

BREEDING & GENETICS

Genetic Variances and Combining Ability of Crosses of American Cultivars, Australian Cultivars, and Wild Cottons

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ABSTRACT

Genes for improved yield and fiber quality are available in Australian cultivars and wild accessions of cotton (*Gossypium hirsutum* L.); however, their combining ability with U.S. cultivars is unknown. We evaluated combining ability and inheritance of yield and fiber traits among nine diverse cotton lines: two cultivars developed in Australia, two experimental lines from wild accessions, and five U.S. cultivars. Parents and F₂'s from a half-diallel cross were grown in Leeper silty clay loam and Marietta sandy clay loam in 1999 and 2000. F₂ hybrids had higher lint yield, heavier bolls and longer fibers than parents. Variance components and genetic effects were calculated utilizing an extended additive dominance model with genotype by environment interaction effects using a mixed norm quadratic unbiased estimation analysis. Parents varied in genetic combining ability (GCA). 'Fibermax 832', developed in Australia, was the best in GCA for yield and fiber quality. 'Stoneville 474' was the best in GCA for yield. Experimental line, B 1388, was good in GCA for fiber strength, although other properties suffered. 'Paymaster 1560' exhibited good GCA ability for yield and fiber length. 'Fibermax 975' exhibited good GCA for fiber length. Lint yield, boll size, and fiber elongation had approximately equal additive and dominance genetic effects. Lint percentage and fiber strength exhibited primarily additive genetic effects. Micronaire and length exhibited primarily dominance genetic effects. A significant residual com-

ponent of the phenotypic variance was present for each trait except lint percentage. The Australian cultivars and wild accessions can combine with cultivars from U.S. breeding programs to provide genes for fiber and/or yield improvement.

New cotton cultivars continue to be developed that are earlier in maturity and higher in yield; however, major improvements in fiber quality have not generally been associated with cultivars developed in breeding programs in the United States in the past 8-10 years (Bowman and Gutierrez, in press). Approximately 30% of the cotton crop in the United States does not meet fiber quality requirements for efficient processing, resulting in an estimated loss to producers of over \$70 million a year (Bradow et al., 1998). The backcross breeding programs used since the early 1990's to develop cultivars with transgenic insect and herbicide resistance have produced cultivars with desired transgenic traits, but many of these have less than desirable fiber quality traits. Agronomic practices and environmental conditions influence the development of cotton fiber, but the genotype of the cultivar can also exert major influences on fiber quality (Perkins et al., 1984).

In the early 1980's, Australian cotton breeders developed higher fiber quality, especially higher strength, cultivars. Since most of the Australian cotton is exported, they focused on increasing fiber quality. Australian cottons currently have a reputation for very good fiber properties, and they continue to provide acceptable yields in Australia (Constable et al., 2001).

Wild cotton accessions are usually photoperiodic, but may be sources of useful fiber traits. Several of the wild accessions have been converted to day neutrality and some of these have been shown to carry genes for increased fiber strength; however, many of these accessions also have undesirable traits such as low lint percentage or short fiber (McCarty et al., 1998a, b; McCarty et al., 2003).

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It seems logical that cotton breeders in the United States should explore ways to incorporate fiber improvement genes from Australian cultivars and wild cotton germplasm into their existing breeding programs to enhance fiber properties of American cultivars. The recent advent of Australian cultivars being sold to growers in the United States, and the release of several day neutral lines of wild cotton with good fiber genes should encourage their use for improved fiber properties in cultivars being bred in the United States. Very little is known about the genetic combining ability of the Australian cultivars, the wild accessions, and U. S. cultivars.

The objective of this research was to measure agronomic and fiber properties and to detect genetic variation and genetic effects associated with five U. S. cultivars, two Australian cultivars, and two day neutral versions of wild cotton accessions and their respective F_2 populations.

MATERIALS AND METHODS

Nine cotton genotypes from diverse breeding programs were selected as parents based on their agronomic performance and fiber properties and crossed in a half-diallel mating design in 1998. The parents were as follows: two cultivars (Fibermax 832 [FM 832] and Fibermax 975 [FM 975]; Aventis Crop Science, Collierville, TN) developed in Australia, which were chosen for their fiber properties, two lines (A 239 and B 1388) derived from day neutral selections from crosses of cultivars with exotic race accessions T-239 (PI 163693) and T-1388 (PI 415112), which were chosen for fiber strength, and five U.S. Delta cultivars (Deltapine 50 [DP 50], Deltapine 90 [DP 90], Paymaster 1560 [PM 1560], Sure-Grow 501 [SG 501]; Delta Pine and Land Co., Scott, MS; and Stoneville 474 [ST 474]; Stoneville Pedigreed Seed Co., Collierville, TN) chosen from diverse breeding programs. Crosses and all subsequent evaluations were conducted at the R. R. Foil Plant Science Research Center at Mississippi State University. The F_1 seed were sent to a winter nursery in Tecoman, Mexico to produce F_2 seed. Seed from the 35 F_2 hybrids (one cross was lost) and the nine parents were planted at two locations each year in 1999 and 2000 at the Plant Science Research Center.

The plots were arranged in a randomized complete block design with four replications at each location. Planting dates were 10 and 12 May 1999

and 11 and 15 May 2000. Environments one and two were grown in 1999 and environments three and four were grown in 2000. Plot size for environments one and three was single rows, 12 m long with row spacing of 0.97 m, and planted in a plant 2 skip 1 row pattern. Plot size for environments two and four was single rows, 9 m long with row spacing of 0.97 m, and planted in a solid planting pattern. The stand density was 10 plants m^{-1} . Soil type at locations one and three was a Leeper silty clay loam (fine smectitic, nonacid, thermic Vertic Eplaquepts). Soil type at locations two and four was a Marietta sandy clay loam (fine-loamy, siliceous, active, thermic, Fluvaquentic Eutrudepts) soil. Insects were controlled on all plots via a full-season insecticide regimen, as needed, and standard production procedures were followed each year.

A 50-boll, sample was harvested by hand from each plot prior to machine harvest. Workers were instructed to harvest first or second position bolls from approximately the middle five fruiting nodes. These sites produce the majority of the seed cotton. These samples were ginned and used to determine lint percentage and boll size. The plots were harvested with a mechanical picker, and the seed cotton was weighed. Seed cotton yields were calculated based on the machine-harvest data. Lint yields were calculated by multiplying seed cotton yield by lint percentage. Yields of solid planting and skip row planting were each expressed as yield per planted hectare.

A 10-gram lint sample was used for fiber analysis. Fiber samples were sent to Starlab Inc. (Knoxville, TN) for single instrument measurements of micronaire, elongation, strength or fiber tenacity (T1), 50% span length, and 2.5% span length.

Environments were considered as a combination of year and location (Environment 1 was Location 1, 1999; Environment 2 was Location 2, 1999; Environment 3 was Location 1, 2000; Environment 4 was Location 2, 2000). Data from 1999 and 2000 were subjected to ANOVA using the General Linear Models (GLM) procedure of SAS (SAS Institute, version 6.12, Cary, NC). Mean separation of parents and F_2 was compared by the F test at 0.05 level of probability. Genotypes and environments were considered as random effects since the five cultivars were selected to represent diverse breeding programs, and two Australian and two day neutral wild accessions were selected to represent these two types of germplasm.

An extended additive-dominance (AD) model proposed by Zhu (1994) was used to analyze the combined data from 1999 and 2000. The genetic assumptions for the AD model are 1) normal diploid segregation; 2) inbred parents are a random sample from a reference population; and 3) no epistatic effects (Zhu, 1994; Tang et al., 1996). This model also made it possible to estimate the proportion of variance attributable to additive genetic effects (A), dominance genetic effects (D), additive by environment effects (AE), dominance by environment effects (DE), block effects (within environment) (B), and random error (e). Genetic analyses were performed using the following mixed linear model, which was extended from Cockerham's (1980) Additive Dominance model to include Genetic × Environment effects:

$$\text{Parents: } Y_{hik} = \mu + E_h + 2A_i + D_{ii} + 2AE_{hi} + DE_{hii} + B_{k(h)} + e_{hik}$$

$$F_2: Y_{hijk(2)} = \mu + E_h + A_i + A_j + \frac{1}{4}D_{ii} + \frac{1}{4}D_{jj} + \frac{1}{2}D_{ij} + AE_{hi} + AE_{hj} + \frac{1}{4}DE_{hii} + \frac{1}{4}DE_{hjj} + \frac{1}{2}DE_{hij} + B_{k(h)} + e_{hijk}$$

A mixed linear model approach, minimum norm quadratic unbiased estimation (MINQUE) procedure with an initial value of 1.0 for each variance component allowed the estimation of genetic variance components based on the extended AD model (Rao, 1971; Zhu, 1992, 1994). The phenotypic variance is $V_P = V_A + V_D + V_{AE} + V_{DE} + V_E$. Standard errors of vari-

ances and predicted genetic effects were estimated by jackknifing over blocks within environments (Miller, 1974; Tang et al., 1996). A one-tailed *t* test was used to test the significance of variance components and a two-tailed *t* test was utilized for genetic effects.

RESULTS

Yield and fiber quality of parents and hybrids:

F₂ hybrids among these nine parents produced significantly greater yields of seedcotton and lint cotton with heavier bolls and longer fibers than the parents; however, lint percentage, micronaire, elongation, and strength for F₂ hybrids were not improved over parents. The mean increases in lint yields (179 kg ha⁻¹) and in fiber length (0.48 mm) by the F₂ were significant (Table 1).

Genetic variance components: The phenotypic variances that show the relative contribution of each genetic and interaction component to the total phenotypic variance were partitioned into the genetic proportions for A, D, AE and DE variances (Table 2). Genetic variance for seed cotton yield, micronaire, and 50 and 2.5% span length were primarily dominance variances. Lint yield, boll size, and elongation variances were approximately equally divided between additive and dominance. Lint percentage and fiber strength variances were

Table 1. Phenotypic means of nine parents and 35 F₂ hybrids for yield and fiber properties in four environments

Envir.	Generation	Seed Cotton (kg ha ⁻¹)	Lint (kg ha ⁻¹)	Lint (%)	Boll weight (g)	Fiber Properties ^z				
						Mic	El (%)	TI (kN mkg ⁻¹)	50% SL	2.5% SL
1	Parental	2520 a ^y	982 a	38.28 a	4.61 a	4.79 a	7.08 a	224.7 a	14.38 a	38.28 a
1	F2	2758 b	1057 a	38.07 a	4.79 b	4.68 a	6.87 a	225.2 a	14.59 b	38.07 a
2	Parental	2452 a	923 a	37.18 a	4.48 a	4.66 a	7.20 a	227.8 a	14.45 a	28.62 a
2	F2	3046 b	1129 b	36.93 a	4.75 b	4.63 a	6.97 a	224.7 a	14.48 a	28.89 a
3	Parental	1984 a	754 a	37.34 a	4.46 a	4.91 a	7.07 a	225.3 a	14.43 a	29.30 a
3	F2	2654 b	997 b	37.33 a	4.86 b	4.72 a	7.00 a	231.0 a	14.69 b	30.00 b
4	Parental	2664 a	989 a	36.57 a	4.60 a	4.60 a	6.90 a	226.5 a	14.44 a	29.51 a
4	F2	3220 b	1182 b	36.56 a	4.95 b	4.39 a	6.91 a	224.0 a	14.70 b	30.05 b
Mean	Parental	2405 a	912 a	37.34 a	4.54 a	4.74 a	7.06 a	226.1 a	14.43 a	28.98 a
Mean	F2	2919 b	1091 b	37.22 a	4.84 b	4.60 a	6.94 a	226.2 a	14.62 b	29.46 b

^z Fiber properties: Mic = micronaire; E1= elongation; T1 = strength; 50% SL = 50% span length; 2.5% SL = 2.5% span length.

^y Means within an environment for a particular trait followed by the same letter are not significantly different ($P \leq 0.05$) according to the *F* test.

primarily due to additive genetic effects. There was no important additive by environment interactions; however, the dominance by environment interactions for seed cotton yield, boll size, fiber strength and 50% span length accounted for 15% or more of the phenotypic variances. Residual variances were important for all fiber and yield traits, except lint percentage, with 21 to 47% of the total variance being due to residual (Table 2). Generally, if the sum of V_A and V_D is greater than sum of V_{AE} and V_{DE} , the trait is considered to be stable across environments. For most all traits in this study the genetic variances were greater than the genetic by environment variances thus the traits were generally stable across these environments.

Genetic Combining Ability (GCA): Positive GCA effects for lint yield were predicted for ST 474, FM 832, and PM 1560; whereas, negative GCA effects were predicted for the wild accession derived lines B 1388 and A 239. Positive GCA effects for boll weight were predicted for FM 832 and PM 1560, the parents with the heaviest bolls. Negative GCA effects for boll weight were predicted for FM 975 and B 1388, the parents with the lightest bolls. Six of nine parents showed positive GCA effects for lint percentage with negative GCA effects predicted for DP 50 and the two accession parents. These three lines have the lowest lint percentage among the parents. No significant GCA effects were detected for micronaire. Parental lines FM 832 and B 1388 were predicted to be the best general combiners for fiber strength. The two weak fiber cultivars DP 50 and ST 474 were predicted to have large negative GCA effects for fiber strength. Although

B 1388 was predicted to have the greatest GCA for fiber strength, crosses with this parent showed reduced yields. Positive GCA effects for 2.5% fiber span length were predicted for three genotypes (FM 832, FM 975, and PM 1560), and negative GCA effects for three genotypes (SG 501, ST 474, and A 239), ranging from -0.83 (A 239) to 0.58 mm (FM 832) (Table 3).

Parental lines varied significantly in GCA. DP 50 did not have any positive GCA effects, but negative GCA effects were predicted for lint percentage, strength, and elongation. DP 90 was predicted to provide positive GCA only for lint percentage. The Australian cultivar FM 832 was predicted to provide positive GCA for lint yield, boll size, lint percentage, strength and 2.5% SL; however, the Australian cultivar FM 975 was predicted to provide positive GCA effects only for lint percentage and 2.5% fiber length. PM 1560 was predicted to provide positive GCA effects for lint yield, boll size, lint percentage, elongation and 2.5% SL. SG 501 only provided positive GCA effects for lint percentage. The highest yielding cultivar among parents was ST 474 which was predicted to provide positive GCA only for seed cotton yield, lint cotton yields, and lint percentage, but to provide negative GCA effects for strength and 2.5% SL. The two wild accession-derived lines each had high strength, low yield, and low lint percentage. B 1388 was predicted to have the largest positive GCA effects for strength among parents, but negative effects on yield, boll size and lint percentage. A 239 was predicted to only have a small effect on strength, but a negative GCA on yield and lint percentage.

Table 2. Proportions of estimated variance components to phenotypic variance for yield components and fiber properties

Ratio ^z	Seed Cotton	Lint Yield	Boll Weight	Lint (%)	Fiber Properties ^x				
					Mic	El	Tl	50% SL	2.5%SL
V_A/V_P	0.05** ^y	0.25**	0.23**	0.81**	0.04**	0.30**	0.47**	0.07**	0.23**
V_D/V_P	0.34**	0.28**	0.29**	0.11**	0.60**	0.23**	0.01**	0.24**	0.55**
V_{AE}/V_P	0.05**	0.04**	0.00	0.01**	0.02**	0.04**	0.00	0.00	0.01*
V_{DE}/V_P	0.15**	0.05**	0.16**	0.00	0.10**	0.00	0.21**	0.21**	0.00
V_e/V_P	0.41**	0.38**	0.32**	0.07**	0.24**	0.44**	0.31**	0.47**	0.21**

^x V_P = phenotypic variance, V_A = additive variance, V_D = dominant variance, V_{AE} = additive × environment variance, V_{DE} = dominant × environment variance, V_e = residual variance, $V_P = V_A + V_D + V_{AE} + V_{DE} + V_e$.

^z Fiber properties: Mic = micronaire; El = elongation; Tl = strength; 50% SL = 50% span length; 2.5% SL = 2.5% span length.

^y*, ** Significantly different from zero at $P \leq 0.05$ and $P \leq 0.01$, respectively, with a one tail t test.

Table 3. Predicted general combining ability effects for yield and fiber properties of nine parents

Genotype	Seed Cotton	Lint	Boll weight	Lint (%)	Fiber Properties ^z				
					Mic	EI	T1	50% SL	2.5% SL
DPL 50	92.24	40.81	-0.01	-0.29**	0.00	0.39**	-17.86**	-0.08**	-0.04
DPL 90	7.52	26.38	0.02	0.80**	0.02	-0.09	0.10	-0.01	0.02
FM 832	38.38	55.55*	0.42**	1.19**	-0.12	-0.09	10.55**	0.12	0.58**
FM 975	4.91	14.51	-0.23**	0.45**	-0.01	-0.37**	-2.54	0.01	0.43**
PM 1560	56.18	64.60*	0.20**	1.30**	0.00	0.31**	-2.46	0.03	0.13**
SG 501	43.39	45.26	-0.07	0.94**	0.04	0.28**	3.17*	0.03	-0.19**
ST 474	157.49** ^y	142.54**	0.03	1.89**	0.04	0.15*	-10.38**	-0.02	-0.12**
B 1388	-228.12**	-227.31**	-0.33**	-3.85**	-0.03	-0.14*	16.53**	0.07*	0.02
A 238	-172.65*	-162.71**	-0.03	-2.45**	0.06	-0.45**	2.83**	-0.17*	-0.83**

^z Fiber properties: Mic = micronaire; EI = elongation; T1 = strength; 50% SL = 50% span length; 2.5% SL = 2.5% span length

^y *,** Significantly different from zero at $P \leq 0.05$ or $P \leq 0.01$, respectively, with a two tail *t* test.

Homozygous Specific Combining Ability (HMSCA): FM 832 exhibited small positive HMSCA effects (D_{ii}) for lint yield (Table 4). Five of the nine parents showed negative HMSCA effects, with ST 474 exhibiting the largest negative HMSCA effect for lint yield. A positive HMSCA effect was observed for FM 832 for boll size, but not for PM 1560, which also has a large boll. Five of the nine parents showed negative HMSCA effects for boll size, with B 1388 exhibiting the greatest negative effect. Positive HMSCA effects were predicted for FM 832, FM 975, SG 501, and ST 474 for lint percentage. A negative HMSCA effect was predicted

for A 239 for lint percentage. Positive HMSCA effects for micronaire were predicted for four of the nine parents with the largest positive effect for B 1388. Positive HMSCA effects for elongation were predicted for A 239. There were no significant HMSCA effects among parents for strength. This reflects the negligible dominance effect for strength (Table 2). Positive HMSCA effects were predicted for parents, FM 832 and SG 501, for 2.5% span length. Negative HMSCA effects, were predicted for five parents with B1388 exhibiting the largest negative SCA effect.

Table 4. Predicted homozygous specific combining ability effects for nine parents

Genotype	Seed Cotton	Lint	Boll weight	Lint (%)	Fiber Properties ^z				
					MIC	EI	TI	50% SL	2.5% SL
DPL 50	-218	-94	-0.03	-0.52	0.27**	0.43	0.29	-0.46**	-0.73**
DPL 90	-473* ^y	-160	-0.51**	0.42	0.18	-0.11	1.72	-0.46*	-0.68*
FM 832	16	15*	0.12**	0.30**	-0.05**	-0.02	-1.59	0.04**	0.18**
FM975	-1143**	-376**	-0.43**	2.39**	0.28**	0.18	-2.90	-0.32*	-0.76**
PM 1560	-958**	-367**	-0.51**	0.09	0.13	0.05	0.56	-0.05	-0.44*
SG 501	-607	-190	-0.26	1.14**	0.10	0.16	-3.74	0.17**	0.33*
ST 474	-1209**	-428**	-0.58**	1.88**	0.18*	-0.14	2.41	-0.29	-0.44
B1388	-1177**	-316**	-0.87**	0.05	0.66**	0.32	-1.90	-0.76**	-3.25**
A238	-1026**	-346**	-0.11	-1.88**	-0.11	-0.67**	-7.64	-0.19	0.05

^z Fiber properties: Mic = micronaire; EI = elongation; T1 = strength; 50% SL = 50% span length; 2.5% SL = 2.5% span length.

^y *,** Significantly different from zero at $P \leq 0.05$ or $P \leq 0.01$, respectively with a two tail *t* test.

DISCUSSION

Cotton breeders continue to explore ways to develop new genotypes that will maintain high yields, reduce the input costs associated with the crop, and improve fiber quality. Successful breeding programs focus initially on yield enhancement, but should also incorporate genes that improve fiber quality.

Variance component analysis indicated that all traits exhibited highly significant additive and dominance variances. The additive by environment effects were not important; however, the dominance by environmental effects were important for boll size, strength and 50% span length. For these traits selection should be based upon evaluation in several environments. Generally, the genotype variances were larger than the genotype by environment variances. GCA effect predictions for the nine parents varied significantly for both yield and fiber traits. Superiority of F_2 hybrids over parents for yield agree in general with other researchers (Baker and Verhalen, 1975; Cheatham 2001; Meredith, 1990a, b; Tang et al., 1993a, b; Shoemaker, 2000). FM 832 was the best overall general combiner, i.e. the best parent to be used in a cross to improve both yield and fiber quality. FM 832 showed positive GCA effects for lint yield, boll size, lint percentage, strength, and 2.5% span length. Micronaire was also lowered significantly when FM 832 was utilized in a cross. FM 832 combined well with the selected U.S. cultivars chosen for this study and would be a good source of parental germplasm for improving fiber quality in cotton breeding programs in the United States. ST 474 was a good general combiner for yield but not for fiber quality traits. The converted wild accession B 1388 was a good general combiner for increased strength; however, other agronomic properties tended to decrease when this parent was used, confirming McCarty's (unpublished data) findings that using exotic germplasm for varietal enhancement may initially result in low yields. One could use B 1388 as a donor parent to provide strength genes and then backcross these strength genes into a high yielding cultivar.

Although A 239 has high fiber strength, it did not exhibit GCA effects as great as some of the other lines such as B 1388 or FM 832. We considered the ranking of the parental lines for yield and fiber properties in relation to GCA effects and found that pa-

rental values did not generally translate to GCA effects rankings. For the two lines derived from wild accession parents, low yield and lint percentage were good indications of their GCA effects for these traits. These two lines had high strength, but a much greater GCA effect for strength was predicted for B 1388 than A 239. Although similar in yield, several cultivars were predicted to vary significantly in GCA for lint yield. There was value added information gained from making the crosses and predicting combining ability that could not be gained from the parental means alone. Gutierrez et al. (2002) in a study with these same lines, plus two additional Australian cultivars, showed that these cultivars had a low genetic distance based upon molecular markers and suggested that genetic distance based upon his set of molecular markers was not a good indication of what to expect from crosses among the lines. For example, the two wild accessions clustered together and some distance from the cultivars. Yet, we show considerable variation in GCA effects among the cultivars and differences in GCA effects between the two wild accessions. U. S. breeders could benefit from using both Australian and wild accessions to improve specific fiber properties; however, FM 832 was better than FM 975 and B 1388 was better than A 239. Since the U. S. cultivars were a sample from four diverse breeding programs, we conclude that U. S. cotton breeding programs should gain from using Australian and/or wild accession germplasm in crosses with their lines.

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DISCLAIMER

Mention of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the United States Department of Agriculture.

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