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Assessment of genotype × environment interactions for yield and fiber quality in cotton performance trials*

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Summary

Plant breeding programs involving a wide range of crop plants routinely practice selection (directly or indirectly) for genotypes that display stability for a given trait or set of traits across testing environments through the genotype evaluation process. Genotype stability for trait performance is a direct measure of the presence and effect of genotype × environment interactions, which result from the differential performance of a genotype or cultivar across environments. The genotype evaluation process also requires selection of the proper field trial locations that best represent the target environments the breeding program is directed toward. In this study, we assessed the extent to which genotype × environment interactions affected agronomic performance (lint yield, gin turnout) and fiber quality (fiber length, fiber strength, uniformity index, micronaire, fiber elongation) in a series of cotton (*Gossypium hirsutum*) performance trials in 12 location–year environments in South Carolina. Genotype × environment interactions affecting lint yield were larger in higher yielding environments, while interactions for fiber strength were greater for genotypes with lower mean fiber strength values. Two regions within the South Carolina cotton production areas were identified as proper testing locations for lint yield performance, while testing for fiber strength can be accomplished in any location within the statewide cotton production areas.

Abbreviations: AMMI: additive main effects and multiplicative interactions model; ANOVA: analysis of variance; G × E: genotype × environment interaction; IPCA: interaction principal component axis

Introduction

The differential response of a genotype or cultivar for a given trait across environments is defined as the genotype × environment interaction (G × E). G × E is an important and essential component of plant breeding programs dedicated to cultivar development. Bilbro and Ray (1976) indicated that a successful breeding program should focus efforts on genotype yield level (average yield compared to standards), adaptation (what environment does the genotype best perform in), and stability (how consistent does the genotype yield compared to others). When identifying improved genotypes and potential cultivars, plant breeders routinely practice selection (directly or indirectly) for genotypes that display stability for a given trait or set of traits across testing environments. Eberhart and Russell (1966) defined stability as the ability to show a minimum interaction with the environment. Hence, the stability of genotype performance is directly related to the effect of G × E.

Breeding for genotype stability is accomplished with repetitive field testing, trait evaluation, and selection of genotypes that rank at or near the top of a series of individual field trials conducted across a range of environments and years. Comparing the ranks of genotypes in individual field trials is an example of

the indirect selection for stability of performance. Directly selecting for genotype stability can also be accomplished by conducting repetitive field testing and trait evaluation while utilizing statistical analyses that directly test for the presence of G × E and measure the stability of an individual genotype. The presence of G × E and the stability of genotype performance can be evaluated using numerous statistical methods. Excellent reviews of current statistics used to test and measure genotype stability are provided by Lin et al. (1986) and Piepho (1999).

Another important part of the genotype evaluation process is selecting the appropriate field trial locations that best represent the target environments for which the breeding program is directed toward. The term mega-environment describes the separation of a crop growing area into different target zones (Gauch & Zobel, 1997). Gauch and Zobel (1997) contend that subdividing a crop's growing region into several mega-environments implies higher heritabilities and faster progress for plant breeders, potentially stronger competitiveness for seed producers, and higher yields for growers. Classifying environments into small groups or mega-environments can be accomplished using various statistical procedures. These procedures include cluster analysis, which categorizes environments using principal component analysis (Carver et al., 1987; Geng et al., 1990), and the additive main effects and multiplicative interaction (AMMI) model that combines analysis of variance and principal component analyses (Gauch & Zobel, 1997).

In upland cotton (*Gossypium hirsutum* L.) cultivar development programs, genotype stability for agronomic performance and fiber quality is an important breeding objective (Geng et al., 1987). Yield stability was documented as the second most important criteria for selecting parents to use in hybridization, with the number one criteria being yield potential, in a 1999 survey of private and public U.S. cotton breeders (Bowman, 2000). Previous research suggests that selection of superior genotypes for lint yield in cotton performance trials is impacted by G × E (Bilbro & Ray, 1976; Geng et al., 1987; Geng et al., 1990; Meredith, 1984; Meredith & Bridge, 1984). G × E also impacts selection of superior genotypes for fiber quality in cotton performance trials, but to a lesser degree than G × E for lint yield (Geng et al., 1987; Paterson et al., 2003).

The objectives of the current study are to evaluate the presence of G × E for agronomic performance (lint yield, gin turnout) and fiber quality (fiber strength, fiber length, uniformity index, micronaire, and fiber elongation) present in data collected from South Carolina cotton performance trials and to determine the value of testing environments where the trials were conducted. Information gained from this assessment should facilitate the design of a testing strategy to assist in selecting superior genotypes for target growing environments.

Materials and methods

Plant materials and trait evaluations

Performance data of eight cultivars evaluated from 2000–2003 in 12 location–year environments was used in this study. The eight cultivars, 'Delta and Pine Land 436R' (DP436R), 'Delta and Pine Land 451BR' (DP451BR), 'Fibermax 958' (FM958), 'Fibermax 966' (FM966), 'Suregrow 215BR' (SG215BR), 'Suregrow 521R' (SG521R), 'Stoneville 4793R' (ST4793R), and 'Stoneville 4892BR' (ST4892BR), were selected from performance trials because each was evaluated in all 12 environments. Performance trials included five test sites representing cotton producing areas in South Carolina, which included the Clemson University Pee Dee Research and Education Center in Darlington County (2000, 2001, 2002), the Clemson University Edisto Research and Education Center in Barnwell County (2000, 2001, 2002, 2003), and on-farm tests in Calhoun (2002), Lee (2002, 2003), and Dillon Counties (2002, 2003).

The experimental design used in each trial was a randomized complete block with four replicates. Each entry was grown in a two-row plot 10.7 m long with 96.5 cm spacing between rows. Plots were managed conventionally and followed the established local practices. Each plot was harvested with a mechanical cotton picker that harvested both rows of each plot, and total seed cotton weight was recorded. A "grab" lint sample was taken from the mechanical picker after harvesting each plot to determine gin turnout and fiber quality properties. Gin turnout was determined by dividing the weight of the lint sample after ginning by the weight of the lint sample before ginning. Lint yield was calculated by multiplying the gin turnout by the seed cotton yield. A portion of the lint sample was sent to Starlab Inc. (Knoxville, TN) for determination of fiber length, fiber strength, uniformity index, fiber elongation, and micronaire by High Volume Instrumentation (HVI) analyses. All traits were measured in each of the 12 location–year environments with the exception of fiber elongation, which was measured in five location–year environments.

Statistical analyses

Data for each trait were analyzed for normality by PROC UNIVARIATE (SAS Institute, 1999). An analysis of variance (ANOVA) was conducted in each environment by PROC GLM coupled with the RANDOM statement to test significant differences among cultivars (SAS Institute, 1999). Homogeneity of variance tests were conducted to determine if data from individual environments (E) could be pooled to evaluate G × E using a combined ANOVA. For the combined analysis, variation was partitioned into relevant sources of variation to test for differences among genotypes and for the presence of G × E.

To evaluate genotype stability and further dissect G × E, stability parameters (Eberhart & Russell, 1966) were estimated, with the 12 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. The regression coefficient (b_i) and deviations from regression (s_d^2) were the parameters used to compare environmental responses of genotypes. G × E sums of squares was partitioned into sums of squares due to (i) regression of cultivars on the environmental index and (ii) pooled deviations from regression. The G × E linear interaction mean square provided a test of genetic differences among cultivars for their response to linearly arrayed environmental productivity. The pooled deviation mean square provided a test of genetic differences among genotypes for their deviation from regression.

Similarities among test environments based on environmental main effects and G × E interaction effects were evaluated using AMMI analyses (Agrobase Generation II, 2004). AMMI analyses use a combination of analysis of variance and principal component analysis. Briefly, analysis of variance is used to partition variance into three components: genotype deviations from the grand mean, environment deviations from the grand mean, and G × E deviations from the grand mean. Subsequently, principal component analysis is used to partition the G × E deviations into different interaction principal component axes (IPCA) that can be tested for statistical significance through ANOVA. Interpretation of AMMI analyses follows by plotting the IPCA of G × E in various types of biplots. In addition, following the approach illustrated by Gauch and Zobel (1997), the relevant portion of G × E was calculated for each trait to avoid spurious interpretation of statistical results. Factoring the errors from uncontrolled variation ("noise") out of the total G × E sums of squares is important because most of the noise appears in the interaction, since the interaction contains a majority of the treatment *df* (Gauch & Zobel, 1997). "Noise" sums of squares, "real structure" sums of squares, and target relevant variation percentage were calculated as described by Gauch and Zobel (1997). The "noise" sums of squares is calculated by the multiplication of MS (Error) × *df* (G × E). Factoring the "noise" sums of squares out of the G × E sums of squares provides the "real structure" sums of squares [SS (G × E) − SS ("noise")]. It follows that the total relevant variation within the total treatment sums of squares [SS (Genotype) + SS (G × E)] is calculated by the addition of SS (Genotype) + SS ("real structure"). Hence, the target percentage of the relevant variation explained by IPCA in the AMMI analysis should equal SS (relevant variation)/SS (treatment). For a full description of AMMI models and discussion of various biplot techniques, see Gauch and Zobel (1996, 1997).

Results and discussion

Homogeneity of variance tests indicated homogeneous error variance for each trait in each of the 12 location–year environments and allowed for a combined, across environment analysis. ANOVA across environments indicated significant variation among genotypes and for the G × E for each of the seven traits measured (Table 1). For each of the traits, the percentage sums of squares remaining among environment, genotype, and G × E ranged from 63% to 95% after removing sums of squares due to error and replication (Table 2). The environment accounted for a high percentage of sums of squares remaining for lint yield (90%) and micronaire (81%), and genotype accounted for a large percentage of sums of squares remaining for fiber elongation (84%). G × E effects accounted for a relatively small amount of the sums of squares remaining for all traits and ranged from 3–24%. However, the G × E sums of squares component was four times larger than the genotype component for lint yield and roughly the same for uniformity index and micronaire.

Significant G × E variation for each of the traits allowed for subsequent analysis of the G × E using ANOVA, genotype stability statistics, and AMMI analyses. Using ANOVA, the linear component of G × E revealed significant differences in slope among the genotypes (linear) for lint yield and fiber strength, with no differences in slope for gin turnout, fiber length,

Table 1. Analysis of variance of seven traits for eight genotypes included in South Carolina cotton variety trials from 2000–2003

		Lint yield (kg ha^{-1})	Gin turnout (%)	Fiber length (cm)	Fiber strength (g tex^{-1})	Uniformity index (%)	Micronaire		Fiber elongation
Source	df	MS	MS	MS	MS	MS	MS	df	MS
Environment (E)	11	4182298.8**	47.4**	0.262**	28.0**	20.7**	4.73**	4	8.8**
Rep (E)	36	95819.3**	4.5	0.012**	3.3**	1.8**	0.07**	15	0.2**
Genotype (G)	7	173201.7**	184.9**	0.396**	204.0**	15.3**	0.92**	7	32.3**
G × E	77	52530.5**	5.9**	0.006**	2.4**	1.4**	0.07**	28	0.3**
Pooled error	252	25539.6	3.8	0.003	0.8	0.7	0.04	105	0.1
Mean		1024.0	39.5	2.750	29.0	82.7	4.44		8.7
CV		15.6	5.0	2.160	3.2	1.1	4.36		3.4

**Significant at the 0.01 level of probability.

Table 2. The portion of sums of squares (SS) attributed to environment, genotype, and genotype × environment interaction (G × E) as a percentage of the total sums of squares remaining after removing sums of squares due to replication and error

	Lint yield	Gin turnout	Fiber length	Fiber strength	Uniformity index	Micronaire	Fiber elongation
Source sums of squares	% SS	% SS	% SS	% SS	% SS	% SS	% SS
Pooled error + Rep (E)	16	33	18	14	27	16	5
Remaining[a]	84	67	82	86	63	84	95
Environment (E)	90	23	47	14	52	81	13
Genotype (G)	2	57	45	63	25	10	84
G × E	8	20	8	8	24	9	3

[a]The percentage sums of squares remaining after that due to error and replication have been subtracted from the total sums of squares.

uniformity index, micronaire, and fiber elongation (Table 3). Hence, genotypes responded dissimilarly across a low to high gradient of environmental indices for lint yield and fiber strength, while responding similarly for gin turnout, fiber length, uniformity index, micronaire, and fiber elongation. Regressing genotype means on an environmental index for lint yield and fiber strength provided a visual representation of the significant G × E detected for those traits (Figure 1). In terms of lint yield, genotypes performed more similar to one another in lower yielding environments, with yield differences becoming greater in more productive, higher yielding environments. The differential between genotypes for fiber strength was similar across environments

Table 3. Partitioning of genotype × environment interactions (G × E) into linear and nonlinear components. Mean squares and significance levels of *F*-tests from the regression analysis of seven traits for eight genotypes combined over 12 environments in South Carolina from 2000–2003

		Lint yield (kg ha^{-1})	Gin turnout (%)	Fiber length (cm)	Fiber strength (g tex^{-1})	Uniformity index (%)	Micronaire		Fiber elongation
Source	df	MS	MS	MS	MS	MS	MS	df	MS
Genotypes	7	60560.1**	46.5**	0.100**	50.7**	3.9**	0.23**	7	8.03**
Environment (linear)	1	11502450.5**	130.9**	0.717**	76.5**	56.8**	12.78**	1	8.76**
G × E (linear)	7	26633.6*	1.2	0.002	1.4**	0.4	0.02	7	0.13
Pooled deviations	80	10322.4	1.3	0.001	0.4	0.3	0.01	24	0.05
Pooled error	252	25539.6	3.8	0.003	0.8	0.8	0.04	105	0.09

*Significant at the 0.05 level of probability.
**Significant at the 0.01 level of probability.

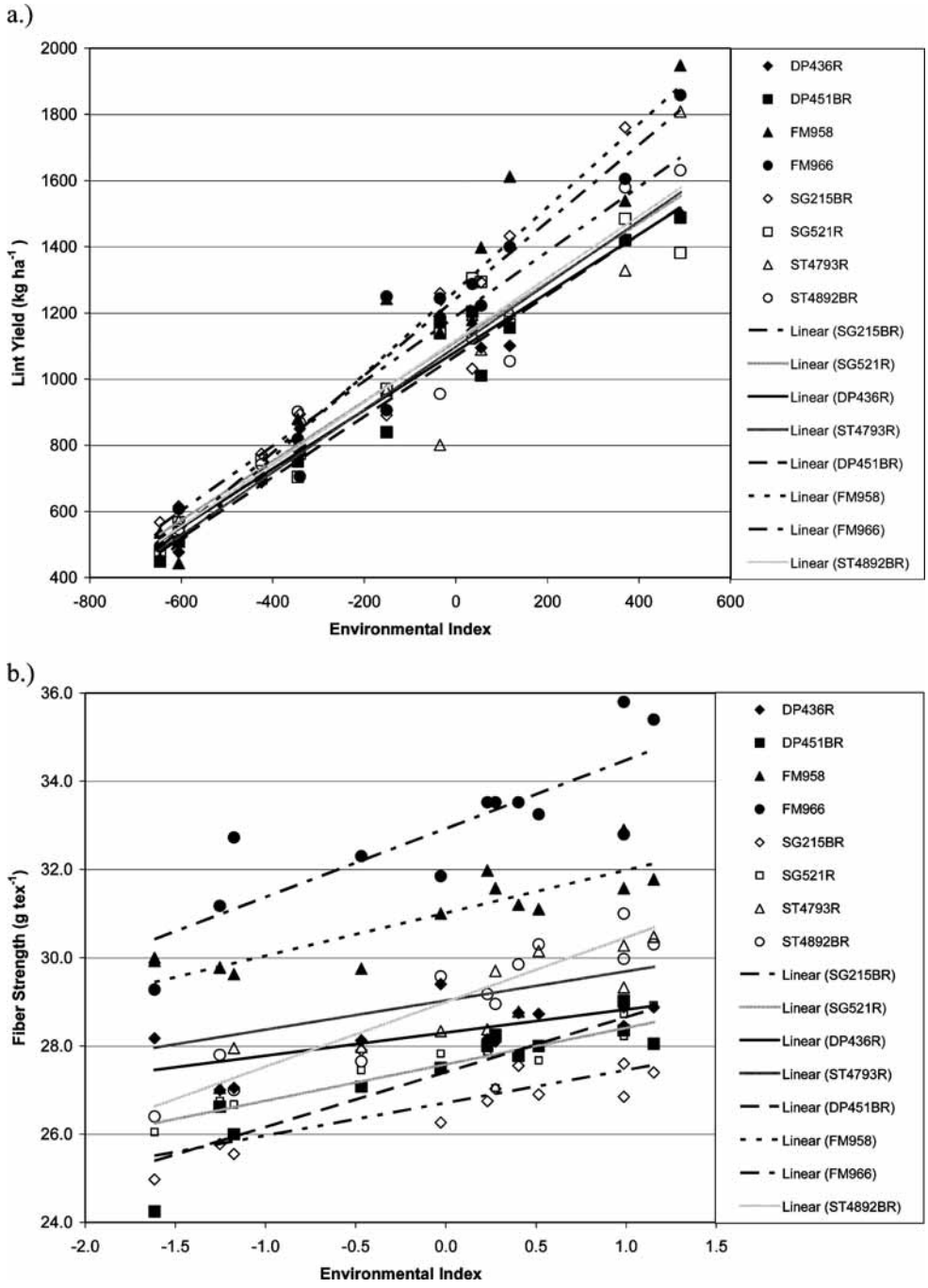

Figure 1. Regressions of eight genotype means on an environmental index estimated from the mean of genotypes grown in each of 12 South Carolina environments minus the grand mean for (a) lint yield and (b) fiber strength.

for most genotypes, although genotypes with lower average fiber strength were more sensitive to the gradient of environmental indices. Interactions due to changes in rank and in magnitude were evident for some of the genotypes evaluated.

AMMI analysis of variance indicated significant variation for environments, genotypes, and G $\times$ E for lint yield and fiber strength (Table 4). The errors from uncontrolled variation were calculated using the methods described by Gauch and Zobel

Table 4. AMMI analysis of variance and percent genotype × environment interaction (G × E) explained for lint yield and fiber strength for eight genotypes included in South Carolina variety trials from 2000–2003. The percent genotype × environment interaction (G × E) explained by each statistically significant interaction principal component axis (IPCA) is given

		Lint yield (kg ha^{-1})				Fiber strength (g tex^{-1})			
Source	df	SS	MS	Prob > *F*	% G × E Explained	SS	MS	Prob > *F*	% G × E Explained
Total	383	61137644.7			–	2240.7			–
Rep (E)	36	3449493.9	95819.3	0.000	–	119.5	3.3	0.000	–
Treatments	95	51252174.0	539496.6	0.000	–	1908.9	20.1	0.000	–
Environment (E)	11	45994850.5	4181350.0	0.000	–	306.3	27.8	0.000	–
Genotype (G)	7	1211552.3	173078.9	0.002	–	1421.1	203.0	0.000	–
G × E	77	4045771.2	52542.5	0.000	–	181.5	2.4	0.000	–
IPCA 1	17	1841922.3	108348.4	0.000	45.5	88.1	5.2	0.000	48.6
IPCA 2	15	1015577.6	67705.2	0.001	25.1	38.3	2.6	0.000	21.1
IPCA 3	13	549135.7	42241.2	0.071	–	26.6	2.0	0.004	14.7
IPCA 4	11	273996.5	24908.8	0.469	–	14.4	1.3	0.114	–
IPCA 5	9	181524.2	20169.4	0.626	–	8.9	1.0	0.312	–
IPCA 6	7	149393.1	21341.9	0.559	–	3.5	0.5	0.762	–
IPCA 7	5	34221.7	6844.3	0.930	–	1.6	0.3	0.863	–
Pooled error	252	6435976.8	25539.6		–	212.3	0.8		–

(1997). For lint yield, the interaction contained 49% noise and 51% real structure, with the relevant (target) variation being 6.4% of the treatment sums of squares. For fiber strength, the interaction contained 34% noise and 66% real structure, with the relevant (target) variation being 81% of the treatment sums of squares. Treatment sums of squares variation explained above target percentages would be attributed to noise.

Using the full AMMI model, the G × E was partitioned into seven interaction principal component axes (IPCA), with the first two IPCA being significant for lint yield, and the first three IPCA significant for fiber strength. For lint yield, the first two IPCA components were significant and explained 45.5 and 25.1% of the G × E interaction, respectively. The first IPCA component explained 6% of the treatment sums of squares ((1841922.3 + 1211552.3)/51252174.0) which was very close to the target percentage sums of squares explained (6.4%). For fiber strength, the first three IPCA components were significant and explained 48.6, 21.1, and 14.7% of the G × E interaction, respectively. The first IPCA component explained 79% of the treatment sums of squares ((88.1 + 1421.1)/1908.9) which was very close to the target percentage sums of squares explained (81%).

To further investigate main effects and interactions across location–year environments, two biplots were constructed for lint yield and fiber strength. One set of biplots focused on locations within a year for lint yield (Figure 2a) and fiber strength (Figure 3a). The other set of biplots focused on year differences across individual testing sites for lint yield (Figure 2b) and fiber strength (Figure 3b). Main effect differences are represented and interpreted in each biplot by comparing the average trait value for each location along the *x*-axis. Main effect differences are evident when large differences exist among average location trait values. Interaction effects are represented and interpreted in each biplot by comparing the interaction score (IPCA) for each location along the *y*-axis. Locations with dissimilar interaction scores indicate dissimilar interaction effects across locations, while locations with interaction scores close to zero indicate negligible interaction effects.

Most of the location–year testing environments displayed similar interaction effects for lint yield, as most environments fell within the upper left-hand quadrant with positive interaction scores and below average lint yields (Figures 2a, 2b). However, the Blackville environments (B00, B01, B02, B03) displayed patterns different than other location–year environments as B00, B01, and B03 fell within the lower right hand quadrant with negative interaction effects and average or above average lint yields. Hence, the Blackville testing environments on average appear to represent a different target environment than Florence, Lee, Calhoun, and Dillon environments evaluated in this study. This indicates

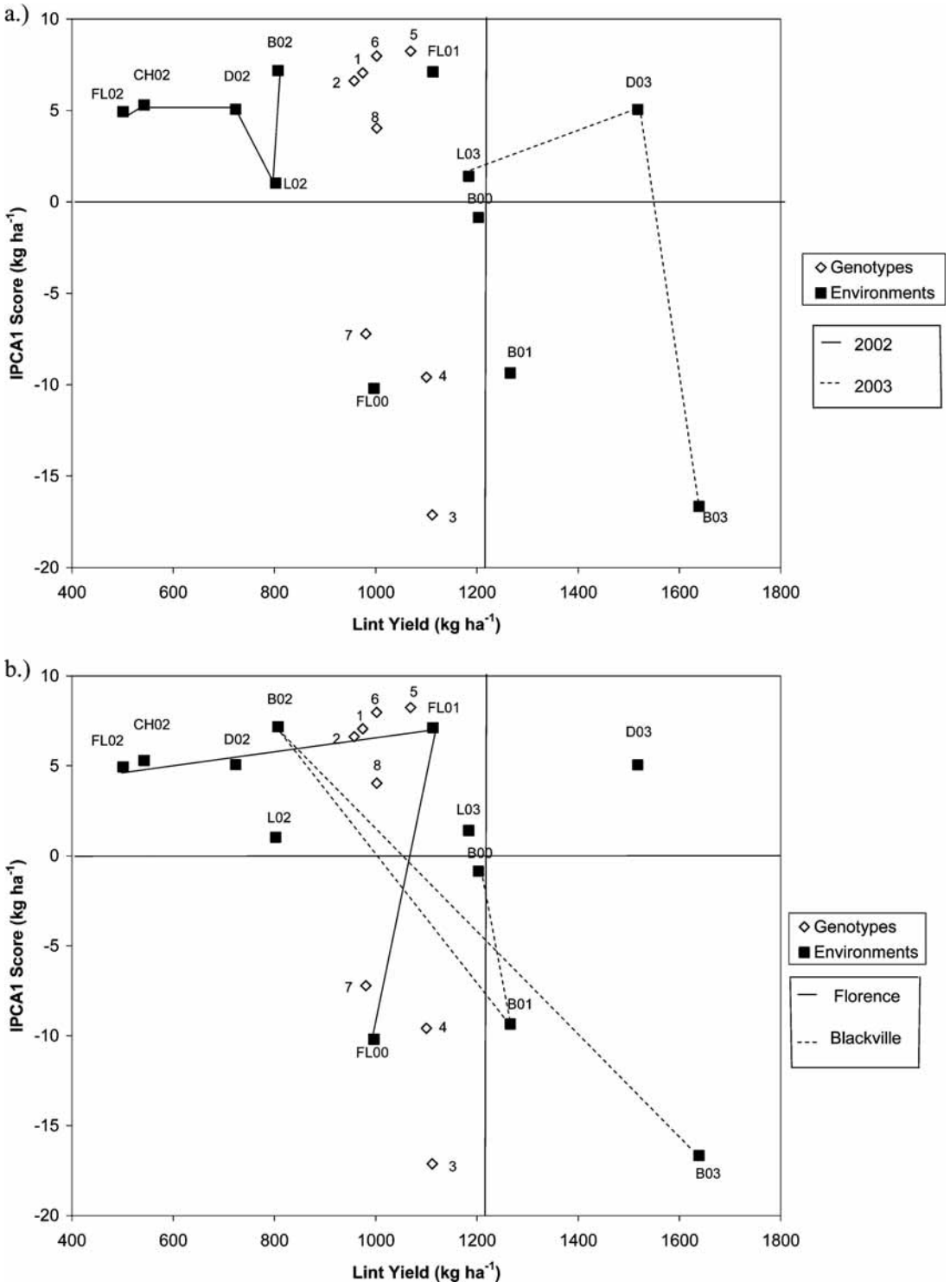

Figure 2. AMMI plots for lint yield of eight genotypes (1, DP436RR; 2, DP451BR; 3, FM958; 4, FM966; 5, SG215BR; 6, SG521RR; 7, ST4793RR; 8, ST4892BR) evaluated at 12 locations (Blackville 2000, 2001, 2002, 2003 (B00, B01, B02, B03); Calhoun 2002 (CH02); Dillon 2002, 2003 (D02, D03); Florence 2000, 2001, 2002 (FL00, FL01, FL02); Lee 2002, 2003 (L02, L03)) presented in terms of (a) years and (b) locations.

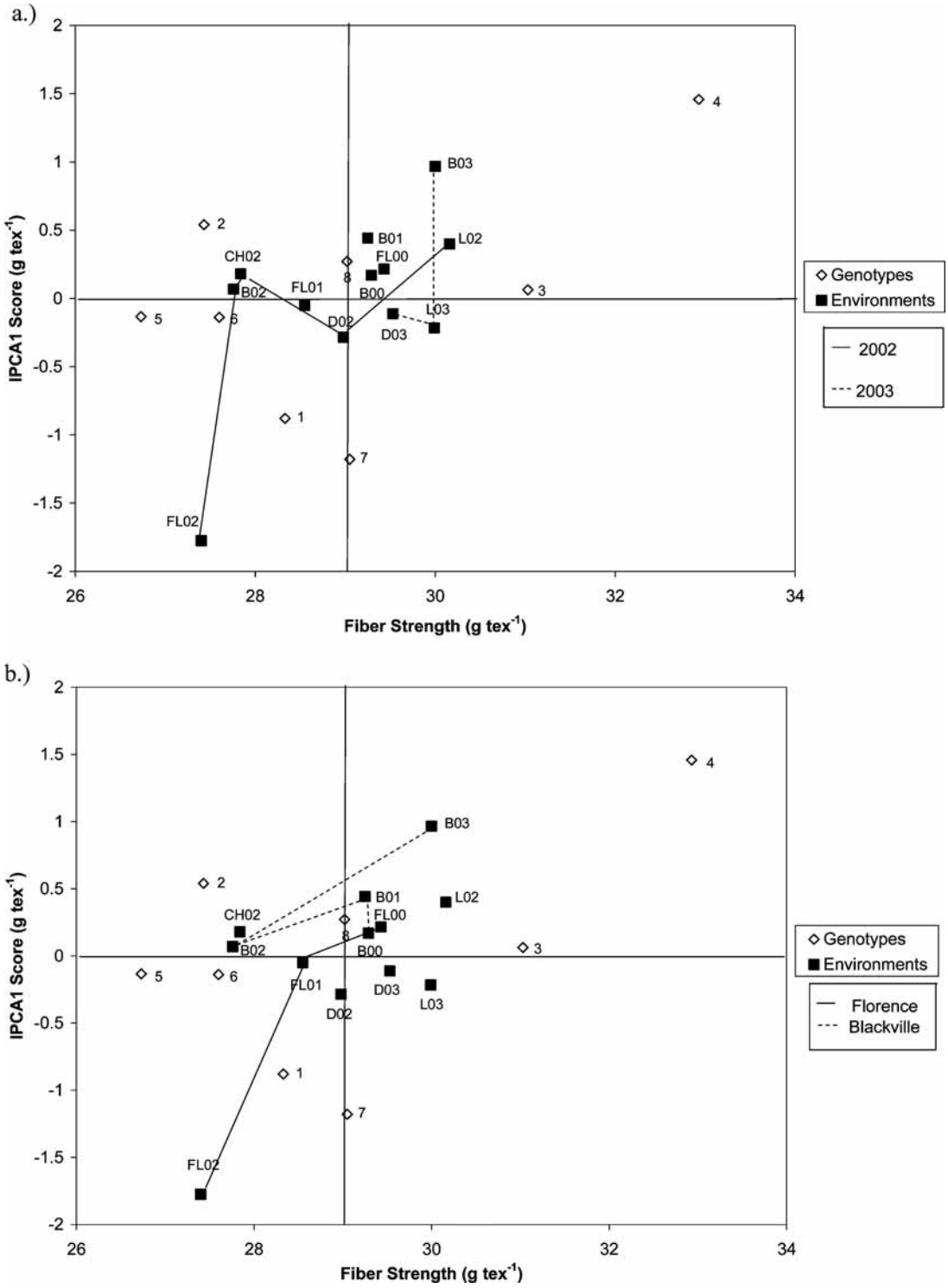

Figure 3. AMMI plots for fiber strength of eight genotypes (1, DP436RR; 2, DP451BR; 3, FM958; 4, FM966; 5, SG215BR; 6, SG521RR; 7, ST4793RR; 8, ST4892BR) evaluated at 12 locations (Blackville 2000, 2001, 2002, 2003 (B00, B01, B02, B03); Calhoun 2002 (CH02); Dillon 2002, 2003 (D02, D03); Florence 2000, 2001, 2002 (FL00, FL01, FL02); Lee 2002, 2003 (L02, L03)) presented in terms of (a) years and (b) locations.

that testing in Blackville and one of the remaining environments (i.e. Florence) should represent two 'mega-environments' within South Carolina cotton producing areas. In 2002, main effect differences in average lint yield were evident across locations, but interaction effects were negligible (Figure 2a). In 2003, interaction effects were greater among the three locations, with main effect differences also being evident. This indicated that dissimilar interaction effects across environments were more prevalent in higher yielding environments such as those in 2003 and similar interaction effects more prevalent in lower yielding environments such as those in 2002. Focusing on Florence (FL00, FL01, FL02) and Blackville (B00, B01, B02, B03) indicates sizeable interaction and main effect differences across years for those two testing sites (Figure 2b). Hence, large differences in interaction effects are present in trials conducted over years at the same location.

In terms of fiber strength, most of the location–year testing environments displayed small interaction effects, as 10 of the 12 environments displayed interaction effects between -0.5 and 0.5 g tex^{-1} (Figures 3a, 3b). In 2002, main effect differences in average fiber strength were evident across locations, but interaction effects were negligible except for the Florence (FL02) environment (Figure 3a). In 2003, main effect differences in average fiber strength were not as distinct, with interaction effects negligible except for the Blackville (B03) environment. Focusing on Florence (FL00, FL01, FL02) and Blackville (B00, B01, B02, B03) testing sites also illustrates primarily main effect differences across years for those two environments with minor interaction effects (Figure 3b). Hence, interaction effects measured within this set of experiments result primarily from the interaction effects accounted for by two of the 12 location–year environments. This indicates that testing genotypes for fiber strength across multiple environments may not be necessary as differences across environments are primarily due to main effects and not interaction effects. However, the larger interaction effects present for FL02 (-1.8 g tex^{-1}) and B03 (1.0 g tex^{-1}) demonstrates that outlier location–year environments do exist and should be noted.

Conclusions

This study demonstrates the importance of implementing direct analyses of G $\times$ E interactions as they relate to genotype performance and classification of testing environments. G $\times$ E interactions were significant for all of the agronomic and fiber quality traits measured, but clearly largest in effect for lint yield as the G $\times$ E sums of squares component was four times larger than the genotype component for lint yield. Genotype stability analysis revealed that genotypes performed dissimilar across the gradient of environmental indices used in this experiment for lint yield and fiber strength. Further analysis indicated that genotypes produced more similar lint yields in lower yielding environments and dissimilar in higher yielding environments. In terms of fiber strength, genotypes with lower average fiber strength performed more dissimilar across environments than genotypes with higher average fiber strength. Similarly, Geng et al. (1987) found that high yielding genotypes showed decreased genotype stability for lint yield and genotypes with higher average fiber quality scores showed increased genotype stability for fiber quality in their analysis of California cotton performance trials. Hence, plant breeding efforts aimed at developing genotypes with high lint yield potential in South Carolina may result in a sacrifice of genotype yield stability or adaptability, as was also proposed by Geng et al. (1987) in California. In contrast, breeding efforts aimed at developing genotypes with higher fiber strength should not result in lower genotype stability for fiber strength.

AMMI analyses conducted in this study provide a framework for identifying target testing environments for breeding efforts in South Carolina. In a similar study aimed at quantifying and classifying location effects on cotton cultivar testing programs using a similar approach, Geng et al. (1990) separated the entire US cotton producing area into four target zones or mega-environments. In the current study, mega-environments within the state of South Carolina are identified as testing environments for cotton performance trials in South Carolina. This study indicates that testing for lint yield should be conducted in two mega-environments within the South Carolina cotton producing areas that include sites located in northeast (e.g. Florence) and southern (e.g. Blackville) areas of the state. In contrast, testing for fiber strength in South Carolina can be accomplished without the need to target genotypes to specific mega-environments within the state. For regionally based plant breeding programs targeted at geographically small growing areas, identifying mega-environments to conduct genotype performance trials that provide the most relevant information is increasingly necessary.

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