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Combining abilities and inheritance of yield components in influential Upland cotton varieties

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Abstract

Influential cotton lines are those that contributed a larger proportion of genes to modern cotton cultivars than any other germplasm lines. The most influential cultivars from 16 cotton breeding programs were identified based on the analysis of the pedigree of 260 cultivars released between 1970 and 1990 in USA. Ten most influential cultivars were selected for a diallel analysis using the procedure in Griffing's Method 2. The parental cultivars varied significantly for bolls per plant, boll weight, lint percentage, seed index, and lint index, and responded consistently to the two different environments. Mean squares of GCA effects were 39.1 for bolls per plant, 6.0 for boll weight, 108.4 for lint percentage, 56.3 for seed index, and 8.2 for lint index, respectively, all of which were highly significant ($P < 0.01$), indicating that additive effects played important roles in inheritance of the traits. SCA effects were highly significant ($P < 0.01$) for boll weight (0.5), lint percentage (3.2), seed index (1.3), and lint index (0.2), suggesting that these traits were also controlled by non-additive effects. The ratios of mean squares, 2GCA / (2GCA + SCA), for bolls per plant, boll weight, lint percentage, seed index, and lint index were 0.96, 0.96, 0.99, 0.99, and 0.99, respectively, indicating that additive effects were much more important in inheritance of the traits than non-additive effects. Narrow-sense heritability ranged from 0.15 to 0.79 and broad-sense heritability from 0.21 to 0.88 for the traits.

Keywords: yield components, combining ability, heritability, influential cotton varieties.
Abbreviations: *ANOVA*, Analysis of Variance, *GCA*, General Combining Ability, *LSD*, Least Significant Difference; *SCA*, Specific Combining Ability.

Introduction

The U.S. cotton yield per unit of area has increased steadily since the thirties of last century. The national average yield of Upland cotton fluctuated around a mean of 213 kg ha^{-1} yr^{-1} of lint with no upward or downward trends from 1866 to 1936 (Miller, 1977). Meredith and Bridge (1982) reported that the national cotton yield rose rapidly from 1936 through 1960, with an average increase of 10.4 kg ha^{-1} yr^{-1}. During the period of 1961 to 1988, the average rate of gain in the national cotton yield was 5.6 kg ha^{-1} yr^{-1} (Culp and Green, 1992). Cotton yield continued to increase but the rate has decreased since 1988 (Meredith, 2000; Lewis, 2001). Yield increases can be attributed to technological advances in production, such as the use of higher yielding cultivars, commercial fertilizer, irrigation, effective pesticides, and mechanization (Culp and Green, 1992).

Several research groups have compared the performance of obsolete and current cultivars for yield and fiber quality. Bridge et al. (1971) and Bridge and Meredith (1983) reported that genetic gain in lint yield averaged 10.2 and 9.5 kg ha^{-1} yr^{-1} in 1968 and 1969, and 1978 and 1979, respectively, in the Mississippi Delta. Hoskinson and Stewart (1977) compared two old cultivars Deltapine A and Carolina Dell with four modern cultivars in Tennessee and found that both obsolete cultivars produced significantly less lint and matured later than the lowest yielding modern cultivars. Bassett and Hyer (1985) estimated genetic gain in lint yield of the Acala cottons in California, since 1939, at 8.0 kg ha^{-1} yr^{-1}. Culp and Green (1992) evaluated 29 commercial cultivars and PD germplasm lines and found lint yield increases of 9.2 kg ha^{-1} yr^{-1}. Cotton yield in Acala 1517 cultivars from the New Mexico State University breeding program increased at an average rate of 1.4% per year from 1930 to 2004 (Zhang et al., 2005). Therefore, the improved cultivars have played an important role in increasing cotton yield.

Between 1970 and 1990, 290 cotton cultivars were released in USA, 285 being Upland cotton cultivars and 5 being Pima cotton cultivars (Calhoun et al., 1994). After investigating on the contribution of various breeding programs to these cultivars, Bowman et al. (1995, 1996, 1997) found that about two-thirds of the cultivars were developed by 17 different breeding programs and every major breeding program had its most influential cultivars that or whose progenies were frequently used for crosses for the development of new cultivars. May et al. (1995) indicated that a germplasm usage trend in the late 1980s was the repeated mating of genetically related materials, or reselection within germplasm to develop proprietary cultivars. Likewise, improvement of fiber strength from 1980 to 2000 was mainly dependent on the Acalas from New Mexico State University and the germplasm from the USDA-ARS Pee Dee program, which supplied 25% and 12.5% of the high fiber strength genes, respectively (Bowman and Gutierrez, 2003). The similar trends were found in other major crops. In dent corn, Mikel and Dudley (2006) determined that most contemporary North American hybrids share ancestry with at least one of eight inbred progenitors. In soybean, the cultivar A3127 is a major progenitor of proprietary cultivars registered from 1999 to 2008 and 23% of 494 cultivars have a

Table 1. Origins of the most influential cotton cultivars used in this study

Most influential cultivar	Breeding program
McNair 235	McNair/Northrup King
Coker 100W	Coker Pedigreed Seed Co
Paymaster 54	Paymaster/Cargill Seeds
Stoneville 2	Stoneville Pedigreed Seed Co.
Lankart 57	Lankart Seed Farms
PD 2165	USDA-ARS & South Carolina AES
Deltapine 15	Delta and Pine Land Co.
CA 614	Texas AES-Lubbock
DES 56	Delta Experiment Station, MS
Delcot 277	Missouri AES

Table 2. Mean squares from analysis of variance and yield components of ten influential cotton varieties at Winnsboro and St. Joseph, LA, in 1997

Source	df	B/P[1]	BW	LP	SI	LI
Location	1	160.3**	4.5**	22.9*	0.02	2.4*
Rep(L)	4	3.4	0.2	1.5	0.48	0.3*
Parent	9	11.4**	3.4**	22.4**	11.72**	1.8**
P x L	9	2.1	0.1	1.3	0.47	0.1
Error	36	2.2	0.1	0.7	0.27	0.1

, * Significant at the 0.05 and 0.01 probability levels, respectively. [1] B/P = bolls per plant; BW = boll weight; LP = lint percentage; SI = seed index; LI = lint index.

Table 3. Mean performance for yield components of ten influential cotton varieties at Winnsboro and St. Joseph, LA, in 1997

Parent	B/P[1]	BW (g)	LP (%)	SI (g)	LI (g)
McNair 235	7.5ab[2]	5.7cd	39.3ab	10.9de	7.1bcd
Coker 100W	6.7abc	5.7cd	35.5ef	11.5cd	6.3e
Paymaster 54	8.1a	5.3d	39.8a	9.6f	6.3e
Stoneville 2	5.0bc	6.5b	34.5f	12.5bc	6.6de
Lankart 57	4.4c	7.8a	35.6def	14.3a	7.9a
PD 2165	4.0c	5.7cd	36.4cde	13.1b	7.5ab
Deltapine 15	7.5ab	5.2d	39.8a	10.0ef	6.6de
CA 614	6.7abc	5.5cd	37.2cd	11.5cd	6.8cde
DES 56	6.8abc	5.5cd	37.7bc	11.9c	7.2bc
Delcott 277	6.7abc	5.9c	38.9ab	11.7cd	7.5ab

[1] B/P = bolls per plant; BW = boll weight; LP = lint percentage; SI = seed index; LI = lint index. [2] Means within column followed by the same letter are not significantly different at the 5% level.

genetic contribution of at least 25% from A3127 (Mikel et al., 2010).

Because the influential cotton cultivars have had great effects on the cultivars released from 1970 to1990 and are expected to continue to contribute genes to new cultivars through their progenies, it is desirable to understand inheritance of agronomically and economically important traits such as yield components and fiber properties in the influential cultivars. The diallel analysis was described in details by Griffing (1956). It is still an important method for evaluation of combining abilities, heterosis, and inheritance of traits (Rehman et al., 2009; Lawati et al., 2010; Sabaghnia et al., 2010; Badu-Apraku et a., 2011). In the present study, we used the diallel analysis to (i) investigate the variation of yield components among some of the most influential cultivars, (ii) determine general combining ability (GCA) and specific combining ability (SCA) for yield components, (iii) evaluate broad sense

Table 4. Mean squares from analysis of variance for yield components of 55 cotton genotypes (10 parents and 45 F_1's) at Winnsboro and St. Joseph, LA, in 1997

Source	df	B/P[1]	BW	LP	SI	LI
Location	1	1046.7**	26.0**	114.9**	1.9*	6.3**
Rep(L)	4	11.4**	1.1**	2.0*	1.9**	1.0**
Genotype	54	9.2**	1.4**	20.8**	10.5**	1.5**
G x L	54	3.6	0.1**	1.5**	0.4**	0.1*
Error	216	2.6	0.1	0.7	0.2	0.1

*, ** Significant at the 0.05 and 0.01 probability levels, respectively. [1] B/P = bolls per plant; BW = boll weight; LP = lint percentage; SI = seed index; LI = lint index.

Table 5. Mean squares from analysis of variance for general (GCA) and specific (SCA) combining ability for yield components among ten influential cotton varieties at Winnsboro and St. Joseph, LA, in1997

Source	df	B/P[1]	BW	LP	SI	LI
GCA	9	39.1**	6.04**	108.4**	56.3**	8.2**
SCA	45	3.3	0.51**	3.2**	1.3**	0.2**
GCA x Loc	9	5.6*	0.17*	4.1**	0.6**	0.2**
SCA x Loc	45	3.2	0.11*	1.0*	0.3*	0.1
Error	216	2.6	0.08	0.7	0.2	0.1

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.[1] B/P = bolls per plant; BW = boll weight; LP = lint percentage; SI = seed index; LI = lint index.

heritability and narrow sense heritability, and (iv) calculate genetic correlations of the traits.

Materials and methods

Plant materials

There are 16 highly influential cultivars from 16 major cotton breeding programs in USA for the period 1970 - 1990 (Bowman et al., 1996). Ten of these cultivars were selected as parents based on the availability of seed and experimental size (Myers and Lu, 1998; Lu and Myers, 2002) (Table 1). The ten cultivars were used in a diallel mating design following the description in Method II of Griffing (1956). The crosses were made in 1996 at Baton Rouge, LA, resulting in 45 F_1s (no reciprocals).

Field experiment

The ten parents and forty five F_1s were planted on 16 May 1997 at Winnsboro and St. Joseph, LA. The soil types are Gigger silt loam at Winnsboro and Commence silt loam at St. Joseph. The experimental design was a randomized complete block with three replications at each location. Plot size at both locations was one row, 6 m long, spaced 1 m apart. Plants were spaced 10-15cm apart within a row. Plots were maintained per Louisiana Cooperative Extension Service recommendations.

Numbers of plants and bolls were counted in one square meter from each plot of parents and F_1's at both locations to determine bolls per plant. A 50-boll sample of open bolls in each plot was handpicked from three replications of each test to obtain boll sample data. Boll sample data included: (i) lint percentage = weight of lint ginned from the samples of seed cotton, expressed as percentage of weight of seed cotton; (ii) boll weight = seed cotton weight (g) per boll; (iii) seed index = weight of 100 seeds (g); and (iv) lint index = fiber weight on 100 seeds.

Statistical analyses

An analysis of variance (ANOVA) was conducted for parental data and significance of differences for each trait among parents was determined by the *F*-protected LSD method (Steel and Torrie, 1980). A SAS (SAS Institute, 1995) program (Zhang and Kang, 1997) for the diallel analysis system was used for analysis of variance and estimates of GCA and SCA effects for yield components. Estimates of GCA and SCA effects were based on the Griffing's (1956) method 2, model 1. The model of combining ability analysis assumed is:$Y_{ijk} = \mu + g_i + g_j + s_{ij} + e_{ijk}$ Where Y_{ijk} is the value of the ijth observation of the cross involving ith row and jth column in kth replication, μ refers to the general mean, g_i represents the GCA effect of the ith row, g_j refers to the GCA effect of the jth column, s_{ij} is the SCA effect of the cross involving the parents of the ith row and jth column, and e_{ijk} is the error of the ijth observation in kth replication.

The relative importance of GCA and SCA effects on inheritance of the yield components was evaluated using the formula 2GCA / (2GCA + SCA) (Baker, 1978). The closer this ratio is to 1, the more important the additive gene effects are in inheritance of the trait. Heritability was calculated using the following formulae: $h_b^2 = \sigma^2_G / \sigma^2_P$ and $h_n^2 = \sigma^2_A / \sigma^2_P$, where

Table 6. Estimates of GCA effects for yield and yield components among ten influential cotton varieties at Winnsboro and St. Joseph, LA, in 1997

Parent	B/P[1]	BW	LP	SI	LI
		g	%	g	
McNair 235	0.59**	-0.16**	1.6**	-0.71**	0.07*
Coker 100W	0	0.10**	-1.4**	0.11*	-0.37**
Paymaster 54	0.70**	-0.35**	1.1**	-1.15**	-0.38**
Stoneville 2	-0.61**	0.25**	-2.0**	0.58**	-0.29**
Lankart 57	-1.26**	0.58**	-1.0**	1.72**	0.69**
PD 2165	-0.83**	-0.04	-0.5**	0.75**	0.30**
Deltapine 15	0.52**	-0.25**	1.3**	-1.04**	-0.22**
CA 614	-0.10	0.03	0.4**	-0.13**	0.05
DES 56	1.06**	-0.34**	0.6**	-0.42**	-0.06*
Delcott 277	-0.07	0.17**	0	0.29**	0.19**

, * Significant at the 0.05 and 0.01 probability levels, respectively. [1] B/P = bolls per plant; BW = boll weight; LP = lint percentage; SI = seed index; LI = lint index.

Table 7. Estimates of broad-sense (h_b) and narrow-sense (h_n)heritability for boll number per plant (B/P), boll weight (BW), line percentage (LP), seed index (SI), and lint index (LI)

Trait	h_b	h_n
B/P	0.21	0.15
BW	0.57	0.40
LP	0.76	0.66
SI	0.88	0.79
LI	0.71	0.64

h_b^2 is the broad sense heritability, h_n^2 is the narrow sense heritability, σ^2_G is the genotypic variance, and σ^2_A is the additive variance, and σ^2_P is the phenotypic variance. Correlation analysis was carried out for GCA effects using SAS PROC CORR (SAS Institute, 1995).

Results and discussion

Variation of traits among parents

ANOVA results showed significant variation for bolls per plant, boll weight, lint percentage, seed index, and lint index among the ten parents (Table 2). Location effects were significant for bolls per plant, lint percentage, boll weight, and lint index. The weather conditions at St. Joseph were poor during early season because of much more rainfall than a normal year but turned to be good for plants to grow and set bolls during late season. The weather at Winnsboro, however, was good at early season and became dry at late season. As a result, plants were higher and set more and bigger bolls at St. Joseph than at Winnsboro, which resulted in higher mean yield for all parents at St. Joseph (data not shown). In this study, no significant interactions of parents × location for yield components were detected, suggesting that the ten influential cultivars responded consistently to the two different environments for all the traits investigated.

The averaged bolls per plant, boll weight, lint percentage, seed index, and lint index of the ten cultivars across the two locations were presented in Table 3. Paymaster 54, Deltapine 15 and McNair 235 had significantly more boll number per plant than PD 2165, Lankart 57, and Stoneville 2. Lankart 57 produced the biggest bolls, followed by Stoneville 2, while bolls of Deltapine 15 and Paymaster 54 were the smallest. Lint percentage varied significantly among the ten cultivars, ranging from 39.8% of Deltapine 15 to 34.5% of Stoneville 2. Seed of Lankart 57 was the largest of the ten cultivars. PD 2165 produced the second largest seed which was not significantly different from those of Stoneville 2. Paymaster 54 and Deltapine 15 had small seeds. Lankart 57 and PD 2165 exhibited higher values for fiber weight per seed as indicated by their higher lint index, while the values of lint index were the lowest in Coker 100W and Paymaster 54.

Table 8. Correlation coefficients between GCA effects among the ten influential cotton cultivars

	B/P[1]	BW	LP	LI	SI	UHM	E_1	Str.	UI	Mic.
B/P	1.00									
BW	-0.88**	1.00								
LP	0.72*	-0.73*	1.00							
LI	-0.61	0.58	-0.08	1.00						
SI	-0.91**	0.90**	-0.76*	0.71*	1.00					
UHM	-0.51	0.41	-0.52	0.48	0.69*	1.00				
E_1	0.00	0.36	-0.01	0.25	0.18	0.27	1.00			
Str.	-0.45	0.20	-0.49	0.26	0.50	0.71*	-0.30	1.00		
UI	-0.48	0.43	-0.34	0.69*	0.69*	0.82**	0.20	0.58	1.00	
Mic.	0.82**	-0.80**	0.75*	-0.33	-0.75*	-0.58	-0.29	-0.50	-0.35	1.00

, * Significant at the 0.05 and 0.01 probability levels, respectively. [1] B/P = bolls per plant; BW = boll weight; LP = lint percentage; SI = seed index; LI = lint index, UHM = upper half mean fiber length (mm); E_1 = fiber elongation; Str. = fiber bundle strength (g/tex); UI = fiber length uniformity index; Mic. = micronaire

Combined ANOVA

A combined analysis of variance was performed on the data of yield components to estimate the amount of variability for these characteristics among parents and their F_1's. Significant differences were observed for every trait studied among genotypes (Table 4). Significant differences were also detected for every trait between locations. Interactions of genotype × location were significant for boll weight, lint percentage, seed index, and lint index.

Analysis of combining ability

GCA effects were significant for every trait evaluated (Table 5), indicating that additive effects were important in inheritance of these traits. Significant GCA × location interactions were also observed for all the traits.

The best general combiners for boll number per plant were DES 56, Paymaster 54, McNair 235, and Deltapine 15, increasing boll number per plant by 1.06, 0.70, 0.59, and 0.52, respectively (Table 6). Lankart 57, PD 2165, and Stoneville 2 exhibited significant negative GCA effects for boll number per plant, reducing boll number per plant by 1.26, 0.83, and 0.61. Lankart 57, Stoneville 2, Delcott 277, and Coker 100W were the positive general combiners for boll weight, while Paymaster 54, DES 56, Deltapine 15, and McNair 235 were the negative general combiners for boll size because they produced progeny whose boll weight was decreased by 0.35, 0.34, 0.25, and 0.16 g, respectively. Five cultivars, McNair 235, Deltapine 15, Paymaster 54, DES 56, and CA 614, had significant positive impact on lint percentage in their F_1 progeny. F_1 hybrids derived from Stoneville 2, Coker 100W, Lankart 57, and PD 2165, however, tended to have decreased lint percentage as indicated by their negative GCA effects of. For seed index, all the ten cultivars showed significant GCA effects, with Lankart 57, PD 2165, Stoneville 2, Delcott 277, and Coker 100W as good general combiners, and others as poor general combiners. Estimates of GCA effects for line index indicated that all the cultivars except for CA 614 had significant GCA. The cultivars contributing increased lint index to their F_1 progeny were Lankart 57, PD 2165, Delcott 277, and McNair 235. The cultivars producing F_1 progeny with decreased lint index included Paymaster 54, Coker 100W, Stoneville 2, Deltapine 15, and DES 56.

SCA effects were significant for all the traits except for boll number per plant (Table 5), indicating that non-additive effects also played roles in inheritance of boll size, lint percentage, seed index, and line index. Significant interactions of SCA effects × locations were detected for boll weight, lint percentage, and seed index. Nine crosses expressed significantly positive SCA effects and six crosses were identified to have negative SCA effects for boll weight (data not shown). Two crosses had higher lint percentage and eight had lower lint percentage than those predicted by GCA effects of their parents. For seed index, nine combinations had significant positive and three had significant negative SCA effects. Significant positive SCA effects for lint index were detected in three crosses while only one cross had significant negative SCA effect for this trait.

Since Sprague and Tatum (1942) refined the concept of combining ability and further defined GCA and SCA, combining ability analysis has been extensively used to determine the inheritance of quantitative traits in plants. In the present study, both additive and non-additive gene effects were important in genetic control of boll weigh, lint percentage, seed index, and lint index. Baker (1978) suggested to use the ratio of mean squares, 2GCA / (2GCA + SCA), to determine the relative importance of GCA and SCA. The closer this ratio is to 1, the more important the additive gene effects are. The ratios of mean squares for boll weight, lint percentage, seed index, and lint index, were 0.96, 0.99, 0.99, and 0.99, respectively. Therefore, additive gene action was much more important than non-additive gene action in the inheritance of these four traits among the ten influential cultivars. For boll number per plant, only additive effects were important. Using the same set of parents and F_1's, Myers and Lu (1998) found that GCA effects were significant for four of the five fiber quality traits and SCA effects were significant only for fiber length. These results indicated that additive effects were important for yield components and fiver properties but non-additive effects were mainly detected in inheritance of yield components.

Estimate of heritability

Narrow-sense heritability across environments ranged from 0.15 – 0.79, and broad-sense heritability ranged from 0.21 – 0.88 for the yield component traits (Table 7). Heritability estimates (h^2) were classified as high (>0.50), medium (0.30-0.50), and low (<0.30) according to Bhateria et al. (2006). In this study, boll weight, lint percentage, seed index, and lint index had high broad-sense heritability. All of these four traits except for boll weight also gave high narrow-sense heritability. Estimates of heritability for lint percentage and boll weight in the present study were similar to those reported in Tang et al. (1996) and McCarty et al. (2004). Boll number per plant expressed both low narrow-sense heritability (0.15) and broad-sense heritability (0.21), suggesting that selection for boll number per plant is less effective than for other traits such as lint percentage and boll weight and thus observation in multi-environments is necessary if the objective is to improve boll number per plant. The molecular bases of the genetic variation among the ten influential cultivars were previously evaluated with the random amplified polymorphic DNA (RAPD) markers (Lu and Myers, 2002). Of 312 DNA fragments amplified with 63 random decamer primers, 13.5% showed polymorphism among the cultivars. Genetic similarities among the ten cultivars were from 92.7% to 97.6% indicating a relatively low genetic diversity at the molecular level.

Correlation analysis of GCA effects

Relationships among GCA effects for yield components obtained in this study and fiber properties analyzed in a previous study (Myers and Lu, 1998) were summarized in Table 8. More correlations were observed in pairs of yield components or between one yield component and one fiber quality trait than in pairs of fiber quality traits. Boll number per plant was significantly positively correlated with lint percentage but negatively with boll weight and seed index. There was a significantly positive correlation of boll weight with seed index and a negative correlation with lint percentage. Lint percentage was negatively correlated with seed index, while lint index was positively correlated with seed index. There were only two significant correlations (both positive) among fiber quality traits, one between upper half mean fiber length and fiber strength and the other between upper half mean fiber length and fiber length uniformity index. Micronaire was significantly correlated with every yield component except with lint index. Fiber length uniformity index was significantly positively correlated with line index and seed index. Upper half mean fiber length had significantly positive relationship with seed index. Fiber strength did not have significant correlations with any yield components in this study. These correlations among the traits should provide cotton breeders with insights on possible impacts of selection for one trait on others.

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