

# Genetic Variation for Agronomic and Fiber Quality Traits in a Population Derived from High-Quality Cotton Germplasm

B.T. Campbell,\* J. Greene, J. Wu, and D.C. Jones

## ABSTRACT

Genetic improvement of fiber quality is necessary to meet the requirements of processors and users of upland cotton (*Gossypium hirsutum* L.) fiber. To foster genetic improvement of cotton fiber quality, adequate genetic variation for the quantitatively inherited physical properties of cotton is required. Additionally, knowledge of the genetic architecture of fiber quality is needed to design effective breeding strategies to further improve fiber quality. In this study, our objective was to estimate genetic variance components and predict genetic effects for agronomic and fiber quality traits in a population derived from four known genotypic sources of high fiber quality. The majority of genetic variation present in a half-diallel population derived from these four sources of high fiber quality was due to additive effects. Predicted genetic effects demonstrated that one of the four parents, MD 15, provides a unique genetic source of high fiber quality alleles that behave additively.

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**Abbreviations:** AD, additive-dominance; HVI, High Volume Instrument; LSD, least significant difference.

**T**O MEET INTERNATIONAL DEMAND from downstream processors and end users of cotton fiber, it is necessary to improve fiber quality. In addition to increased globalization of cotton production and processing, competition from manmade fibers has increased demand for high cotton fiber quality (Smith et al., 2008). Access to genetic variation for the physical properties of cotton fiber is required for continued improvement of upland cotton (*Gossypium hirsutum* L.). The physical properties of cotton, including fiber length, strength, and micronaire (combination of fiber maturity and fineness), are known to behave as quantitatively inherited traits (Chee and Campbell, 2009).

Quantitative genetic analyses have shown that both additive and dominance effects contribute fiber property genetic variation. Campbell and Myers (2015) summarized recent studies reporting components of variance for fiber properties and found the mean additive to dominance variance ratio for length, strength, and micronaire as 1:1, 2:1, and 1:1, respectively. They also reported mean narrow-sense heritability estimates of 0.4 for length, 0.4 for strength, and 0.3 for micronaire. The proportions of additive and dominance variance components and estimates of heritability vary among different studies, but generally, the impact of additive effects is the most notable for fiber strength, followed by fiber length, and the lowest for micronaire.

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Numerous studies have shown increased fiber quality over the last century. For example, Kuraparthy and Bowman (2013) reported positive gains in US cotton fiber quality for fiber length, fiber strength, and micronaire. Determining the genetic sources of improved fiber quality is of great interest to cotton breeders and geneticists. Assuming multiple sources of fiber quality are available and results from different favorable alleles, attempts can be made to pyramid the multiple, favorable alleles to further increase fiber quality.

Based on examining the pedigrees of widely grown commercial cultivars from 1980 through 2000, Bowman and Gutierrez (2003) noted the majority of increased fiber strength was accounted for by the New Mexico State University Acala breeding program (50%), transgressive segregation (25%), and the USDA-ARS Pee Dee breeding program (12.5%). The breeding histories of both the New Mexico State University Acala (Zhang et al., 2005) and USDA-ARS Pee Dee breeding programs have been well documented (Campbell et al., 2009, 2011, 2012). Both programs focused heavily on improving fiber quality with similar breeding foundations established using a diversity of germplasm resources including accessions involving the triple hybrid (Beasley, 1940; *G. arboreum* L., *G. thurberi* Tod., *G. hirsutum* L.), *G. barbadense* L., and *G. hirsutum*. Although not tested empirically, it is assumed that the sources of high fiber quality in both programs were derived from *G. thurberi* (fiber strength) via the triple hybrid and *G. barbadense* (fiber length) (Bowman and Gutierrez, 2003). In addition, the Cotton Improvement Lab at Texas A&M University has recently developed a series of extra long staple upland germplasm lines and cultivars (Smith et al., 2008). Upon inspection of breeding history, the source of beneficial fiber quality alleles is believed to come from either the USDA-ARS Pee Dee breeding program or transgressive segregation.

In this report, we examined the performance and genetic effects of breeding populations derived from four known sources of fiber quality and an upland cotton genetic standard. The objective of this study was to estimate genetic variance components and predict genetic effects for agronomic and fiber quality traits in a population derived from four known sources of fiber quality.

## MATERIALS AND METHODS

### Development of Genetic Families

In 2006, a total of four high fiber quality genotypes and an upland genetic standard TM-1 (PI 607172) were crossed in a half-diallel mating design without reciprocals. The seeds of F<sub>1</sub> hybrids and their parental lines were sent to a winter nursery in Tecoman, Mexico, and manually self-pollinated to produce enough seeds for multilocation trials using F<sub>2</sub> populations and parental lines. The four high-quality genotypes included 'Deltapine 90' (PI 529529), 'DES 119' (PI 606809; Bridge, 1986), MD 15 (PI 642769; Meredith, 2006), and PD 2164 (PI 529617;

Culp and Harrell, 1980a). The genotypes were selected to represent known sources of high fiber quality. For better understanding of these genotypes, their pedigrees are detailed below.

### Deltapine 90

Deltapine 90 (DP 90) was developed from a four-way cross (AZ 5909-7-1/'Deltapine 16')/(Deltapine 16/John Cotton Polycross). The origin of AZ 5909-7-1 is not known. Deltapine 16 was derived from a cross involving 'Deltapine Smoothleaf' and 'Fox 4'. Both of these strains trace to 'Deltapine 10', 'Deltapine 11', and 'Stoneville 2'. John Cotton Polycross was derived from a complex intercross involving several Acala strains, 'Auburn 56', 'Stoneville 213', Deltapine Smoothleaf, and 'Paymaster 111'.

### DES 119

DES 119 was developed from the cross 'DES 24'/DES 2134-047. DES 24 was developed from a cross involving 'Stoneville 603'/'Delcote 277'. DES 2134-047 was a sister line of 'DES 56', which was developed from the cross Stoneville 213/PD 62-164. Collectively, materials on both sides of the DES 119 pedigree trace back to 'Lone Star', 'Empire', and Pee Dee origins.

### MD 15

MD 15 was developed from a cross of 'Fibermax 832' (PVP 9800258) and MD 51neOKRA. Fibermax 832 was developed by the Commonwealth Scientific and Industrial Research Organisation in Australia and commercialized in the United States in the late 1990s. Fibermax 832 was derived from a cross involving 'Sicala V-1' and 'Siokra 1-4', which trace back to 'Blightmaster' and Acala germplasm. MD 51neOKRA was a BC<sub>5</sub> derived line from 'MD 51ne', which was derived from the cross MD 65\_11ne/Deltapine 90 and ultimately traces back to FTA 263 (Culp and Harrell, 1980b) of the Pee Dee breeding program.

### PD 2164

PD 2164 was derived from the cross AC 239/FJA 348. Collectively, AC 239 and FJA 348 were derived from complex crosses involving AHA-6-1-4, C6-5, TH 108, TH 171, Sealand 7, Sealand 542, and Earlistaple (Culp and Harrell, 1980b). FJA 348 was also derived from a complex cross involving Sealand 542, TH 108, AHA 6-1-4, Earlistaple, TH 171, and Sealand 7. Collectively, these complex crosses involved a wide range of genetic diversity involving Acala cottons, extra long staple upland cottons, and triple hybrid cottons developed from *G. arboreum*, *G. thurberi*, *G. barbadense*, and upland cotton.

### Field Evaluations

The 10 F<sub>2</sub> hybrids and five parental lines were evaluated in four environments during 2007 and 2008. In each year, the trial was conducted at the Clemson University Pee Dee Research and Education Center near Florence, SC, and the Clemson University Edisto Research and Education Center in Blackville, SC. In each trial, the F<sub>2</sub> hybrids and parental lines were randomly assigned to a single replicate of a replicated, randomized complete block field design. Three and four replicates were used in 2007 and 2008, respectively. In all trials, plots consisted of two rows 10.6 m long with 96 cm row spacing. Trial management followed the established local production practices for

rained cotton production at each location. Each plot was harvested with a spindle-type mechanical cotton picker, and total seed cotton weight was recorded. A 25-boll sample was hand-harvested from each plot before harvest to determine yield components and fiber quality properties. Boll weight was determined by dividing the 25-boll seed cotton weight by 25. All samples from each location were ginned on a common 10-saw laboratory gin, and lint percentage 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 percentage by the total seed cotton yield for each plot accordingly. Seed index was measured by recording the mass of 100 fuzzy seeds. Bolls per square meter was calculated by dividing seed cotton yield by boll weight. 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 included micronaire, upper-half mean fiber length, fiber length uniformity, fiber strength, and short fiber content.

## Data Analysis

### Analysis of Phenotypic Data

First, all agronomic and fiber quality data were analyzed using a mixed model and the PROC GLM module of SAS ver. 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, data were analyzed using two analysis of variance procedures. Block and environment (each year–location) were considered random effects. Genotypes were considered fixed effects. Fisher's protected LSD was calculated and used to make planned comparisons among least square means.

### Genetic Analysis

The data were analyzed by an additive–dominance genetic model with genotype  $\times$  environment interaction following the procedures described by Jenkins et al. (2006). As a result of some coefficients for genetic effects being fractions rather than 0 and 1, a mixed linear model approach, minimum norm quadratic unbiased estimation 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 environment ( $V_E$ ), block within environment ( $V_B$ ), additive ( $V_A$ ), dominance ( $V_D$ ), additive  $\times$  environment ( $V_{AE}$ ), dominance  $\times$  environment ( $V_{DE}$ ), and residual ( $V_\rho$ ); they were expressed as proportions of the total phenotypic variance (Tang et al., 1996; Wu et al., 2010, 2014). 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). An approximate one-tailed *t*-test with nine of degrees of freedom was used to detect the significance of variance components. A two-tailed *t*-test was used to detect the significance of genetic

**Table 1. Mean agronomic performance for 10 half-diallel families combined over four environments.**

Family	Lint percentage	Lint yield	Seed index	Boll weight	No. bolls
	%	kg ha <sup>-1</sup>	g		m <sup>-2</sup>
DP 90/DES 119	39.55	1409	9.69	5.53	62.3
MD 15/DES 119	40.43	1431	10.40	5.74	60.1
MD 15/DP 90	40.33	1445	10.07	5.86	61.0
PD 2164/DES 119	38.60	1296	10.88	5.73	56.6
PD 2164/DP 90	38.40	1294	10.50	5.88	54.8
PD 2164/MD 15	40.16	1376	11.24	6.32	52.7
TM-1/DES 119	36.69	1156	10.95	5.68	53.6
TM-1/DP 90	37.48	1255	10.65	5.81	55.9
TM-1/MD 15	37.13	1212	11.14	5.93	53.7
TM-1/PD 2164	35.63	1150	11.77	6.46	49.0
LSD (0.05)	0.48	113	0.29	0.19	5.3

effects (Miller, 1974). Similar to Campbell et al. (2013), lower and upper limits of 95% confidence interval for parameters of interest were calculated to make multiple comparisons among parameters of interest (i.e., additive effects) 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 effects for each of the five parental lines. The 95% confidence intervals for additive effects were compared among the parental lines. All of these genetic analyses were conducted using the Qgtools package in R (Wu et al., 2012, 2014).

## RESULTS

### Mean Comparisons among Hybrids

Table 1 provides mean agronomic trait values for each of the  $F_2$  hybrids combined across four environments. Hybrids derived from MD 15/DES 119, MD 15/DP 90, and PD 2164/MD 15 had the highest lint percentage and lint yield. The DP 90/DES 119 hybrid also produced high lint yield. The TM-1/PD 2164 hybrid had the highest seed index and boll weight. In addition, PD 2164/MD 15 also produced a high boll weight. In terms of bolls per square meter, DP 90/DES 119, MD 15/DES 119, and MD 15/DP 90 were the highest. Overall, the hybrids derived from TM-1 showed poor agronomic performance.

Table 2 provides the mean fiber quality trait values for each of the  $F_2$  hybrids across four environments. Hybrids derived from MD 15/DES 119, MD 15/DP 90, and PD 2164/MD 15 had the lowest micronaire and longest fibers. In addition, TM-1/MD 15 produced long fibers. The  $F_2$  hybrids MD 15/DES 119 and MD 15/DP 90 had the highest uniformity. MD 15/DP 90 produced the strongest fibers and MD 15/DES 119, MD 15/DP 90, and PD 2164/MD 15 produced the lowest short fiber content. Considering these physical fiber properties, overall, hybrids derived from MD 15 produced the highest quality fiber.

**Table 2. Mean fiber quality performance for 10 half-diallel families combined over four environments.**

Family	Micro- naire	Fiber length	Unifor- mity	Fiber strength	Short fiber content
	units	mm	%	kN m kg <sup>-1</sup>	%
DP 90/DES 119	4.6	28.45	83.4	283	8.21
MD 15/DES 119	4.3	29.46	84.3	302	8.06
MD 15/DP 90	4.3	29.06	84.1	321	7.70
PD 2164/DES 119	4.5	28.11	83.5	268	8.19
PD 2164/DP 90	4.5	28.53	82.8	280	8.41
PD 2164/MD 15	4.2	29.10	83.7	300	7.92
TM-1/DES 119	4.6	28.22	83.6	265	8.36
TM-1/DP 90	4.6	28.29	83.0	270	8.49
TM-1/MD 15	4.5	29.36	83.7	293	8.15
TM-1/PD 2164	4.5	28.49	82.8	269	8.52
LSD (0.05)	0.1	0.42	0.43	6.4	0.36

## Variance Components

Variance components were estimated and expressed as proportions of the phenotypic variance. Considering the agronomic traits, variance components for environment, additive effects, and residuals were significant ( $p < 0.01$ ) for all agronomic traits (Table 3). Dominance effects were significant for lint yield and boll weight ( $p < 0.01$ ). Additive  $\times$  environment interactions were significant only for seed index ( $p < 0.05$ ). Dominance  $\times$  environment interactions were significant for lint yield ( $p < 0.01$ ) and seed index ( $p < 0.05$ ). Additive effects accounted for between 2.2 (lint yield) and 48.3% (lint percentage) of the total variance. Of the total variance, dominance effects were responsible for 4.7% for lint yield and 15.6% for boll weight. Additive  $\times$  environment interactions accounted for 2.4% of the total variation for seed index. Of the total variation, dominance  $\times$  environment interactions accounted for 23.7% for lint percentage and 6.4% for seed index. Environmental effects accounted for between 12.5 (lint percentage) and 77.0% (lint yield) of the total variance. Residuals were responsible for between 7.8 (lint percentage) to 17.1% (bolls m<sup>-2</sup>) of the total variance.

Table 4 provides the components of variance for fiber quality traits. Variance components for environment, additive effects, and residuals were significant ( $p < 0.01$  for all except  $p < 0.05$  for short fiber content). Dominance effects were not significant for any of the fiber quality traits. Additive  $\times$  environment interactions were significant only for micronaire ( $p < 0.05$ ). Dominance  $\times$  environment interactions were significant for micronaire ( $p < 0.01$ ) and fiber strength ( $p < 0.05$ ). Additive effects accounted for between 1.7 (short fiber content) and 30.6% (fiber strength) of the total variance. Additive  $\times$  environment interactions accounted for 9.2% of the total variation for micronaire. Of the total variation, dominance  $\times$  environment interactions accounted for 24.9% for micronaire and 7.2% for fiber strength. Environment accounted for between 39.6 (micronaire) and 84.7% (short fiber content) of the total

variance. Residuals were responsible for between 8.5 (fiber length) to 16.5% (micronaire) of the total variance.

Collectively, variance component analysis for agronomic and fiber quality traits indicates that additive effects represent the majority of genetic variation in this population. The lack of significant additive  $\times$  environment interactions was consistent with other recent cotton combining ability studies (Campbell et al., 2014; Jenkins et al., 2009; Zeng and Wu, 2012). The proportion of the total variance attributed to each variance component differed from previously conducted studies (Campbell et al., 2014; Jenkins et al., 2009; Zeng and Wu, 2012). This difference likely was due to differences in the genetic populations and field environments used for these studies.

## Predicted Genetic Effects

To assess the breeding potential of the parental lines used in this study, we predicted additive and dominance effects for each trait. As noted by Jenkins et al. (2009), genetic effects 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, which is deviated from its population mean, we tested if the effect was significantly different than zero. In addition, these predicted genetic effects were compared among the four high-quality lines and TM-1.

## Agronomic Traits

Predicted additive effects and their standard errors on a per-trait basis are provided in Fig. 1. For lint percentage, all five genotypes displayed significant additive effects ( $p < 0.01$ ). MD 15 displayed the highest additive effect. For lint yield, DP 90, MD 15, and TM-1 displayed significant additive effects ( $p < 0.01$ ). DP 90 and MD 15 displayed the highest additive effects. TM-1 displayed the lowest additive effect for lint percentage and lint yield. Additive effects for each genotype were significant ( $p < 0.01$ ) for seed index, boll weight, and bolls per square meter with the exception of MD 15 for seed index and bolls per square meter. DP 90 displayed the greatest additive effect for seed index and lowered seed index. DES 119 displayed the greatest additive effect for boll weight and reduced boll weight. DP 90 and DES 119 displayed additive effects that increased the number of bolls per square meter.

## Fiber Quality Traits

Additive effects and their standard errors were also predicted on a per-trait basis for fiber quality and are provided in Fig. 2. All genotypes, with the exception of DES 119, displayed significant additive effects for micronaire ( $p < 0.01$ ). For fiber length, uniformity, and fiber strength, all genotypes displayed significant additive effects ( $p < 0.01$  for all except  $p < 0.05$  DES 119 for fiber

**Table 3. Variance components and standard errors expressed as proportions of the phenotypic variances for agronomic traits.**

	Lint percentage	Lint yield	Seed index	Boll weight	Bolls m <sup>-2</sup>
$V_E/V_P$ †	0.125 ± 0.008**	0.770 ± 0.019**	0.554 ± 0.012**	0.559 ± 0.020**	0.691 ± 0.027**
$V_B/V_P$	0.012 ± 0.003*	0.001 ± 0.001	0.007 ± 0.003	0.001 ± 0.001	0.002 ± 0.002
$V_A/V_P$	0.483 ± 0.015**	0.022 ± 0.005**	0.246 ± 0.011**	0.076 ± 0.008**	0.058 ± 0.007**
$V_D/V_P$	0.034 ± 0.016	0.047 ± 0.014**	0.000 ± 0.000	0.156 ± 0.021**	0.000 ± 0.000
$V_{AE}/V_P$	0.029 ± 0.012	0.003 ± 0.004	0.024 ± 0.007*	0.009 ± 0.009	0.004 ± 0.006
$V_{DE}/V_P$	0.237 ± 0.021**	0.066 ± 0.024	0.064 ± 0.018*	0.079 ± 0.029	0.074 ± 0.042
$V_e/V_P$	0.078 ± 0.004**	0.090 ± 0.007**	0.105 ± 0.005**	0.120 ± 0.010**	0.171 ± 0.016**

\* Significantly different at the 0.05 level of probability.

\*\* Significantly different at the 0.01 level of probability.

†  $V_E$ , environment variance;  $V_B$ , block (environment) variance;  $V_A$ , additive variance;  $V_D$ , dominance variance;  $V_{AE}$ , additive × environment variance;  $V_{DE}$ , dominance × environment variance;  $V_e$ , error variance;  $V_P$ , phenotypic variance.

**Table 4. Variance components and standard errors expressed as proportions of the phenotypic variances for fiber quality traits.**

	Micronaire	Fiber length	Uniformity	Fiber strength	Short fiber content
$V_E/V_P$ †	0.396 ± 0.019**	0.774 ± 0.011**	0.779 ± 0.012**	0.515 ± 0.012**	0.847 ± 0.013**
$V_B/V_P$	0.031 ± 0.005**	0.013 ± 0.049**	0.009 ± 0.004	0.012 ± 0.003*	0.006 ± 0.002
$V_A/V_P$	0.066 ± 0.009**	0.047 ± 0.005**	0.052 ± 0.007**	0.306 ± 0.013**	0.017 ± 0.004*
$V_D/V_P$	0.000 ± 0.000	0.002 ± 0.004	0.000 ± 0.000	0.007 ± 0.008	0.001 ± 0.003
$V_{AE}/V_P$	0.092 ± 0.024*	0.010 ± 0.005	0.018 ± 0.008	0.000 ± 0.000	0.014 ± 0.007
$V_{DE}/V_P$	0.249 ± 0.035**	0.052 ± 0.016	0.012 ± 0.017	0.072 ± 0.020*	0.023 ± 0.019
$V_e/V_P$	0.165 ± 0.011**	0.085 ± 0.005**	0.130 ± 0.009**	0.087 ± 0.007**	0.092 ± 0.009**

\* Significantly different at the 0.05 level of probability.

\*\* Significantly different at the 0.01 level of probability.

†  $V_E$ , environment variance;  $V_B$ , block (environment) variance;  $V_A$ , additive variance;  $V_D$ , dominance variance;  $V_{AE}$ , additive × environment variance;  $V_{DE}$ , dominance × environment variance;  $V_e$ , error variance;  $V_P$ , phenotypic variance.

length). For short fiber content, MD 15 ( $p < 0.01$ ), PD 2164 ( $p < 0.05$ ), and TM-1 ( $p < 0.01$ ) displayed significant additive effects. Across all fiber quality traits measured, MD 15 provided the greatest additive effect and resulted in reduced micronaire, increased fiber length, increased uniformity, increased fiber strength, and reduced short fiber content. Although significantly different than zero, additive effects for the other three high-quality genotypes (DES 119, DP 90, and PD 2164) were negligible. TM-1 displayed negative additive effects by increasing micronaire and short fiber content while decreasing fiber length, uniformity, and fiber strength. Collectively, these fiber quality data suggest that MD 15 alone is primarily responsible for the significant additive genetic variation detected in this study.

## DISCUSSION

In this study, our objective was to estimate genetic variance components and predict genetic effects for agronomic and fiber quality traits using a half-diallel population derived from four known genotypic sources of high fiber quality. Most of the genetic variation measured for agronomic and fiber quality traits was explained by additive effects. In terms of agronomic traits, our study showed that additive genetic variation was present and presumably should be accessible to further agronomic performance improvement. In terms of fiber quality traits, this study showed that

additive genetic variation exists in crosses derived from different genotypic sources of high fiber quality. Consistent with previous reports summarized by Campbell and Myers (2015), this would suggest that within these four high quality genotypes multiple genetic sources of high fiber quality are present that primarily behave additively.

The predicted genetic effects of fiber quality for these genotypes indicate that most of the additive variation present is explained by MD 15. Hence, it would appear that MD 15 contains unique high fiber quality alleles complementary to those present in the other three high quality genotypes. For each of the fiber quality traits measured in this study, the predicted additive effect of MD 15 was significant and favorable. Compared with the mean of all  $F_2$  hybrids evaluated in this study, the predicted additive effect of MD 15 corresponds to 3% lower micronaire, 2% longer fibers, 1% higher uniformity, 9% higher fiber strength, and 3% lower short fiber content.

The genetic architecture and origin of the favorable fiber quality alleles present in MD 15 is not clearly known. Studies designed to dissect the genetic basis of physical cotton fiber properties generally indicate quantitative inheritance, and quantitative trait locus (QTL) mapping studies using genetic populations derived from an assortment of *Gossypium* spp. germplasm have identified an array of chromosomal regions associated with cotton fiber properties. These studies indicate a large number of QTL

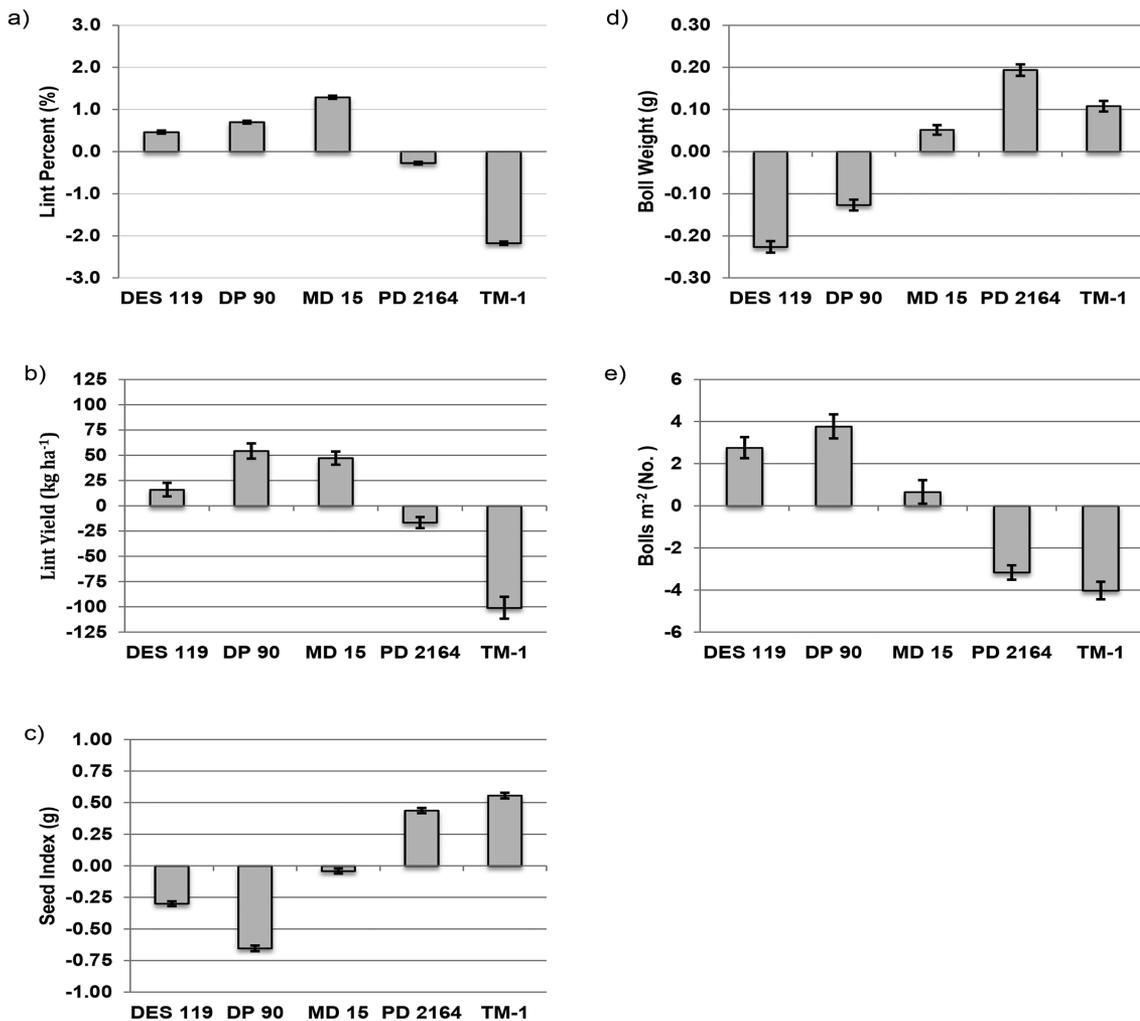


Fig. 1. Additive effects for agronomic traits expressed as deviations from the grand mean.

or genes associated with cotton fiber properties. Chee and Campbell (2009) summarized fiber property QTL mapping studies and reported the total number of QTL as (i) 107 QTL for fiber length, (ii) 13 QTL for short fiber content, (iii) nine QTL for fiber uniformity, (iv) 84 QTL for fiber strength, and (v) 112 QTL for micronaire.

Based solely on inspection of the pedigree of MD 15, there are three different plausible sources of improved fiber quality (Fig. 3). These would include DP 90, FTA 263-20, and Fibermax 832. The source of DP 90 fiber quality likely traces back to the John Cotton Polycross, which was developed through a complex intercrossing among a number of Acala germplasm lines and upland cotton lines (Zeng et al., 2010). Kuraparthy and Bowman (2013) noted that DP 90 was a key contributor of improved fiber quality in recent cultivars. FTA-263-20 was developed in the Pee Dee program and involved a wide range of genetic diversity involving Acala cottons, extra long staple upland cottons, *G. barbadense*, and triple hybrid cottons developed from *G. arboreum*, *G. thurberi*, and *G. hirsutum*. The source of favorable fiber quality alleles in Fibermax 832 is not known, but

it is likely attributed to DP 90 and Acala germplasm (Greg Constable, personal communication, 2015).

Considering the other three high-quality genotypes used in this study (DP 90, DES 119, and PD 2164), it is interesting that they share plausible sources of high fiber quality with MD 15. MD 15 directly contains DP 90 in its pedigree and shares common Pee Dee program origins with PD 2164. Similarly, based on examination of its pedigree, the most plausible source of DES 119 fiber quality would trace to a Pee Dee breeding line PD 62-164. Consequently, when considering the collective ancestral sources of high fiber quality among these four high-quality lines, there does not appear to be a single unique source of favorable fiber quality alleles present only in MD 15's breeding history.

Meredith (2005) indicated that the  $F_{2:3}$  progeny row selection (No. 120), which ultimately led to MD 15, displayed significantly longer and stronger fiber than either of its original parents (MD 51neOKRA and Fibermax 832). Also, four  $F_6$  strains derived from the original No. 120  $F_{2:3}$  progeny row selection consistently produced significantly higher fiber strength and lower short fiber

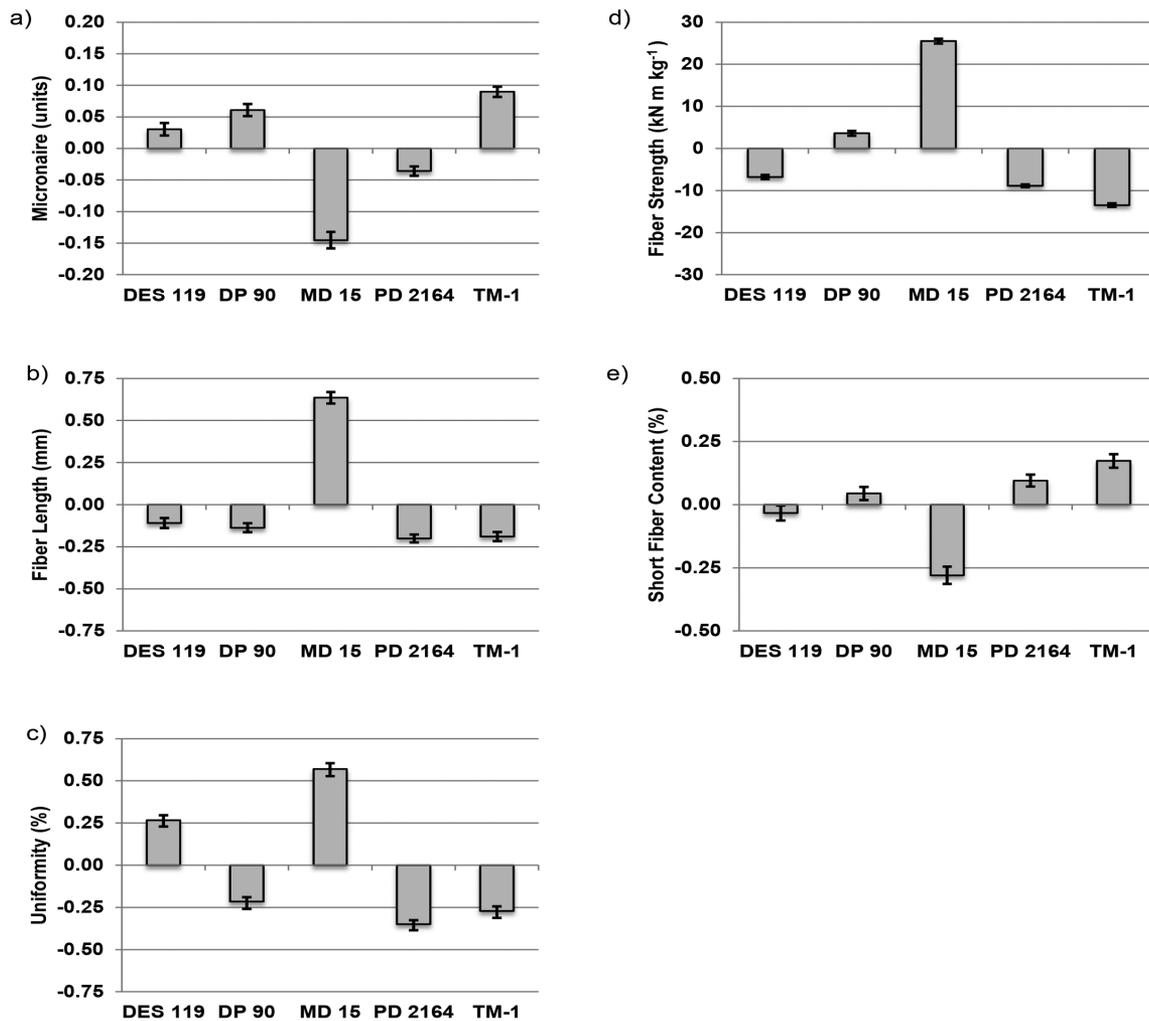


Fig. 2. Additive effects for fiber quality traits expressed as deviations from the grand mean.

content than either MD 51neOKRA or Fibermax 832. Hence, these data would support the hypothesis that the beneficial fiber quality alleles present in MD 15 resulted from transgressive segregation.

Studies have been conducted to determine the genetic architecture of the high fiber quality (especially fiber strength) present within MD 15's lineage. Using the Castle–Wright approach developed by Wright (1968) as modified by Cockerham (1986), Meredith (2005) evaluated three sets of backcross populations segregating for high fiber strength and estimated the minimum number of genes for fiber strength to be 1.23. Islam et al. (2014) mapped QTL associated with fiber quality in two  $F_2$  populations derived from MD 90ne and MD 52ne (a sister line of MD 51ne). They identified a small-effect QTL located on chromosome 3 associated with fiber strength. Two other QTL were identified that were associated with fiber length on chromosome 24 and short fiber index on chromosome 14. Using a microarray approach to identify gene expression differences at several time points during fiber elongation and secondary wall biosynthesis between MD 90ne and MD 52ne, Hinchliffe et al. (2010; 2011)

found that high fiber strength was associated with an earlier transition into secondary cell wall biosynthesis.

Overall, the results of this study provide promising information that can be used by breeders and geneticists alike to further improve fiber quality. This study suggests that MD 15 contains and transmits unique, additive alleles associated with improved fiber quality, especially fiber strength. Although the number of genotypes evaluated in this study is limited and not wholly representative of the available breeding resources, it does suggest that breeders can readily increase fiber quality with novel alleles present in MD 15. One strategy to further increase fiber quality would be to use an inbreeding and selection approach to pyramid the favorable alleles present in MD 15 with other genetic sources of high fiber quality. Future research should continue studying the genetic architecture of the high-quality trait present in MD 15. Recent advances in our increased knowledge of the sequence, structure, and organization of the cotton genomes (Paterson et al., 2012; Wang et al., 2012; Li et al., 2014, 2015; Liu et al., 2015; Zhang et al., 2015;) will facilitate such efforts.

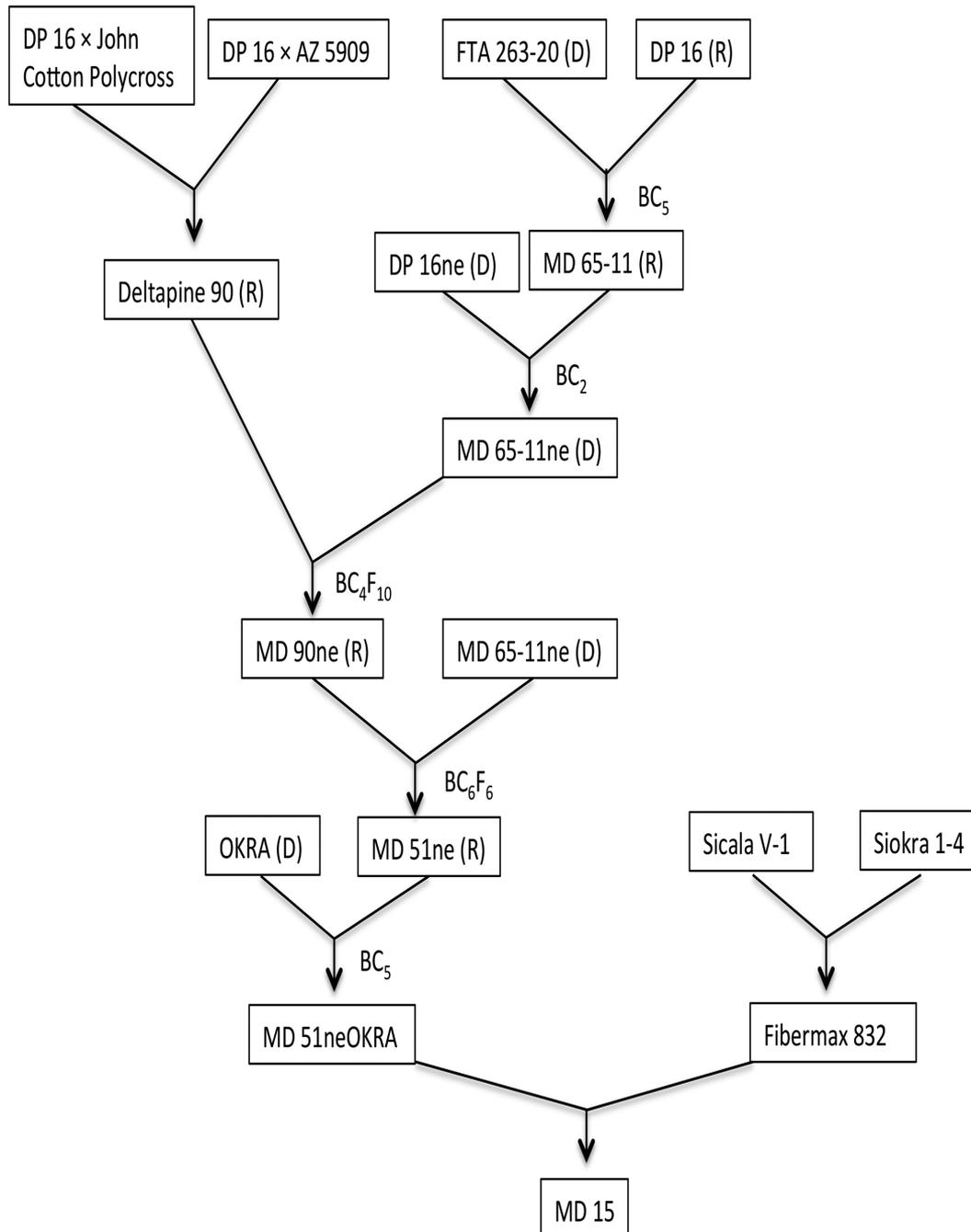


Fig. 3. Breeding history of MD 15.

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