgia, and Mississippi. The experimental design for each trial consisted of two to four replicates arranged in an alpha-lattice incomplete block design. In 2004, trials were conducted at three locations in South Carolina; these locations included the Clemson University Edisto Research and Education Center in Blackville, the Clemson University Pee Dee Research and Education Center in Florence, and the

Monsanto Company research station in Hartsville. These trials included the check cultivars Deltapine 491 and FiberMax 958. Florence and Blackville trials consisted of four replicates and 14 incomplete blocks of size six. The Hartsville trial contained two replicates and 21 incomplete blocks of size four.

In 2005 and 2006, trials were conducted across North Carolina, South Carolina, Georgia, and Mississippi. Each trial included all six check cultivars. For North Carolina, three replicate trials in each year were conducted at the NC State Upper Coastal Plains Research Station in Rocky Mount, NC. In both years, three replicate trials were conducted at the University of Georgia research station in Tifton, GA. Two replicate trials were conducted at the USDA-ARS Jamie Whitten Research Center in Stoneville, MS. Trials in South Carolina were conducted in Florence (four replicates), Blackville (three replicates), and Hartsville (two replicates), with the exception that 2006 included Florence and Blackville only. In 2005 and 2006, with the exception of Blackville 2006, each replicate of the alpha-lattice designs contained 22 incomplete blocks of size four. Blackville 2006 contained eight incomplete blocks of size 11.

With the exception of the Stoneville location, plots were two rows 10.6 m to 15.0 m by 76 cm to 100 cm. At the Stoneville location, plots were single rows 10.6 m by 96.5 cm. Trial management followed the established local practices for cotton production at each location. Each plot was harvested with a spindle-type mechanical cotton picker, and total seed cotton weight was recorded. A 25-boll sample was hand-harvested from each plot prior to harvest to determine boll weight, bolls m^{-2}, seed index, lint percent, and fiber quality properties. Boll weight was determined by dividing the seed cotton weight of the boll sample by 25. Bolls m^{-2} was determined by dividing the seed cotton yield by the boll weight. All samples from each location were ginned on a common 10-saw laboratory gin, and lint percent was determined by dividing the weight of the lint sample after ginning by the weight of the seed cotton sample before ginning. Lint yield was calculated by multiplying the lint percent by the seed cotton yield. In addition, a portion of the lint sample was sent to the Cotton Incorporated Fiber Testing Laboratory (Cary, NC) for determination of high-volume instrument (HVI) and Advanced Fiber Information System (AFIS) fiber properties. Fiber properties measured include HVI fiber length, HVI fiber strength, HVI elongation, HVI uniformity, HVI micronaire, and AFIS fineness.

Statistical Analyses

The importance of G × E interactions for each agronomic and fiber quality trait was first evaluated by comparing each source of variation's contribution to the adjusted total sums of squares calculated from the combined ANOVA provided in Campbell et al. (2011). Total sums of squares were adjusted by removing sums of squares due to blocks, replications, and pooled error. For each trait, the percentage sums of squares for environment, genotype, and G × E interactions was calculated relative to the adjusted total sums of squares.

To evaluate genotype stability and dissect G × E interactions, stability parameters (Eberhart and Russell 1966) were estimated, with the 14 environments, by regressing genotype means on an environmental index. The environmental index was estimated as the mean of all genotypes at a specific environment minus the grand mean over all environments. The regression coefficient (b_i)

and deviations from regression (s^2d) were used to compare environmental responses of genotypes. A *t*-test was conducted to determine if $b_i = 1$ for each genotype. The G × E sums of squares calculated in Campbell et al. (2011) was partitioned into sums of squares due to (i) regression of genotypes on the environmental index and (ii) pooled deviations from regression for each of the eight breeding cycles (germplasm groups). The G × E linear interaction mean square provided a test of genetic differences among the nine groups of germplasm (eight breeding cycles + checks) and within each germplasm group for their response to linearly arrayed environmental productivity. The pooled deviation mean square provided a test of genetic differences among groups and within groups for their deviation from regression.

Genotypic correlations and their standard errors were calculated among all agronomic and fiber quality traits using SAS version 9.2 (SAS Institute, 2008) as described by Holland (2006). Check cultivars were excluded from correlation analyses.

RESULTS AND DISCUSSION
Genotype × Environment Interactions and Genotype Stability

Table 1 shows the percentage sums of squares remaining for environment, genotype, and G × E interactions. On average, the environment sums of squares accounted for the largest amount of total variation for each trait. Environment ranged from 32% for length to 82% for micronaire. The percentage sums of squares accounted for by genotype ranged from 6% for fineness to 33% for length. The percentage sums of squares accounted for by G × E interaction ranged from 11% for micronaire to 46% for boll weight. The ratio of Pee Dee line × environment interaction and Pee Dee line sums of squares revealed the importance of G × E for lint yield (3:1), bolls m^{-2} (5:1), boll weight (5.5:1), uniformity (3:1), micronaire (2:1), and fineness (3:1). However, this ratio indicated the impact of Pee Dee line × environment interactions was less for lint percent (1:1), seed index (1.5:1), strength (1:1), length (1:1), and elongation (1.5:1).

Table 2 shows the summary of ANOVA results for linear and nonlinear components of G × E. Overall, the linear component of G × E was significant for lint percent, boll weight, and elongation. The nonlinear component (pooled deviation) was not significant for any of the traits measured. The linear and nonlinear components of G × E were further partitioned to compare differences among and within the eight breeding cycle groups and check cultivars. Slopes were significantly different among breeding cycle groups for lint yield, lint percent, boll weight, seed index, strength, length, elongation, and micronaire. Hence, on average, genotypes representing the eight breeding cycles responded dissimilarly across a low to high gradient of environmental indices for these traits.

In terms of lint yield and lint percent, the regression of breeding cycle group mean on environmental index showed that the differential between groups was greatest in high lint yield or lint percent environments (Fig. 1a and 1b).

Table 1. Percentage sums of squares explained by environment, genotype, and genotype × environment interactions from total sums of squares after removing sums of squares due to blocks, replication, and pooled error. Components of genotype and genotype × environment interactions also shown. Sums of squares were obtained from the analysis of variance of Pee Dee cotton germplasm lines and check cultivars combined over 14 location–year environments from 2004 to 2006 (Campbell et al., 2011).

Source	Lint yield	Bolls m^{-2}	Lint percent	Boll weight	Seed index	Strength	Length	Elongation	Uniformity	Micronaire	Fineness
					percentage sums of squares (%)						
Environment (E)	72	59	67	44	43	58	32	72	45	82	80
Genotype (G)	9	9	20	10	29	22	33	12	14	7	6
Pee Dee lines (PD)	5	6	12	8	18	19	30	10	13	5	4
Checks	1	1	1	1	7	2	2	2	1	1	1
PD vs. check	3	2	7	1	4	1	1	0	0	1	1
G × E	19	32	13	46	28	20	35	16	41	11	14
PD × E	17	29	11	44	27	18	33	15	38	10	13
Check × E	1	2	1	1	1	1	2	1	2	0	0
PD vs. check × E	1	1	1	1	0	1	0	0	1	1	1

These G × E interactions were primarily due to changes in magnitude rather than change in rank. However, there were a few cases of change in rank. For lint yield, the Group 6 mean displayed a slight change in rank relative to other breeding cycle groups. For lint percent, the Group 5 mean changed in rank relative to other breeding cycle groups.

In terms of length and strength, the regression of breeding cycle group mean on environmental index showed the differential between groups was similar across low and high length/strength environments (Fig. 1c and 1d). Although G × E interactions were primarily due to changes in magnitude, there were a few instances of changes in rank. For length, Groups 3, 4, and 7 showed changes in rank. For strength, Group 7 showed a change in rank relative to other breeding cycle groups.

Significant within breeding cycle group linear G × E variation was negligible and only found for lint percent (Group 6), boll weight (Groups 4 and 8), strength (Group 3), length (Group 1), elongation (Group 1), and fineness (Checks). Overall pooled deviations (nonlinear components of G × E) were not significant for any trait. Component pooled deviations were significant only for lint yield (Checks) and micronaire (Checks and Group 1). These findings indicated genotypes and breeding cycle deviations from regression were not a large contributor to G × E interactions.

Table 3 provides a listing of trait stability parameters calculated for each genotype with slope (b_i) not equal to 1. Each genotype–trait combination with b_i not equal to 1 was considered environmentally sensitive and impacted significantly by G × E interactions (Eberhart and Russell, 1966). A genotype was considered stable when b_i was equal to 1. This analysis detected specific genotype information as well as possible stability trends across the eight breeding cycles of the Pee Dee germplasm enhancement program.

For lint yield, a total of six Pee Dee lines displayed slopes different from 1. The six consisted of one Pee Dee line in Groups 1, 2, 4, and 8. Two Pee Dee lines in Group 6 displayed slopes different from 1. For bolls m^{-2}, four Pee Dee lines displayed slopes different from 1; these included one line in Group 4 and three lines in Group 6. For lint percent, a total of 14 Pee Dee lines displayed slopes different from 1. This included one line in Groups 4 and 7, two lines in Groups 1, 3, and 5, and three lines in Groups 6 and 8. For boll weight, four Pee Dee lines showed slopes different from 1. The four lines consisted of one line each in Groups 3, 4, 6, and 8. For seed index, a total of three Pee Dee lines showed slopes different from 1. One of the three lines was present each in Groups 2, 4, and 6. For strength, eight total Pee Dee lines showed slopes different from 1. The eight consisted of one line each in Groups 4, 5, 6, and 7 and two lines each in Groups 3 and 8. For length, a total of seven Pee Dee lines showed slopes different from 1. The seven consisted of two lines each in Groups 1 and 2 and three lines in Group 3. For elongation, a total of 14 Pee Dee lines showed slopes different from 1. The 14 consisted of one line in each of Groups 2, 4, 6, and 8, two lines in Group 3, and four lines in each of Groups 1 and 5. For uniformity, a total of three Pee Dee lines showed slopes different from 1. These included two lines in Group 6 and one line in Group 8. There were only two Pee Dee lines with slopes different from 1 for micronaire and fineness. For micronaire, there was one Pee Dee line in each of Groups 7 and 8. For fineness, there was one Pee Dee line in each of Groups 2 and 8.

Overall, summed across traits, Group 7 had the lowest number of Pee Dee lines (three) with slopes different from 1 and Group 6 had the largest number (14). Five Pee Dee lines were found to display slopes different from 1 for three or more traits. In breeding cycle Group 1, AC 241 was environmentally sensitive for lint yield, lint percent, and length. FTA 266 was environmentally sensitive for lint percent, length, and elongation. In Group 5, PD 7586 was environmentally sensitive for lint percent, strength, and elongation. In Group 6, PD 0781 was environmentally sensitive for lint yield, boll m^{-2}, boll weight, and uniformity. In Group 8, PD 93034 was environmentally sensitive for lint yield, lint percent, and strength. Eight Pee Dee lines

Table 2. Partitioning of genotype × environment interactions into linear and nonlinear components. Mean squares and significance levels of *F*-tests from the regression analysis of all traits for eight groups of Pee Dee cotton germplasm lines and check cultivars combined over 14 location–year environments in North Carolina, South Carolina, Georgia, and Mississippi from 2004 to 2006.

Source	Lint yield	Bolls m⁻²	Lint percent	Boll weight	Seed index	Strength	Length	Elongation	Uniformity	Micronaire	Fineness
Genotypes (G)	13,432**	213**	28.2**	0.52**	3.93**	1,391**	5.6**	1.38**	3.2**	0.35**	139**
Environment (linear) (E)	56,554,456**	67,185**	4961.1**	137.21**	280.55**	175,799**	292.4**	378.90**	476.7**	180.85**	89,321**
G × E (linear)	26,569	44	1.7**	0.20**	0.17	81	0.2	0.23**	0.3	0.03	14
Among groups	68,789**	82	4.7**	0.39**	0.45*	174**	0.6*	1.56**	0.6	0.08*	12
Checks	25,393	13	1.2	0.01	0.28	93	0.4	0.15	0.7	0.05	55*
Group 1	22,423	31	1.1	0.10	0.18	75	0.7*	0.24**	0.2	0.03	14
Group 2	35,695	59	1.4	0.29	0.32	85	0.5	0.14	0.3	0.01	17
Group 3	14,415	36	1.5	0.20	0.05	151*	0.3	0.05	0.3	0.02	14
Group 4	30,505	53	1.5	0.28*	0.18	38	0.1	0.11	0.4	0.02	12
Group 5	16,437	52	1.6	0.06	0.12	72	0.2	0.14	0.1	0.02	20
Group 6	17,005	38	1.7*	0.23	0.14	60	0.1	0.08	0.3	0.01	7
Group 7	11,802	27	0.4	0.07	0.13	42	0.1	0.05	0.3	0.03	11
Group 8	26,182	33	1.2	0.31**	0.11	69	0.1	0.05	0.4	0.05	15
Pooled dev.†	23,990	62	1.0	0.17	0.23	77	0.3	0.10	0.5	0.04	25
Checks dev.	22,409**	61	1.0	0.18	0.23	76	0.3	0.11	0.5	0.04*	23
Group 1 dev.	45,062	77	1.5	0.10	0.15	83	0.4	0.07	0.6	0.06*	36
Group 2 dev.	45,062	77	1.5	0.10	0.14	70	0.4	0.06	0.5	0.07	44
Group 3 dev.	11,617	41	0.8	0.19	0.18	90	0.3	0.14	0.4	0.02	18
Group 4 dev.	21,902	60	1.0	0.17	0.26	64	0.3	0.07	0.4	0.05	14
Group 5 dev.	20,485	52	0.6	0.14	0.17	57	0.2	0.08	0.3	0.05	14
Group 6 dev.	23,936	60	1.3	0.14	0.18	51	0.2	0.07	0.4	0.05	23
Group 7 dev.	34,878	91	0.7	0.12	0.23	62	0.2	0.06	0.4	0.02	18
Group 8 dev.	17,931	57	0.6	0.16	0.16	61	0.3	0.12	0.4	0.03	19
Pooled error	27,416	79	1.5	0.29	0.45	136	0.5	0.17	1.1	0.05	46

* Significant at 0.05 level of probability.

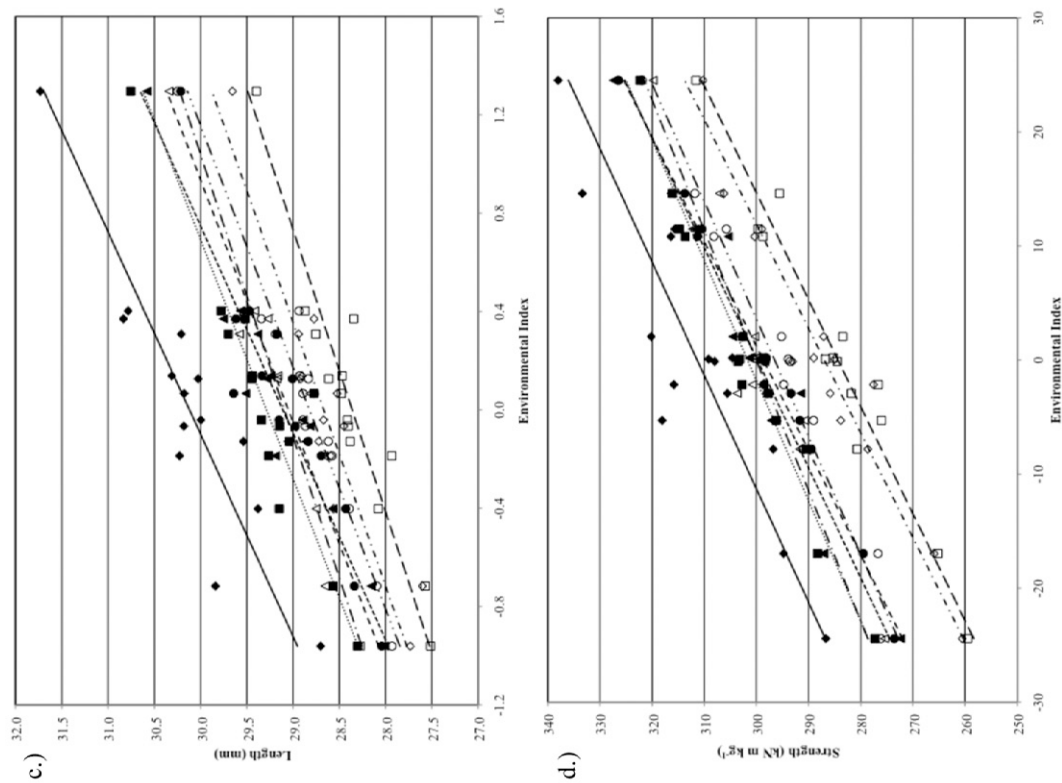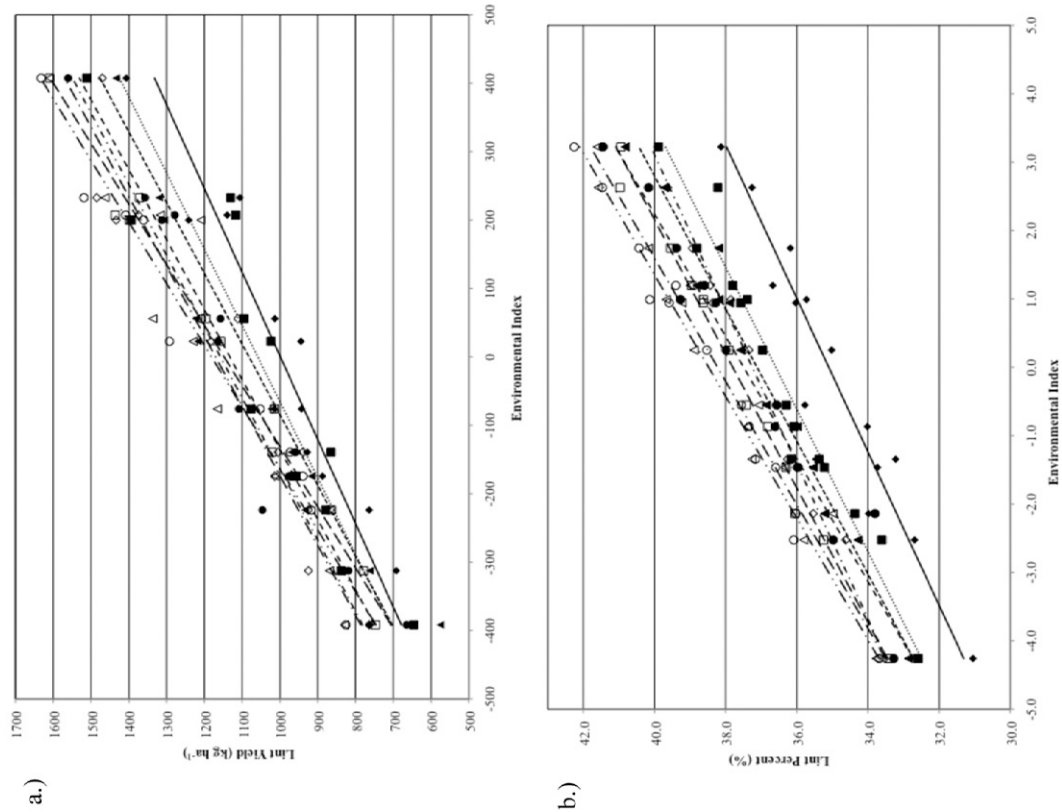** Significant at 0.01 level of probability.

† Deviations (dev,).

Figure 1. Regressions of eight Pee Dee cotton group means on an environmental index estimated from the mean of genotypes grown in each of 14 environments minus the grand mean for (a) lint yield, (b) lint percent, (c) fiber length, and (d) fiber strength.

Table 3. Agronomic and fiber quality trait stability parameters of cotton genotypes with slope (*b*) not equal to 1. Genotypes were evaluated in 14 location–year environments from 2004 to 2006.

Trait	Genotype (Group)[†]	*b*	Trait	Genotype (Group)	*b*	Trait	Genotype (Group)	*b*
Lint yield	AC 241 (1)	0.62**	Boll weight	PD 9223 (3)	1.81**	Elongation	Earlistaple 7 (1)	0.46**
	PD 2165 (2)	0.32*		PD 6186 (4)	2.12*		Hybrid 330-278 (1)	0.23**
	PD 875 (4)	0.71*		PD 0781 (6)	1.47*		FTA 266 (1)	0.47**
	PD 0741 (6)	1.39*		PD 94042 (8)	−0.05*		Sealand 542 (1)	0.35**
	PD 0781 (6)	1.35*	Seed index	PD 2165 (2)	1.71*		PD 2164 (2)	0.57**
	PD 93034 (8)	1.32*		PD 6044 (4)	0.52*		PD 0109 (3)	0.61*
Bolls m^{-2}	PD 875 (4)	0.59*		PD 0753 (6)	1.43*		PD 9363 (3)	0.70*
	PD 0741 (6)	1.52**		DP444BR (C)	0.65*		PD 6142 (4)	1.37*
	PD 0762 (6)	1.63*		FM960BR (C)	0.43**		PD 7388 (5)	1.24*
	PD 0781 (6)	1.54*		ST5599BR (C)	0.37**		PD 7496 (5)	1.15*
Lint percent	AC 241 (1)	0.71*	Strength	PD 0113 (3)	0.56**		PD 7501 (5)	1.46*
	FTA 266 (1)	0.75**		PD 9223 (3)	1.60*		PD 7586 (5)	1.26*
	PD 9364 (3)	1.28**		PD-2 (4)	1.11*		PD 0771 (6)	1.43*
	SC-1 (3)	1.30*		PD 7586 (5)	1.36*		PD 93057 (8)	1.38**
	PD 6142 (4)	1.18**		PD 0778 (6)	1.47*	Uniformity	PD 0683 (6)	1.46*
	PD 7586 (5)	0.72*		PD 5256 (7)	0.66*		PD 0781 (6)	0.44*
	PD 7723 (5)	0.59*		PD 93009 (8)	0.62*		PD 93021 (8)	0.33**
	PD 0648 (6)	1.35*		PD 93034 (8)	0.73*	Micronaire	PD 5358 (7)	0.59*
	PD 0747 (6)	0.76*		FM960BR (C)	0.48**		PD 94042 (8)	0.65**
	PD 0785 (6)	0.60**	Length	AC 241 (1)	0.45*	Fineness	PD 4381 (2)	0.80*
	PD 5246 (7)	1.19*		FTA 266 (1)	1.76**		PD 93046 (8)	0.77*
	PD 93009 (8)	1.26**		PD 0259 (2)	1.53**			
	PD 93034 (8)	1.24**		PD 3246 (2)	0.38*			
	PD 94045 (8)	1.50*		PD 0109 (3)	1.44*			
				PD 0111 (3)	1.61**			
				PD 9232 (3)	0.55*			

* Significant at 0.05 level of probability.

** Significant at 0.01 level of probability.

† Pee Dee Group 1–8 (1–8) and commercial check (C).

were environmentally sensitive for two traits and included PD 2165 (Group 2), PD 0109 and PD 9223 (Group 3), PD 875 and PD 6142 (Group 4), PD 7586 (Group 5), PD 0741 (Group 6), and PD 93009 and PD 94042 (Group 8). The check cultivar FM960B2R displayed slopes different from 1 for seed index and strength. Group 7 contained no Pee Dee lines with slopes different from 1 for more than one trait.

Genotypic Correlations

Genotypic correlations and their standard errors were calculated to determine the genetic relationships between traits among the Pee Dee germplasm lines surveyed in this experiment. Table 4 provides a summary of the genotypic correlations. In terms of the agronomic traits, lint yield was correlated with lint percent (0.82), boll weight (−0.30), seed index (−0.80), and bolls m^{-2} (0.84). These data suggest that selections for higher lint yield are accompanied by lower seed weight and smaller boll size. The data also suggest that selecting for high lint percent and/or bolls m^{-2} is associated with increased yield.

For fiber quality traits, length and strength were highly and positively correlated (0.84). Uniformity was negatively correlated with length (−0.51) and positively correlated with strength (0.80). Elongation was negatively correlated with length (−0.62). Micronaire and fineness were highly and positively correlated (0.94), and both were negatively correlated with length (−0.59 and −0.55) and strength (−0.40 and −0.44). These data suggest that selections can be made that simultaneously improve length and strength, while also lowering micronaire and increasing fineness (lower values are more fine). Correlated selection effects on uniformity and elongation were not clear.

When comparing correlations between agronomic and fiber quality traits, several key findings are evident. Lint percent, lint yield, and bolls m^{-2} are each negatively and unfavorably correlated with length and strength. Correlations between agronomic traits and length were −0.65 (lint percent), −0.60 (lint yield), 0.75 (seed index), and −0.35 (bolls m^{-2}). For strength, correlations with these agronomic traits were −0.44 (lint percent), −0.48 (lint yield), 0.71 (seed index), and −0.29 (bolls m^{-2}). Lint percent, lint yield, and bolls m^{-2} were each positively and unfavorably correlated with micronaire and fineness. Correlations between agronomic traits and micronaire were 0.55 (lint percent), 0.48 (lint yield), −0.40 (seed index), and 0.25 (bolls m^{-2}). For fineness, correlations with agronomic traits

Table 4. Genotypic correlations and their standard errors among cotton agronomic and fiber quality traits.

	Lint yield	Boll weight	Seed index	Bolls m⁻²	Length	Strength	Uniformity	Elongation	Micronaire	Fineness
Lint percent	0.82 (0.06)	−0.30 (0.13)	−0.71 (0.06)	0.53 (0.12)	−0.65 (0.07)	−0.44 (0.09)	0.10 (0.12)	0.72 (0.06)	0.55 (0.09)	0.55 (0.09)
Lint yield	—	−0.30 (0.16)	−0.80 (0.13)	0.84 (0.05)	−0.60 (0.10)	−0.48 (0.11)	0.01 (0.15)	NE†	0.48 (0.12)	0.44 (0.13)
Boll weight	—	—	0.53 (0.11)	−0.65 (0.12)	0.18 (0.14)	0.03 (0.14)	−0.32 (0.14)	−0.39 (0.13)	0.00 (0.15)	0.01 (0.02)
Seed index	—	—	—	−0.76 (0.09)	0.75 (0.05)	0.71 (0.06)	0.27 (0.12)	−0.73 (0.06)	−0.40 (0.11)	0.04 (0.03)
Bolls m⁻²	—	—	—	—	−0.35 (0.14)	−0.29 (0.14)	0.17 (0.15)	0.66 (0.11)	0.25 (0.15)	0.20 (0.16)
Length	—	—	—	—	—	0.84 (0.04)	−0.51 (0.09)	−0.62 (0.07)	−0.59 (0.08)	−0.55 (0.09)
Strength	—	—	—	—	—	—	0.80 (0.05)	NE	−0.40 (0.04)	−0.44 (0.10)
Uniformity	—	—	—	—	—	—	—	−0.01 (0.13)	−0.09 (0.13)	−0.04 (0.13)
Elongation	—	—	—	—	—	—	—	—	0.34 (0.11)	NE
Micronaire	—	—	—	—	—	—	—	—	—	0.94 (0.11)

† NE, not estimated because Restricted Maximum Likelihood (REML) convergence criteria not met.

were 0.55 (lint percent), 0.44 (lint yield), and 0.20 (bolls m⁻²). These data indicate that selections to simultaneously increase lint yield and fiber quality properties continue to be hampered by unfavorable correlations. However, as noted by Campbell et al. (2011), there are specific Pee Dee germplasm lines, including PD 2164 in Group 2, PD 7723 in Group 5, and PD 94042 in Group 8, that combine high lint percent/lint yield and high length/strength.

Attempts were made to evaluate changes in genotypic correlations between agronomic and fiber quality traits across breeding cycles. However, as noted in Holland (2006), small sample sizes within each breeding cycle group prevented accurate genotypic correlation estimates and their 95% confidence intervals. Holland (2006) recommended sample sizes of 75 or greater to accurately estimate genotypic correlations and their 95% confidence intervals. As an alternative, scatterplots were constructed for each breeding cycle group to observe relationships between agronomic and fiber quality traits. Figure 2 shows the relationship between lint percent and length separated by breeding cycle group. Moderate linear relationships were fitted for Groups 1, 2, 3, 4, and 6. In each of these breeding cycle groups, the trend between lint percent and length was negative. For Groups 5, 7, and 8, a linear trend between lint percent and length could not be fitted. These breeding cycle group trends suggest that the negative relationship between lint percent and length decreased across breeding cycles. Scatterplots were also constructed for each breeding cycle group to observe relationships between lint percent and strength, lint yield and length, and lint yield and strength. These plots showed relationships similar to those shown in Figure 2 (data not shown).

CONCLUSIONS

This study demonstrates the impact of G × E interactions and genotypic correlations among agronomic and fiber quality traits for germplasm representative of the 70-yr Pee Dee germplasm enhancement program. Based on a proportional comparison of sums of squares, G × E interactions have significant effects on lint yield, bolls m⁻², boll weight, uniformity, micronaire, and fineness (Table 1). Dissecting the Pee Dee line × environment interaction further showed that the eight breeding cycle groups of the Pee Dee program responded dissimilarly across low to high environmental indices for lint yield, lint percent, boll weight, seed index, strength, length, elongation, and micronaire. Fortunately, it appears that, on average, G × E interactions were due to changes in magnitude rather than change in rank. This has important breeding implications as G × E interactions due to changes in rank make progress very difficult in breeding programs. Such interactions typically require a greater number of field evaluations that ensure target growing environments are adequately represented.

The Pee Dee germplasm line–specific stability parameters estimated in this study demonstrate that the majority of Pee Dee germplasm lines surveyed in this report display slopes
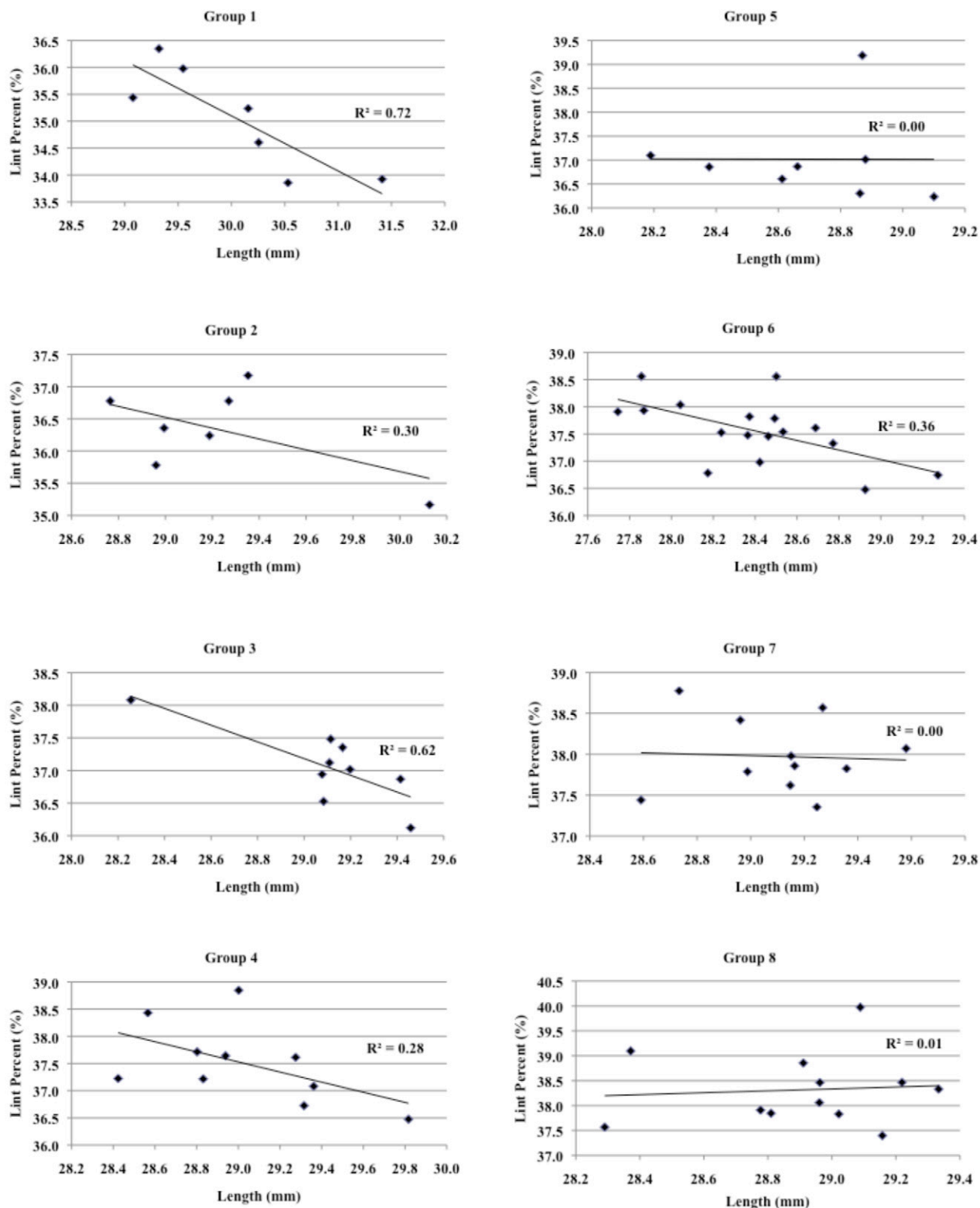
Figure 2. Relationship between mean lint percent and length for eight Pee Dee cotton germplasm groups.

equal to 1. Hence, most of the Pee Dee germplasm lines display relatively stable agronomic and fiber quality performance across the southeastern U.S. growing environments represented in this study. However, there were several Pee Dee lines that displayed instability for specific traits across these growing environments. Overall, Pee Dee line instability was most prevalent for lint percent and elongation. Pee Dee

line stability was most prevalent for micronaire and fineness. Stability trends across the eight breeding cycle groups were not obvious, although Group 7 contained the fewest number of unstable Pee Dee lines. This indicates that repeated rounds of selection for fiber quality traits has not led to changes in stability in Pee Dee germplasm. This is likely a consequence of selection practices being focused on improving fiber traits

rather than fiber trait stability over eight cycles of breeding. Stability analysis identified several Pee Dee lines that appear to be unstable for three or more traits. These include AC 241 and FTA 266 in Group 1, PD 7586 in Group 5, PD 0781 in Group 6, and PD 93034 in Group 8.

The genotypic correlations calculated in this study correspond to those reported in previous studies. The correlations among lint yield and yield component traits confirm that lint yield progress reported by Campbell et al. (2011) corresponds to increased lint percent and bolls m^{-2}. The favorable correlations among strength, length, micronaire, and fineness provide evidence that future breeding efforts based on intermated Pee Dee germplasm lines can result in the simultaneous improvement of all four traits. However, several of the negative genotypic correlations between agronomic and fiber quality performance continue to impede progress to simultaneously increase lint yield and fiber quality. Although genotypic correlations could not be calculated and directly compared across the eight breeding cycle groups, a visual inspection of scatterplots suggests that the negative relationship between agronomic performance and fiber quality is lessening over time to some degree. This supports the report by Culp et al. (1979) that repeated intermating among Pee Dee germplasm has been successful in breaking the negative linkage between agronomic performance and fiber quality in rare cases. In that study, Culp et al. (1979) cited the work of Hanson (1959), which predicted intermating would be expected to break up small linkage blocks in self-pollinated crops. Several Pee Dee lines appear to be rare recombination products of intermating that can be further exploited to simultaneously increase lint yield and fiber quality performance. These include PD 2164 in Group 2, PD 7723 in Group 5, and PD 94042 in Group 8. Culp et al. (1979) also identified PD 2164 as a putative, rare recombinant. Interestingly, Culp and Green (1992) noted that PD 2164 was a key parent used to develop the elite DES germplasm pool that is present in the pedigrees of many current commercial cultivars (W.R. Meredith, Jr., unpublished data, 2011). Cotton breeders can readily use the information provided herein as a resource to select specific Pee Dee germplasm lines for specific breeding purposes. This would include the ability to select Pee Dee germplasm lines for agronomic performance and fiber quality stability. It would also include the selection of unique germplasm lines that appear to represent rare recombination events that break the negative linkage between agronomic performance and fiber quality.

Acknowledgments

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