

# Breeding Potential of Elite Pee Dee Germplasm in Upland Cotton Breeding Programs

B. T. Campbell,\* D. B. Weaver, R. Sharpe, J. Wu, and D. C. Jones

## ABSTRACT

Successful plant breeding programs begin with parental line selection. Effective parental line selection is facilitated when the breeding potential of candidate parental lines is known. Using topcross families involving germplasm from eight U.S. public cotton (*Gossypium hirsutum* L.) breeding programs, we evaluated the breeding potential of recently developed, elite Pee Dee germplasm. Based on parental line mean performance, hybrid performance, and genetic effect estimates, the breeding potential for recently developed, elite Pee Dee germplasm was similar to or better than the breeding potential of two well-known, commercial cultivars. Results suggest that crosses involving germplasm from the USDA-ARS, Stoneville, MS, and USDA-ARS, Maricopa, AZ, cotton germplasm enhancement programs offer high fiber quality potential. In addition, our results suggest that recently developed, elite Pee Dee germplasm can be used to generate offspring with a lessened or absent negative relationship between agronomic performance and fiber quality. Cotton breeders can use the information provided herein to facilitate their efforts to develop elite breeding lines, recurrent parents, and/or commercial cultivars.

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**Abbreviations:** MINQUE, minimum norm quadratic unbiased estimation.

CONTINUED GENETIC IMPROVEMENT OF COTTON (*Gossypium* L. spp.) is essential to increase both the quantity and quality of cotton production systems. Today, the globalization of cotton textile manufacturing and the adoption of high-speed fiber spinning machinery have increased the global demand for improved quality fiber (Campbell et al., 2011). Hence, increasing pressure is being placed on cotton breeding programs to increase yields while simultaneously increasing fiber quality. Efforts to meet these demands through genetic improvement begin with effective parental line selection.

Historically, public breeding and germplasm enhancement programs have been a key source of parental lines used to develop new commercial cultivars. Bowman and Gutierrez (2003) found that two public germplasm programs (New Mexico Acala and Pee Dee) accounted for over 50% of fiber strength improvements present in commercial cotton cultivars. However, the negative relationship between agronomic performance and fiber quality traits has made efforts to increase yields while simultaneously increasing fiber quality difficult (Campbell et al., 2012; May, 1999; Meredith, 1984a).

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Previously, studies were conducted to retrospectively examine genetic properties of the 70-yr Pee Dee cotton germplasm enhancement program. Campbell et al. (2009) examined genetic relationships based on molecular marker and field performance data within the Pee Dee germplasm collection and found that useful genetic variation remains. Campbell et al. (2011) found that incremental genetic gains for agronomic performance while maintaining fiber quality performance occurred over eight cycles of organized breeding. Campbell et al. (2012) found that negative genetic correlations among agronomic and fiber quality traits have lessened following eight cycles of breeding to increase yield while simultaneously improving fiber quality.

Each of these studies provides information about the Pee Dee germplasm collection that is useful to public and private cotton breeding programs. However, mean germplasm line performance across environments may not adequately predict their value for use in plant breeding. Designing studies that allow for the estimation of genetic effects including additive, dominance, and their interactions with environment can provide information on the general and specific combining ability of specific genotypes. As suggested by Meredith (1984b), combining ability studies can produce information about gene action in a base population and thereby aid parental line selection for producing crosses and segregating populations. Combining ability studies using an array of experimental designs have been performed in cotton (Cheatham et al., 2003; Hinze et al., 2011; Jenkins et al., 2009, 2007, 2012; McCarty et al., 2004a, 2004b; Meredith and Brown, 1998; Zeng et al., 2011; Zeng and Wu, 2012).

In this report, we examine the mean performance and genetic effects of breeding populations derived from crosses involving recently developed elite Pee Dee germplasm lines. Since Pee Dee germplasm has been used almost exclusively as a source of improved fiber quality, one might hypothesize that the well-known negative relationship between agronomic performance and fiber quality has negatively affected the breeding potential of high quality Pee Dee germplasm for improved agronomic performance. Relative to other possible parental lines, the breeding potential or combining ability of Pee Dee germplasm for agronomic performance could be comparatively low. The objective of this study was to estimate genetic variance components and predict agronomic and fiber quality performance genetic effects for breeding populations derived from recently developed, elite Pee Dee germplasm.

## MATERIALS AND METHODS

### Development of Topcross Families

A total of 120 topcross families were developed using four elite Pee Dee breeding lines and two elite commercial cultivars. The Pee Dee breeding lines included two unreleased breeding lines (PD 97019 and PD 97047) and two released germplasm lines, PD

98066, registered as GA 98066 (PI 635119) (May et al., 2005), and PD 99035 (PI 653111) (Campbell et al., 2009). The two elite commercial cultivars included Deltapine Acala 90 (DP 90 [PI 564767]) and DES 119 (PI 606809) (Bridge, 1986). Both commercial cultivars were selected based on their widespread use as parental lines in cotton breeding programs (Bowman and Gutierrez, 2003). In 2006, the four Pee Dee breeding lines and two commercial cultivars were each topcrossed as males onto twenty elite breeding lines from U.S. public sector breeding programs. The elite breeding lines were obtained from eight U.S. public sector breeding programs including (i) USDA-ARS, Maricopa, AZ (AGC85 [PI 641928], AGC375 [PI 641930], and AGC208 [PI 641929]) (Percy et al., 2006), (ii) University of Arkansas (AR 9704-13-08, AR 9706-38-06 [PI 654510] [Bourland and Jones, 2009], AR 9715-33-03, and AR 9720-47-09), (iii) University of Georgia (GA 200035 and GA 200036), (iv) Louisiana State University (LA03404171, LA00405016, LA03404148, and LA03404065), (v) Mississippi State University (8824-1-2-25-192-8 and 8824-1-2-25-192-10), (vi) USDA-ARS, Stoneville, MS (MD09ne [PI 6595070] [Meredith and Nokes, 2011] and MD15 [PI 642769] [Meredith, 2006]), (vii) New Mexico State University (NM1155 [PI 659506] [Zhang et al., 2011]), and (viii) Texas A&M University (00WA-104 and 01WM-27). The majority of elite breeding lines were obtained from entries evaluated in the 2006 Regional Breeders Testing Network trial (<http://www2.msstate.edu/~tpw6/current/home.html> [accessed 22 Sept. 2012]). The F<sub>1</sub> and parental lines were planted in the USDA Cotton Winter Nursery in Tecoman, Mexico, and manually self-pollinated to produce F<sub>2</sub> and additional parental line seed.

### Field Design and Procedures

The 120 F<sub>2</sub> hybrids, 26 parental lines, and four commercial checks were evaluated in four environments in 2007, 2008, and 2009. In 2007 and 2008, the trial was conducted at the Clemson University Pee Dee Research and Education Center near Florence, SC. In 2008 and 2009, the trial was conducted at the E. V. Smith Research Center, Plant Breeding Unit in Tallahassee, AL. In each trial, the hybrids, parental lines, and commercial checks were randomly assigned to a single replicate of a replicated,  $\alpha$ -lattice incomplete block field design for each trial. With the exception of the 2007 trial in Florence, SC, that included three replicates, all trials consisted of four replicates. In each trial, the  $\alpha$ -lattice consisted of 15 incomplete blocks of size 10. Because of limited seed amounts, plots consisted of single rows 10.6 m long planted in skip row fashion (i.e., no adjacent border rows). Trial management followed the established local production practices for dry-land cotton production at each location. Each plot was harvested with a spindle-type mechanical cotton picker, and total seed cotton weight recorded. A 25-boll sample was hand harvested from each plot before harvest to determine lint percent and fiber quality properties. 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 lint percent by 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 fiber properties. The fiber properties measured include upper half mean fiber length, fiber strength, and micronaire.

## Data Analysis

### Analysis of Phenotypic Data

Agronomic and fiber quality data were analyzed using a mixed model and the PROC GLM module of SAS version 9.2 (SAS Institute, 2008). The RANDOM statement was included to identify random effects and make *F*-tests using the appropriate error term. Initially, individual year–location data were analyzed and homogeneity of variance tests were conducted to determine if a combined analysis of variance could be conducted for each trait. After confirming homogenous error variance for each trait, the data were analyzed using two analysis of variance procedures. For ease of analysis, the replicate and incomplete block terms were combined to form a single “block” term; the block term was considered a random effect. Each year–location trial was considered a single environment; environment was considered a random effect. Genotypes were considered fixed effects. Fisher’s protected LSD was calculated and used to make planned comparisons among least square means.

### Genetic Analysis

An additive–dominance genetic model with genotype  $\times$  environment interaction was used for data analysis following the procedures described by Jenkins et al. (2006). In this study, some coefficients for genetic effects were fractions rather than 0 and 1; therefore, analysis of variance and general linear model methods were not appropriate. Therefore, a mixed linear model approach, minimum norm quadratic unbiased estimation (MINQUE) with an initial value of 1.0 called MINQUE1, was used to estimate the variance components (Zhu, 1989). Genetic variances and genetic effects were calculated for each genetic component. The phenotypic variance was partitioned into components for additive variance, dominance variance, additive by environment variance, dominance by environment variance, and error variance; they were expressed as proportions of the total phenotypic variance (Tang et al., 1996; Wu et al., 2010). Genetic effects were predicted by the adjusted unbiased prediction approach (Zhu, 1993). Standard errors of variance components and genetic effects were estimated by randomized 10-fold jackknife resampling (Wu et al., 2008, 2012; Zhu, 1993). An approximate one-tailed *t* test was used to detect the significance of variance components. A two-tailed *t* test was used to detect the significance of genetic effects (Miller, 1974). In addition, lower and upper limits of 95% confidence interval for parameters of interest were calculated so that multiple comparisons among parameters (i.e., additive effects) could be made accordingly.

The predicted genetic effects were deviations from the respective population grand mean. A *t* test was used to detect the significance of genetic effects from zero. These effects are measures of the additive or homozygous dominance effects for each of the 26 topcross parents. The 95% confidence intervals for additive and homozygous dominance effects were compared between the four Pee Dee combiners and the two commercial combiners. Heterozygous dominance effects were estimated for each combiner  $\times$  elite breeding line combination. For each cross with a given elite breeding line, heterozygous dominance effects were compared between the Pee Dee and commercial combiners. The 95% confidence intervals for each heterozygous dominance effect were compared between the four Pee Dee combiners and the two commercial combiners.

**Table 1. Mean agronomic and fiber quality performance for 20 elite U.S. breeding lines and six combiners (four Pee Dee lines and two commercial cultivars) combined over four environments.**

Parental line	Lint percent	Lint yield	Fiber strength	Fiber length	Micronaire
	%	kg ha <sup>-1</sup>	kN m kg <sup>-1</sup>	mm	units
Female parent					
AR 9704-13-08	43.13	1792	271.7	28.02	4.9
AR 9706-38-06	43.72	1988	293.2	28.33	5.1
AR 9715-33-03	38.09	1523	284.7	27.73	4.1
AR 9720-47-09	41.91	1982	272.2	27.47	4.6
GA200035	35.73	1427	299.6	28.61	4.4
GA200036	42.49	1819	311.4	29.62	4.8
LA03404171	38.85	1546	296.7	29.45	4.7
LA00405016	39.22	1728	284.3	26.65	4.5
LA03404148	40.70	1682	306.0	27.98	4.6
LA03404065	41.56	1705	282.5	27.08	4.1
AGC85	40.65	1836	311.9	29.14	4.4
AGC375	41.55	1605	297.7	29.55	4.2
AGC208	39.17	1650	313.0	30.14	4.3
00WA-104	40.18	1734	306.3	28.76	4.5
01WM-27	40.11	1818	281.9	28.07	4.2
8824-1-2-25-192-8	42.41	2000	282.2	27.33	4.6
8824-1-2-25-192-10	41.58	1750	286.9	28.62	4.7
MD09ne	39.08	1684	321.1	27.72	4.4
MD15	38.57	1321	363.1	29.56	3.9
NM1155	39.83	1464	301.3	29.66	4.2
Male parent					
PD 97019	37.98	1461	284.8	28.82	4.0
PD 97047	38.15	1682	307.7	26.68	4.8
PD 98066	35.65	1770	310.3	30.90	4.1
PD 99035	39.53	1815	309.7	28.99	4.7
DP 90	39.39	1594	303.0	28.78	4.1
DES 119	37.76	1550	302.7	29.20	4.3
LSD (0.05)	0.87	217	8.5	0.52	0.2

## RESULTS

### Mean Comparisons among Topcross Parents and F<sub>2</sub> Hybrids

Table 1 provides mean trait values for each topcross parent combined across four environments. Among the 20 U.S. breeding lines, AR 9706-38-06 and AR 9704-13-08 had the highest lint percent. Among the six male combiners, PD 99035 and DP 90 had the highest lint percent. Among the 20 U.S. breeding lines, AR 9704-13-08, AR 9720-38-06, AR 9720-47-09, GA200036, AGC85, 01WM-27, and 8824-1-2-25-192-8 had the highest lint yield. Among the six male combiners, PD 97047, PD 98066, and PD 99035 had the highest lint yield. MD15 had the highest fiber strength. Considering the six male combiners, PD 97019 had the lowest fiber strength. Among the 20 U.S. breeding lines, GA200036, AGC208, and NM1155 had the longest fiber lengths. Among the six male combiners, PD 98066 had the longest fiber length. Among the 20 U.S. breeding line parents, AR 9715-33-03, LA03404065, and MD15 had

**Table 2. Lint percent (%) of F<sub>2</sub> hybrids derived from crosses of 20 elite U.S. breeding lines and six combiners including four Pee Dee lines and two commercial cultivars. The least significant difference between means at the two-tailed 95% probability level is 0.87%.**

Female parent	Male combiners						Female parent mean
	PD 97019	PD 97047	PD 98066	PD 99035	DP 90	DES 119	
AR 9704-13-08	41.21	41.02	40.29	40.49	40.95	42.23	41.03
AR 9706-38-06	40.76	42.29	40.89	42.38	40.74	41.36	41.40
AR 9715-33-03	40.13	38.64	38.44	38.16	39.73	38.88	39.00
AR 9720-47-09	40.81	40.29	40.63	39.95	40.88	40.95	40.59
GA200035	39.54	39.67	40.44	37.30	37.90	42.13	39.50
GA200036	40.71	39.29	40.29	43.80	42.60	37.78	40.75
LA03404171	40.33	39.11	38.77	38.28	39.46	36.01	38.66
LA00405016	40.63	39.11	39.60	39.70	39.85	40.04	39.82
LA03404148	39.90	39.96	38.45	38.17	39.79	39.48	39.29
LA03404065	40.97	39.75	41.80	39.86	41.19	41.36	40.82
AGC85	38.78	39.60	40.05	39.36	41.00	35.68	39.08
AGC375	40.23	39.68	38.04	40.95	40.92	39.33	39.86
AGC208	38.78	39.01	38.02	37.84	40.12	36.55	38.39
00WA-104	39.40	39.71	40.38	38.61	39.77	37.58	39.24
01WM-27	39.66	37.97	41.40	40.61	39.93	37.33	39.48
8824-1-2-25-192-8	40.37	41.93	41.03	40.28	41.12	38.18	40.49
8824-1-2-25-192-10	39.47	41.04	39.36	40.58	40.69	39.95	40.18
MD09ne	41.39	38.53	37.30	40.11	39.56	35.83	38.79
MD15	40.21	38.26	38.21	39.08	39.65	37.36	38.80
NM1155	39.42	38.85	39.95	39.58	38.71	40.93	39.57
Male combiner mean	40.14	39.69	39.67	39.75	40.23	38.95	

**Table 3. Lint yield (kg ha<sup>-1</sup>) of F<sub>2</sub> hybrids derived from crosses of 20 elite U.S. breeding lines and six combiners including four Pee Dee lines and two commercial cultivars. The least significant difference between means at the two-tailed 95% probability level is 217 kg ha<sup>-1</sup>.**

Female parent	Male combiners						Female parent mean
	PD 97019	PD 97047	PD 98066	PD 99035	DP 90	DES 119	
AR 9704-13-08	1729	2173	1913	1869	1822	1801	1885
AR 9706-38-06	1751	1954	1874	2076	1995	2016	1944
AR 9715-33-03	1811	1817	1659	1536	1997	1704	1754
AR 9720-47-09	2033	1974	1909	1703	1790	1349	1793
GA200035	1865	2020	2109	1194	1429	1928	1758
GA200036	1930	1693	1902	1964	1851	1550	1815
LA03404171	1871	1723	1882	1688	1711	1551	1738
LA00405016	2005	1784	1963	1912	1691	1694	1842
LA03404148	1769	1936	1940	1872	1790	1732	1840
LA03404065	1949	1696	1905	1519	1874	1969	1819
AGC85	1748	1612	1790	1804	1987	1695	1773
AGC375	1731	1847	1688	1814	1535	1606	1704
AGC208	1663	1699	1884	1687	1797	1600	1722
00WA-104	1848	2034	1834	1906	1875	1885	1897
01WM-27	1638	1761	1900	2064	1705	1846	1819
8824-1-2-25-192-8	1840	2097	1794	1929	1920	1853	1906
8824-1-2-25-192-10	1641	2070	1851	2025	2133	1878	1933
MD09ne	1729	1593	1845	1864	1987	1632	1775
MD15	1607	1744	1794	1675	1709	1442	1662
NM1155	1564	1923	1764	1860	1637	1270	1670
Male combiner mean	1786	1858	1860	1798	1812	1700	

the lowest micronaire. Among the six male combiners, PD 97019, PD 98066, and DP 90 had the lowest micronaire.

Tables 2, 3, 4, 5, and 6 provide mean trait values for all 120 F<sub>2</sub> hybrids combined across environments. The

highest lint percent was produced by the GA200036 × PD 99035 hybrid (Table 2). Averaged across each of the six combiners, five U.S. breeding lines produced hybrids that displayed equally high lint percent. These included

**Table 4. Fiber strength (kN m kg<sup>-1</sup>) of F<sub>2</sub> hybrids derived from crosses of 20 elite U.S. breeding lines and six combiners including four Pee Dee lines and two commercial cultivars. The least significant difference between means at the two-tailed 95% probability level is 8.5 kN m kg<sup>-1</sup>.**

Female parent	Male combiners						Female parent mean
	PD 97019	PD 97047	PD 98066	PD 99035	DP 90	DES 119	
AR 9704-13-08	295.9	295.6	301.7	287.1	284.0	283.3	291.3
AR 9706-38-06	296.0	294.5	297.4	302.0	304.7	293.3	298.0
AR 9715-33-03	296.5	300.5	302.8	309.0	309.8	287.8	301.1
AR 9720-47-09	293.9	290.1	290.3	305.5	295.2	291.6	294.4
GA200035	292.3	292.7	308.4	323.4	309.7	293.8	303.4
GA200036	303.1	305.8	295.1	303.9	306.0	333.7	307.9
LA03404171	303.6	313.0	298.3	313.4	301.9	312.3	307.1
LA00405016	295.6	303.5	305.3	304.1	298.7	297.0	300.7
LA03404148	314.0	327.7	325.8	321.5	313.9	319.7	320.4
LA03404065	286.8	288.1	285.4	313.5	289.9	279.5	290.5
AGC85	307.7	310.2	306.1	318.2	310.3	324.6	312.9
AGC375	299.4	305.3	305.4	320.4	305.7	304.6	306.8
AGC208	303.9	316.3	310.8	312.2	308.2	325.7	312.9
00WA-104	303.4	311.9	302.8	323.7	302.2	322.8	311.1
01WM-27	283.4	301.0	299.5	305.6	298.9	312.0	300.1
8824-1-2-25-192-8	281.6	299.7	295.7	319.3	295.1	305.7	299.5
8824-1-2-25-192-10	296.1	292.9	288.6	300.2	290.8	310.8	296.6
MD09ne	315.5	308.3	325.8	317.2	327.7	332.1	321.1
MD15	316.8	326.9	325.8	326.1	338.3	337.5	328.6
NM1155	290.0	301.9	306.8	300.1	300.6	292.5	298.6
Male combiner mean	298.8	304.3	303.9	311.3	304.6	308.0	

**Table 5. Fiber length (mm) of F<sub>2</sub> hybrids derived from crosses of 20 elite U.S. breeding lines and six combiners including four Pee Dee lines and two commercial cultivars. The least significant difference between means at the two-tailed 95% probability level is 0.52 mm.**

Female parent	Male combiners						Female parent mean
	PD 97019	PD 97047	PD 98066	PD 99035	DP 90	DES 119	
AR 9704-13-08	28.45	27.85	29.89	28.87	28.63	28.48	28.70
AR 9706-38-06	29.30	29.13	29.21	29.30	28.92	28.76	29.10
AR 9715-33-03	28.44	29.33	30.01	30.45	29.40	27.76	29.23
AR 9720-47-09	27.46	27.92	29.24	30.24	28.40	27.71	28.50
GA200035	28.46	28.57	29.95	30.27	29.19	28.31	29.13
GA200036	29.13	29.07	29.47	28.89	29.10	30.49	29.36
LA03404171	28.12	28.42	29.13	29.95	29.29	29.89	29.13
LA00405016	28.37	27.34	29.10	28.84	28.33	27.96	28.32
LA03404148	28.82	28.85	29.74	30.28	28.81	29.76	29.38
LA03404065	27.68	28.50	28.88	30.10	27.83	28.25	28.54
AGC85	30.12	28.76	29.16	30.37	28.40	30.51	29.55
AGC375	29.99	29.03	30.92	31.02	28.94	29.63	29.92
AGC208	30.21	28.98	30.79	30.63	29.04	31.06	30.12
00WA-104	28.20	28.37	28.62	30.23	28.74	29.67	28.97
01WM-27	28.29	29.12	29.29	29.30	28.43	28.99	28.90
8824-1-2-25-192-8	27.09	27.28	28.83	29.72	28.46	28.42	28.30
8824-1-2-25-192-10	28.54	28.51	29.39	29.06	28.32	29.01	28.81
MD09ne	28.42	27.85	30.69	28.72	28.63	28.63	28.82
MD15	28.65	27.59	30.06	29.39	29.05	30.84	29.26
NM1155	28.58	29.61	30.41	29.68	28.39	28.50	29.20
Male combiner mean	28.62	28.50	29.64	29.77	28.72	29.13	

one from Louisiana, one from Georgia, and three from Arkansas. Averaged across each of the 20 U.S. breeding lines, five of the six combiners produced hybrids with similar lint percent. On average, DES 119 produced

hybrids with the lowest mean lint percent. Out of the total 120 F<sub>2</sub> hybrids, 21 hybrid combinations shared the highest lint yield (Table 3). Averaged across each of the six combiners, 16 of the 20 U.S. breeding lines resulted

**Table 6. Micronaire (units) of F<sub>2</sub> hybrids derived from crosses of 20 elite U.S. breeding lines and six combiners including four Pee Dee lines and two commercial cultivars. The least significant difference between means at the two-tailed 95% probability level is 0.2 units.**

Female parent	Male combiners						Female parent mean
	PD 97019	PD 97047	PD 98066	PD 99035	DP 90	DES 119	
AR 9704-13-08	4.8	4.7	4.4	4.4	4.7	4.6	4.6
AR 9706-38-06	4.6	4.8	4.5	4.8	4.7	4.6	4.7
AR 9715-33-03	4.4	4.7	4.3	4.2	4.4	4.4	4.4
AR 9720-47-09	4.7	4.6	4.4	4.3	4.4	4.4	4.5
GA200035	4.0	4.2	4.7	4.3	4.5	4.7	4.4
GA200036	4.3	4.5	4.6	4.7	4.8	4.3	4.5
LA03404171	4.6	4.8	4.6	4.5	4.7	4.4	4.6
LA00405016	4.6	4.4	4.3	4.4	4.5	4.6	4.5
LA03404148	4.4	4.5	4.2	4.2	4.3	4.3	4.3
LA03404065	4.4	4.5	4.3	4.1	4.3	4.3	4.3
AGC85	4.3	4.6	4.6	4.4	4.5	4.4	4.5
AGC375	4.2	4.3	4.3	4.1	4.7	4.2	4.3
AGC208	4.4	4.4	4.3	4.3	4.5	4.2	4.4
00WA-104	4.7	4.4	4.5	4.2	4.2	4.5	4.4
01WM-27	4.4	4.3	4.3	4.4	4.3	4.3	4.3
8824-1-2-25-192-8	4.4	4.9	4.4	4.5	4.7	4.3	4.5
8824-1-2-25-192-10	4.3	4.5	4.5	4.6	4.4	4.5	4.5
MD09ne	4.4	4.6	4.2	4.5	4.6	4.5	4.5
MD15	4.0	4.0	4.1	4.1	4.4	4.0	4.1
NM1155	4.0	4.5	4.2	3.9	4.3	4.5	4.2
Male combiner mean	4.4	4.5	4.4	4.3	4.5	4.4	

in hybrids with similar lint yield. On average, AGC375, AGC208, MD15, and NM1155 resulted in hybrids with the lowest lint yield. Averaged across hybrids, each of the six combiners resulted in hybrids of similar lint yield.

Four F<sub>2</sub> hybrids had equally high fiber strength (Table 4). Three of the four highest in fiber strength involved hybrids with DES 119 (GA200036, MD09ne, and MD15) and the other with DP 90 (MD15). Hybrids involving LA03404148, MD09ne, and MD15 exhibited the highest fiber strength. Compared to hybrids derived from the other five combiners, those involving PD 97019 produced lower fiber strength. For fiber length, seven individual F<sub>2</sub> hybrids exhibited the longest fibers (Table 5). These seven hybrids were derived from PD 98066, PD 99035, and DES 119 as the combiner and AGC375, AGC208, MD09ne, and MD15 as the U.S. breeding line parent. Considering the 20 U.S. breeding lines, averaged across each of the six combiners, AGC85, AGC375 and AGC208 produced hybrids with the longest fibers. Compared to the other four combiners, hybrids with PD 98066 and PD 99035 had the longest fibers. Table 6 shows that all F<sub>2</sub> hybrids produced micronaire values below the 5.0 discount range (Hake et al., 1990). Averaged across the 20 U.S. breeding lines, each combiner produced F<sub>2</sub> hybrids with similar micronaire values.

A primary goal of cotton breeding programs is to simultaneously combine desirable agronomic and fiber quality performance. The well-known, negative relationship among agronomic and fiber quality performance traits hinders the ability to develop germplasm with desirable values for both

traits (Campbell et al., 2012). To determine the ability of the six male combiners used in this study to generate offspring with desirable agronomic and fiber quality performance, we investigated per combiner the relationship between lint percent and both strength and length. Figures 1 and 2 show the scatter plot of strength (Fig. 1) and length (Fig. 2) regressed on lint percent for the 20 offspring derived from each of the six male combiners. The strongest negative relationship between lint percent and strength was found for offspring derived from both PD 98066 ( $R^2 = 0.49$ ) and DES 119 ( $R^2 = 0.65$ ). There appeared to be a weak or no linear relationship between lint percent and strength for offspring derived from four male combiners including (i) PD 97019 ( $R^2 = 0.00$ ), (ii) PD 97047 ( $R^2 = 0.19$ ), (iii) PD 99035 ( $R^2 = 0.22$ ), and (iv) DP 90 ( $R^2 = 0.11$ ). Similarly for lint percent and length, the strongest negative relationship was found for offspring derived from both PD 98066 ( $R^2 = 0.51$ ) and DES 119 ( $R^2 = 0.40$ ). There appeared to be a weak or no linear relationship between lint percent and length for offspring derived from four male combiners including (i) PD 97019 ( $R^2 = 0.21$ ), (ii) PD 97047 ( $R^2 = 0.04$ ), (iii) PD 99035 ( $R^2 = 0.28$ ), and (iv) DP 90 ( $R^2 = 0.07$ ). Considering the six male combiners, these data suggest that the negative relationship between lint percent and strength or length was more frequently found in offspring derived from PD 98066 and DES 119.

### Variance Components and Genetic Effects

Variance components were estimated and expressed as proportions of the phenotypic variance. These can be

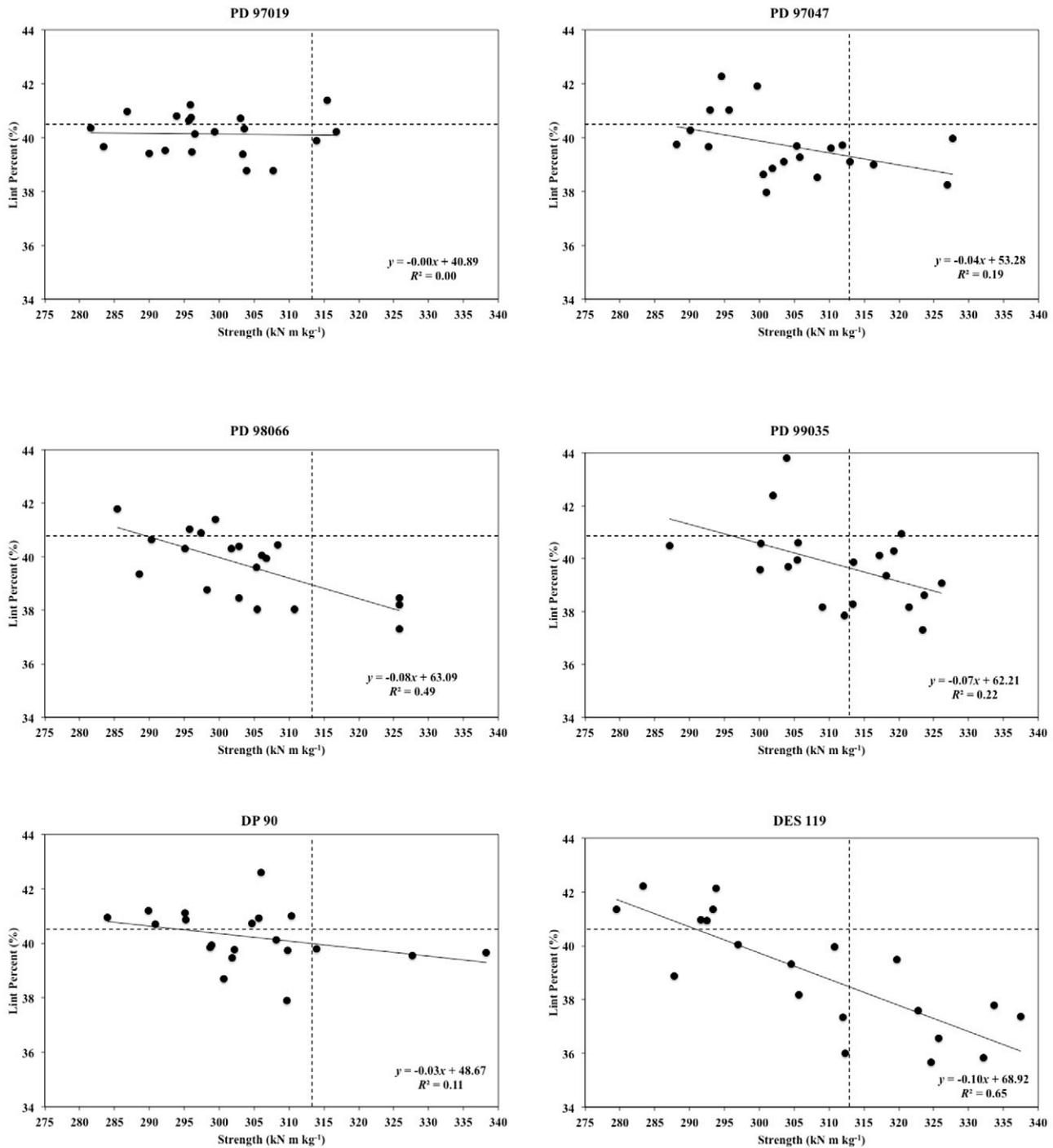


Figure 1. Relationship between lint percent and fiber strength for 20 hybrids derived from each of the six male combiners. Dashed lines represent one least significant difference above the grand mean for lint percent and fiber strength.

considered as measures of heritability (Table 7). Variance components for additive, dominance, dominance  $\times$  environment interaction effects, and residuals were significant ( $p < 0.01$ ) for all phenotypic traits. Additive  $\times$  environment interactions were only significant for micronaire. Additive effects accounted for between 1.9 (lint yield) and 21.8% (fiber strength) of the total variance. Dominance effects accounted for between 7.8 (lint yield) and 49.4% (lint percent) of the total variance. Dominance  $\times$  environment interactions accounted for between 16.4 (micronaire) and 51.3% (lint

yield) of the total variance. Residuals accounted for between 20.7 (lint percent) to 52.0% (micronaire) of the total variance. The lack of significant additive  $\times$  environment interactions was consistent with other recent cotton combining ability studies (Jenkins et al., 2009; Zeng and Wu, 2012). Not surprisingly, the proportion of the total variance attributed to each variance component differed from previously conducted studies (Jenkins et al., 2009; Zeng and Wu, 2012). As noted in Zeng et al. (2011), variance component proportions often differ depending on the genotypes being evaluated.

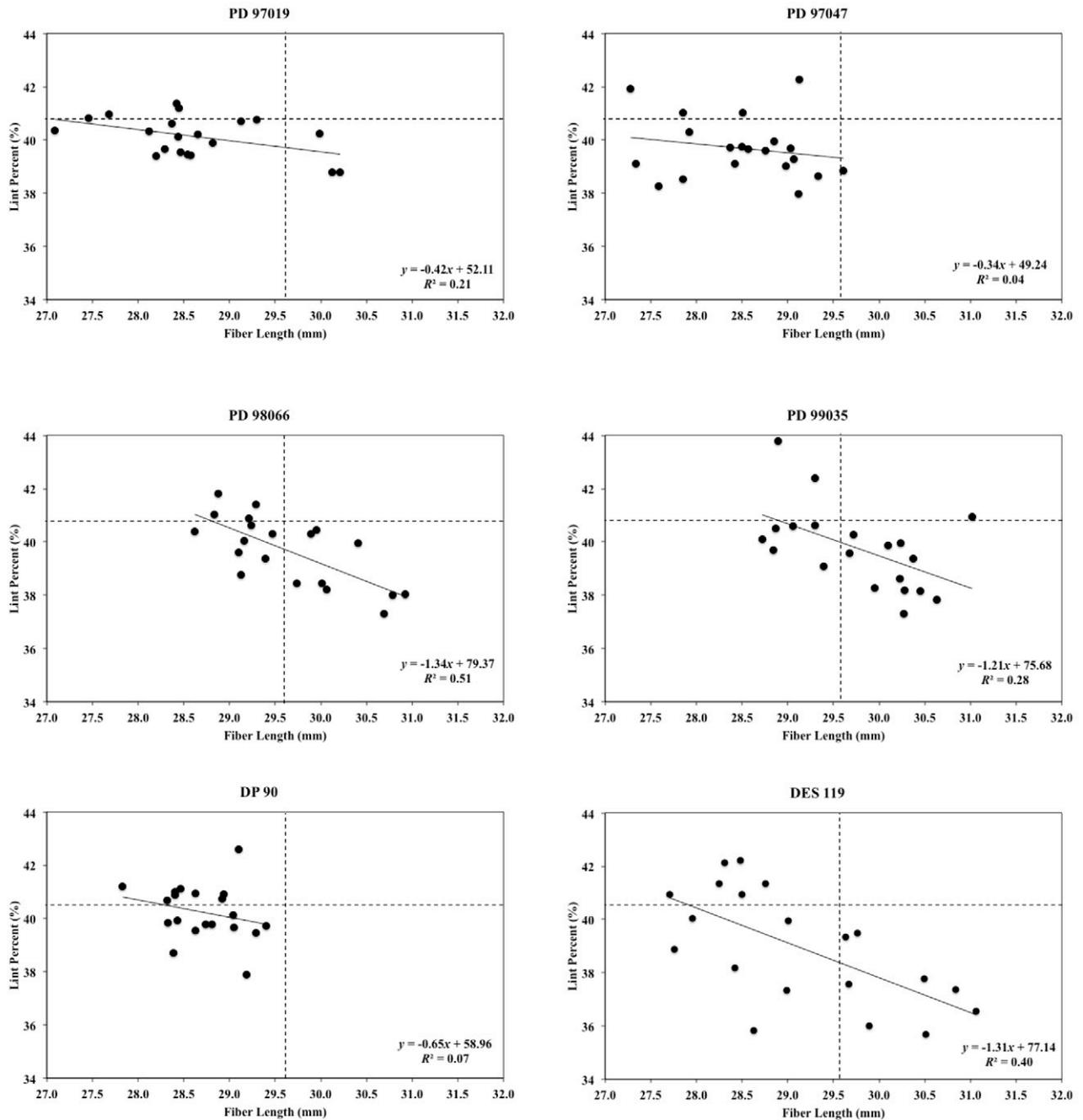


Figure 2. Relationship between lint percent and fiber length for 20 hybrids derived from each of the six male combiners. Dashed lines represent one least significant difference above the grand mean for lint percent and fiber length.

To assess the breeding potential of the six male combiners used in this study, we estimated the additive and dominance effects of each combiner. As noted in Jenkins et al. (2009), genetic effect estimates can be translated as follows: (i) additive effects represent general combining ability, (ii) homozygous dominance effects represent inbreeding depression, and (iii) heterozygous dominance effects represent specific combining ability. For each genetic effect, we tested if the effect was different than zero. Estimated genetic effects were also compared between the four Pee Dee lines and the two commercial cultivars.

Additive effects and their standard errors were estimated on a per-trait basis. Additive effects for each of the six male combiners were compared; these effects represent general combining ability (Table 8). PD 97047 and PD 99035 had lower additive effects than DP 90 for lint percent; PD 98066 had an additive effect higher than DP 90. For this trait, the four Pee Dee lines had higher additive effects than DES 119. PD 97047 had an additive effect higher than DP 90 for lint yield; three of the four Pee Dee lines had additive effects higher than DES 119. For fiber strength, PD 97019 had an additive effect lower than DP 90; PD 99035 had an additive effect higher than

**Table 7. Variance components and standard errors expressed as proportions of the phenotypic variances for agronomic and fiber quality traits.<sup>†</sup>**

	Lint percent	Lint yield	Fiber strength	Fiber length	Micronaire
$V_A/V_P$	0.086 ± 0.007**	0.019 ± 0.004**	0.218 ± 0.008**	0.159 ± 0.06**	0.086 ± 0.007**
$V_D/V_P$	0.494 ± 0.013**	0.078 ± 0.014**	0.219 ± 0.014**	0.372 ± 0.012**	0.200 ± 0.015**
$V_{AE}/V_P$	0.012 ± 0.003	0.000 ± 0.000	0.001 ± 0.002	0.001 ± 0.002	0.030 ± 0.007*
$V_{DE}/V_P$	0.202 ± 0.014**	0.513 ± 0.018**	0.299 ± 0.017**	0.257 ± 0.015**	0.164 ± 0.024**
$V_e/V_P$	0.207 ± 0.006**	0.390 ± 0.015**	0.263 ± 0.007**	0.210 ± 0.006**	0.520 ± 0.015**

\*Significant at the 0.05 probability level.

\*\*Significant at the 0.01 probability level.

<sup>†</sup> $V_A$ , additive variance;  $V_D$ , dominance variance;  $V_{AE}$ , additive by environment variance;  $V_{DE}$ , dominance by environment variance;  $V_e$ , error variance;  $V_P$ , phenotypic variance.

**Table 8. Additive effects for agronomic and fiber quality traits expressed as deviations from the grand mean. Significant effects are different from zero.**

Trait	Combiner	Effect estimate	Versus DP 90	Versus DES 119
Lint percent, %	DP 90	-0.03 ± 0.03	-	-
	DES 119	-1.14 ± 0.06*	-	-
	PD 97019	0.14 ± 0.04*	Not different	Higher
	PD 97047	-0.41 ± 0.04**	Lower	Higher
	PD 98066	0.12 ± 0.03	Higher	Higher
	PD 99035	-0.51 ± 0.03**	Lower	Higher
Lint yield, kg ha <sup>-1</sup>	DP 90	28.56 ± 10.08	-	-
	DES 119	-43.18 ± 13.50*	-	-
	PD 97019	44.46 ± 10.05*	Not different	Higher
	PD 97047	112.95 ± 15.91**	Higher	Higher
	PD 98066	59.78 ± 10.20**	Not different	Higher
	PD 99035	-13.61 ± 8.88	Not different	Not different
Strength, kN m kg <sup>-1</sup>	DP 90	0.50 ± 0.46	-	-
	DES 119	8.14 ± 0.54**	-	-
	PD 97019	-2.07 ± 0.47**	Lower	Lower
	PD 97047	1.84 ± 0.59	Not different	Lower
	PD 98066	0.08 ± 0.45	Not different	Lower
	PD 99035	10.14 ± 0.56**	Higher	Not different
Length, mm	DP 90	0.01 ± 0.03	-	-
	DES 119	0.44 ± 0.02**	-	-
	PD 97019	-0.22 ± 0.03**	Lower	Not different
	PD 97047	0.06 ± 0.02	Not different	Lower
	PD 98066	0.61 ± 0.03**	Higher	Higher
	PD 99035	1.19 ± 0.04**	Higher	Higher
Micronaire, units	DP 90	0.05 ± 0.01**	-	-
	DES 119	-0.03 ± 0.01	-	-
	PD 97019	0.03 ± 0.01	Not different	Not different
	PD 97047	0.03 ± 0.01	Not different	Not different
	PD 98066	0.00 ± 0.01	Lower	Not different
	PD 99035	-0.18 ± 0.01**	Lower	Lower

\*Significant at the 0.05 probability level.

\*\*Significant at the 0.01 probability level.

DP 90, PD 97019, PD 97047, and PD 98066 had additive effects lower than DES 119. For fiber length, PD 97019 had an additive effect lower than DP 90; PD 97047 had an additive effect lower than DES 119. PD 98066 and PD 99035 had additive effects higher than DP 90 and DES 119. For micronaire, PD 98066 had an additive effect lower than DP 90; PD 99035 had an additive effect lower than DP 90 and DES 119.

**Table 9. Homozygous dominance effects for agronomic and fiber quality traits expressed as deviations from the grand mean. Significant effects are different from zero.**

Trait	Combiner	Effect estimate	Versus DP 90	Versus DES 119
Lint percent, %	DP 90	-0.56 ± 0.19	-	-
	DES 119	0.61 ± 0.21	-	-
	PD 97019	-2.78 ± 0.24**	Lower	Lower
	PD 97047	-0.46 ± 0.17	Not different	Lower
	PD 98066	-5.04 ± 0.24**	Lower	Lower
	PD 99035	1.24 ± 0.24**	Higher	Not different
Lint yield, kg ha <sup>-1</sup>	DP 90	-175.44 ± 27.80**	-	-
	DES 119	-79.06 ± 54.19	-	-
	PD 97019	-250.24 ± 42.52**	Not different	Not different
	PD 97047	-338.0 ± 39.71**	Not different	Lower
	PD 98066	-176.37 ± 27.73**	Not different	Not different
	PD 99035	-6.83 ± 34.52	Higher	Not different
Strength, kN m kg <sup>-1</sup>	DP 90	0.06 ± 1.68	-	-
	DES 119	-18.61 ± 2.83**	-	-
	PD 97019	-10.79 ± 1.82**	Lower	Not different
	PD 97047	0.25 ± 1.91	Not different	Higher
	PD 98066	9.99 ± 1.65**	Higher	Higher
	PD 99035	-8.92 ± 2.77	Not different	Not different
Length, mm	DP 90	-0.63 ± 0.10**	-	-
	DES 119	-1.06 ± 0.13**	-	-
	PD 97019	0.37 ± 0.15	Higher	Higher
	PD 97047	-2.21 ± 0.12**	Lower	Lower
	PD 98066	0.27 ± 0.10	Higher	Higher
	PD 99035	-3.06 ± 0.19**	Lower	Lower
Micronaire, units	DP 90	-0.35 ± 0.05**	-	-
	DES 119	-0.08 ± 0.06	-	-
	PD 97019	-0.41 ± 0.05**	Not different	Lower
	PD 97047	0.23 ± 0.04**	Higher	Higher
	PD 98066	-0.26 ± 0.07*	Not different	Not different
	PD 99035	0.67 ± 0.05**	Higher	Higher

\*Significant at the 0.05 probability level.

\*\*Significant at the 0.01 probability level.

Homozygous dominance effects were predicted and their standard errors estimated on a per-trait basis. These effects were compared for each of the six male combiners to represent inbreeding depression effects (Table 9). For lint percent, PD 97019 and PD 98066 had lower inbreeding depression effects compared to DP 90 and DES 119; PD 97047 had a lower effect compared to DES 119. PD 99035 had a higher inbreeding depression effect compared to

DP 90. For lint yield, PD 99035 had a higher inbreeding depression effect compared to DP 90; PD 97047 had an inbreeding depression effect lower than DES 119. For fiber strength, PD 97019 had an inbreeding depression effect less than DP 90; PD 98066 had an effect higher than DP 90. PD 97047 and PD 98066 had inbreeding depression effects higher than DES 119. For fiber length, PD 97019 and PD 98066 had higher inbreeding depression effects than DP 90 and DES 119; PD 97047 and PD 99035 had lower inbreeding depression effects than DP 90 and DES 119. For micronaire, PD 97047 and PD 99035 had inbreeding depression effects higher than DP 90 and DES 119. PD 97019 had a lower inbreeding depression effect than DES 119.

For each trait and cross combination, heterozygous dominance effects were predicted and their standard errors estimated (Supplemental Tables S1, S2, S3, and S4). No strong trends specific to any of the male combiners were evident. However, for fiber length and micronaire, topcrosses involving PD 99035 appear to transmit more beneficial specific combining ability effects. Of 20 topcross combinations, 11 combinations involving PD 99035 displayed positive specific combining ability for fiber length (beneficial) whereas only one combination displayed positive specific combining ability for micronaire (detrimental). In general, these results suggested heterozygous dominance effects differ depending on the specific topcross parent  $\times$  male combiner cross combination.

## DISCUSSION

Progress in plant breeding can be greatly facilitated with knowledge of the breeding potential of specific germplasm or germplasm pools. In this study, when used in topcrosses with a subset of breeding lines developed in eight different public U.S. cotton breeding programs, we evaluated the breeding potential of Pee Dee germplasm. Considering four Pee Dee germplasm line combiners and two commercial combiners, we compared parental line mean performance, hybrid performance, and estimated genetic effects. Compared to well-known, commercial combiners DP 90 and DES 119, the Pee Dee germplasm combiners showed similar or better breeding potential. Previously, cotton topcross studies have been effective in determining the breeding potential of specific germplasm. A topcross design was used to determine the breeding potential of exotic, converted day-neutral accessions (McCarty et al., 2004a, 2004b). Topcross designs have been used successfully to determine the breeding potential of interspecies chromosome substitution lines (Jenkins et al., 2006, 2012). Zeng and Wu (2012) successfully used a topcross design to determine the breeding potential breeding lines with exotic origins.

To determine if any obvious trends existed among hybrids derived from crosses using 20 breeding lines from eight different U.S. cotton breeding programs represented in this study, we compared the mean of hybrids from

each of the eight breeding programs, averaged both across combiners and per male combiner, to the overall hybrid mean. It is important to note that these inferences pertain to the breeding potential of each of the 20 breeding lines used in this study and do not necessarily represent the broader breeding potential of all germplasm developed in each of the eight U.S. breeding programs. For lint percent, hybrids averaged across combiners involving USDA-ARS, Stoneville, MS, germplasm were greater than one LSD below the overall hybrid mean. Hybrids involving three of the six combiners were one LSD below the overall hybrid lint percent mean. Averaged across male combiners, hybrids involving University of Arkansas germplasm were greater than one LSD below the overall hybrid mean for strength. University of Arkansas hybrids involving three of the six combiners were one LSD below the overall hybrid strength mean. Averaged across male combiners, hybrids involving USDA-ARS, Stoneville, MS, germplasm were greater than one LSD above the overall hybrid strength mean. The USDA-ARS, Stoneville, MS, hybrids involving all six combiners were one LSD above the overall hybrid strength mean. Averaged across male combiners, hybrids involving USDA-ARS, Maricopa, AZ, germplasm were greater than one LSD above the overall length hybrid mean. The USDA-ARS, Maricopa, AZ, hybrids involving four of the six combiners were one LSD above the overall length hybrid mean. For lint yield and micronaire, hybrids derived from the eight different U.S. breeding programs and averaged across combiners did not differ from the overall hybrid mean. Considering the eight U.S. breeding programs represented in this study, excellent sources of fiber quality are clearly provided from hybrids derived from the elite breeding lines used in this study from the USDA-ARS, Stoneville, MS (strength), and USDA-ARS, Maricopa, AZ (length), germplasm enhancement programs.

Pearson correlation coefficients were calculated between the mean of crosses involving each of the six male combiners and the mean performance of each male combiner to investigate the ability of parental line mean performance to predict the agronomic and fiber quality performance of hybrid offspring. The correlation coefficients were 0.32 for lint percent, 0.52 for lint yield, 0.71 for strength, 0.70 for length, and  $-0.10$  for micronaire. These data suggested that parental line performance was a fairly good predictor for strength and length; however, it was a weaker predictor for lint percent and micronaire.

Overall when using Pee Dee germplasm in early stages of a breeding program, our results suggested no detrimental effects for agronomic and fiber quality performance. Based on the scatter plots in Fig. 1 and 2, both PD 98066 and DES 119 appear to generate offspring that maintain the negative relationship between agronomic and fiber quality performance. The negative relationship among offspring derived from PD 97019, PD 97047, and DP

90 appears to have weakened. However, the weakened, negative relationship appears to be associated with lower strength and/or length.

Our results suggested a good candidate for generating high fiber quality potential with a weakened negative relationship with agronomic performance is PD 99035. Interestingly, Campbell et al. (2012) identified several Pee Dee germplasm lines representing rare recombination events that overcome the negative linkage between agronomic and fiber quality performance. Although not included in that study, it is plausible that PD 99035 represents such a rare recombinant. In a half-diallel involving four older Pee Dee germplasm lines and a commercial cultivar, Green and Culp (1990) identified two Pee Dee germplasm lines (PD 3249 and 'SC-1') as sources to simultaneously improve yield and fiber quality. In terms of specific crosses, AGC375 × PD 99035 generated offspring with high lint percent, strength, and length that was one LSD higher than the overall mean for each trait. MD09ne × PD 97019 generated offspring with lint percent and strength one LSD higher than the overall mean for each trait. The mean lint yield for both cross combinations did not differ from than the overall mean. GA20035 × PD 98066 generated offspring with lint yield and length one LSD higher than the overall mean for each trait. Compared to the overall mean, the mean for GA20035 × PD 98066 offspring was not different for lint percent and strength. In summary, cotton breeders can use the information provided herein as an informative parental line selection tool. This information should facilitate the development of elite breeding lines, recurrent parents, and/or commercial cultivars.

## Supplemental Information Available

Supplemental material is included with this manuscript.

Supplemental Tables 1 through 5 provide heterozygous dominance effects for each trait and are available.

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## References

Bourland, F.M., and D.C. Jones. 2009. Registration of Arkot 9704 and Arkot 9706 germplasm lines of cotton. *J. Plant Reg.* 3:289–292. doi:10.3198/jpr2008.12.0708crg

Bowman, D.T., and O.A. Gutierrez. 2003. Sources of fiber strength in the U.S. upland cotton crop from 1980–2000. *J. Cotton Sci.* 7:164–169.

Bridge, R.R. 1986. Registration of 'Des 119' cotton. *Crop Sci.*

26:646–647. doi:10.2135/cropsci1986.0011183X002600030050x

Campbell, B.T., P.W. Chee, E.L. Lubbers, D.T. Bowman, W.R. Meredith, J. Johnson, and D.E. Fraser. 2011. Genetic improvement of the Pee Dee cotton germplasm collection following seventy years of plant breeding. *Crop Sci.* 51:955–968. doi:10.2135/cropsci2010.09.0545

Campbell, B.T., P.W. Chee, E. Lubbers, D.T. Bowman, W.R. Meredith, J. Johnson, D. Fraser, W. Bridges, and D.C. Jones. 2012. Dissecting genotype × environment interactions and trait correlations present in the Pee Dee cotton germplasm collection following seventy years of plant breeding. *Crop Sci.* 52:690–699. doi:10.2135/cropsci2011.07.0380

Campbell, B.T., V. Williams, and W. Park. 2009. Using molecular markers and field performance data to characterize the Pee Dee cotton germplasm resources. *Euphytica* 169:285–301. doi:10.1007/s10681-009-9917-4

Cheatham, C.L., J.N. Jenkins, J.C. McCarty, C.E. Watson, and J. Wu. 2003. Genetic variances and combining ability of crosses of American cultivars, Australian cultivars, and wild cottons. *J. Cotton Sci.* 7:16–22.

Green, C.C., and T.W. Culp. 1990. Simultaneous improvement of yield, fiber quality, and yarn strength in Upland cotton. *Crop Sci.* 30:66–69. doi:10.2135/cropsci1990.0011183X003000010015x

Hake, K., K. Bragg, J. Mauney, and B. Metzger. 1990. Causes of high and low micronaire. *Phys. Today* 1:12.

Hinze, L.L., B.T. Campbell, and R.J. Kohel. 2011. Performance and combining ability in cotton (*Gossypium hirsutum* L.) populations with diverse parents. *Euphytica* 181:115–125. doi:10.1007/s10681-011-0442-x

Jenkins, J.N., J.C. McCarty, S. Saha, O. Gutierrez, R. Hayes, and D.M. Stelly. 2006. Genetic effects of thirteen *Gossypium barbadense* L. chromosome substitution lines in topcrosses with upland cotton cultivars: I. Yield and yield components. *Crop Sci.* 46:1169–1178. doi:10.2135/cropsci2005.08-0269

Jenkins, J.N., J.C. McCarty, J. Wu, and O.A. Gutierrez. 2009. Genetic variance components and genetic effects among eleven diverse upland cotton lines and their F<sub>2</sub> hybrids. *Euphytica* 167:397–408. doi:10.1007/s10681-009-9902-y

Jenkins, J.N., J.C. McCarty, J. Wu, O.A. Gutierrez, R. Hayes, and D.M. Stelly. 2007. Genetic effects of thirteen *Gossypium barbadense* L. chromosome substitution lines in topcrosses with upland cotton cultivars: II. Fiber quality traits. *Crop Sci.* 47:561–571. doi:10.2135/cropsci2006.06.0396

Jenkins, J.N., J.C. McCarty, J. Wu, R. Hayes, and D. Stelly. 2012. Genetic effects of nine *Gossypium barbadense* L. chromosome substitution lines in top crosses with five elite upland cotton *G. hirsutum* L. cultivars. *Euphytica* 187:161–173. doi:10.1007/s10681-011-0580-1

May, L. 1999. Genetic variation in fiber quality. In: A.S. Basra, editor, *Cotton fibers, development biology, quality improvement and textile processing*. Food Products Press, New York, NY. p. 183–230

May, O.L., R.G. Cantrell, and D.C. Jones. 2005. Registration of GA98066 upland cotton germplasm line. *Crop Sci.* 45:1175–1176. doi:10.2135/cropsci2004.0556GP

McCarty, J.C., J.N. Jenkins, and J. Wu. 2004a. Primitive accession derived germplasm by cultivar crosses as sources for cotton improvement: I. Phenotypic values and variance components. *Crop Sci.* 44:1226–1230. doi:10.2135/cropsci2004.1226

McCarty, J.C., J.N. Jenkins, and J. Wu. 2004b. Primitive accession derived germplasm by cultivar crosses as sources for cotton

- improvement: II. Genetic effects and genotypic values. *Crop Sci.* 44:1231–1235. doi:10.2135/cropsci2004.1231
- Meredith, W.R. 1984a. Genotype  $\times$  environment interactions. In: R.J. Kohel and C.F. Lewis, editors, *Cotton*. American Society of Agronomy, Madison, WI. p. 138–141.
- Meredith, W.R. 1984b. Quantitative genetics. In: R.J. Kohel and C.F. Lewis, editors, *Cotton*. American Society of Agronomy, Madison, WI. p. 132–147.
- Meredith, W.R., Jr. 2006. Registration of MD 15 upland cotton germplasm. *Crop Sci.* 46:2722. doi:10.2135/cropsci2006.05.0354
- Meredith, W.R., and J.S. Brown. 1998. Heterosis and combining ability of cottons originating from different regions of the United States. *J. Cotton Sci.* 2:77–84.
- Meredith, W.R., and W.S. Nokes. 2011. Registration of MD 9ne and MD 25 high-fiber-quality germplasm lines of cotton. *J. Plant Reg.* 5:202–206. doi:10.3198/jpr2010.06.0333crg
- Miller, R.G. 1974. The jackknife – A review. *Biometrika* 61:1–15.
- Percy, R.G., O.L. May, M. Ulloa, and R.G. Cantrell. 2006. Registration of AGC85, AGC208, and AGC375 upland cotton germplasm lines. *Crop Sci.* 46:1828–1829. doi:10.2135/cropsci2005.12-0483
- SAS Institute. 2008. SAS 9.2 for Windows. SAS Institute, Cary, NC.
- Tang, B., J.N. Jenkins, and C.E. Watson. 1996. Evaluation of genetic variances, heritability, and correlations for yield and fiber properties among cotton  $F_2$  hybrids. *Euphytica* 91:315–322. doi:10.1007/BF00033093
- Wu, J., J.N. Jenkins, and J.C. McCarty. 2008. Testing variance components by two jackknife techniques. In: *Proceedings of Applied Statistics in Agriculture*, Manhattan, KS. 27–29 Apr. 2008. Kansas State University, Manhattan, KS. p. 1–17.
- Wu, J., J.N. Jenkins, and J.C. McCarty. 2010. A generalized approach and computer tool for quantitative genetics study. In: *Proceedings of Applied Statistics in Agriculture*, Manhattan, KS. 25–27 Apr. 2010. Kansas State University, Manhattan, KS. p. 85–106.
- Wu, J., J.N. Jenkins, J.C. McCarty, and K. Glover. 2012. Detecting epistatic effects associated with cotton traits by a modified MDR approach. *Euphytica* 187:289–301. doi:10.1007/s10681-012-0770-5
- Zeng, L., W.R. Meredith, and D.L. Boykin. 2011. Germplasm potential for continuing improvement of fiber quality in upland cotton: Combining ability for lint yield and fiber quality. *Crop Sci.* 51:60–68. doi:10.2135/cropsci2010.07.0413
- Zeng, L., and J. Wu. 2012. Germplasm for genetic improvement of lint yield in upland cotton: Genetic analysis of lint yield and yield components. *Euphytica* 187:247–261. doi:10.1007/s10681-012-0708-y
- Zhang, J., R. Flynn, S.E. Hughs, S. Bajaj, and D.C. Jones. 2011. Registration of ‘Acala 1517–09R’ cotton. *J. Plant Reg.* 5:164–169. doi:10.3198/jpr2010.05.0268crg
- Zhu, J. 1989. Estimation of genetic variance components in the general mixed model, Ph.D. diss. North Carolina State University, Raleigh, NC.
- Zhu, J. 1993. Methods of predicting genotype value and heterosis for offspring of hybrids. *J. Biomath.* 8:32–40.