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Genetic Effects of Chromosomes 1, 4, and 18 from Three Tetraploid *Gossypium* Species in Topcrosses with Five Elite Cultivars

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ABSTRACT

Chromosome substitution lines (CSLs) have been developed for selected chromosomes from two tetraploid species of *Gossypium* and are effective ways to target introgression of alleles from exotic tetraploid species into Upland cotton (*G. hirsutum* L.) Genetic effects of chromosomes 1, 4, and 18 from Upland cotton (TM-1), Pima cotton (*G. barbadense* L.), and Hawaiian cotton (*G. tomentosum* Nutt. ex Seem) were estimated by topcrossing TM-1 and six isochromosomal CSLs with five upland cultivars and comparing F_2 and F_3 hybrids for agronomic and fiber traits. Data were analyzed according to an additive–dominance (AD) model. Additive genetic effects were greater than dominance effects for lint percentage, fiber uniformity, fiber strength, and elongation; whereas, dominance effects were greater than additive effects for boll weight, lint yield, fiber length, and fiber micronaire. All additive × environment effects were small. Dominance × environment effects were only significant for boll weight, lint yield, and fiber micronaire. Chromosome B04 and B18 from Pima cotton and T01 from Hawaiian cotton had significantly greater additive effects for lint percentage than homologs. Chromosomes 1, 4, and 18 from the three species generally showed negative additive effect on lint yield compared with cultivars. Chromosome 1 from Hawaiian cotton had greater additive effects on fiber length than homologs. Chromosomes 1 and 4 from Pima cotton showed greater additive effects on fiber strength than homologs. The magnitude of additive effects on important agronomic and fiber traits show that Pima cotton and Hawaiian cotton harbor useful alleles for Upland cotton breeding programs.

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Abbreviations: AD, additive–dominance; CS-B, chromosome substitution line from *G. barbadense*; CSL, chromosome substitution line; CS-T, chromosome substitution line from *G. tomentosum*; QTL, quantitative trait loci; UHM, upper-half mean; UI, uniformity index.

CHROMOSOME SUBSTITUTION LINES provide a unique way to effectively introgress alleles from alien *Gossypium* tetraploid species into Upland cotton by avoiding some of the problems experienced with conventional methods of interspecific crosses, for example, hybrid breakdown (Zhang, 2014). Endrizzi (1963) initially outlined methods for development of interspecific chromosome substitution lines in Upland cotton and several of the initially discovered monosomics were used to substitute Pima cotton chromosomes into Upland cotton (Endrizzi 1963, Kohel et al., 1977; Ma and Kohel, 1983). Through the use of chromosome substitution lines, chromosome 6 was associated with higher lint percentage, finer fiber, and later flowering, while chromosome 17 was associated with short fiber length (Kohel et al., 1977; Ma and Kohel 1983).

Currently, there have been 17 CSLs developed by hypoaneuploid-based chromosome substitution, each of which contains a whole chromosome or a segment of a chromosome arm from Pima cotton line 3-79 substituted into Upland cotton line TM-1.

These were designated as chromosome substitution bar-badense (CS–B), (Stelly et al., 2005). Line 3-79 is a Pima cotton doubled haploid genetic standard (Endrizzi et al., 1985), and TM-1 is a Upland cotton genetic standard derived from 'Deltapine 14' that has been self-pollinated for over 40 generations, (Kohel et al., 2001). In developing these CSLs, individual TM-1 chromosome pairs were replaced with their respective 3-79 chromosome pair with the remaining 25 chromosome pairs remaining primarily TM-1 chromosomes (Stelly et al., 2005). Additional CS–B lines have been developed and CSLs for some chromosomes from Hawaiian cotton (CS–T) and *G. mustelinum* Miers ex G. Watt (CS–M) have been developed following similar procedures (Saha et al., 2011a).

In addition to cotton, CSLs have been used extensively to identify genetic effects of individual chromosomes associated with quantitative traits in wheat (*Triticum aestivum* L.; $2n = 6 = 42$) (Berke et al., 1992a,b) followed by fine mapping of associated QTL within an individual chromosome (Campbell et al., 2003, 2004). Berke et al. (1992a,b) evaluated a full set of reciprocal chromosome substitution lines between two winter wheat cultivars, 'Wichita' and 'Cheyenne', for grain yield and demonstrated chromosome 3A from Wichita increased grain yield ~15% when placed in Cheyenne background. At the same time, their analysis demonstrated a reciprocal effect of chromosome 3A from Cheyenne (~15% decrease) when placed in Wichita background. Following, recombinant inbred chromosome lines (or chromosome-specific recombinant inbred lines) were developed for both chromosomes and allowed for a much finer dissection of genomic regions associated with the chromosome 3A effects for grain yield from Wichita 3A in Cheyenne background (Campbell et al., 2003, 2004) and Cheyenne 3A in Wichita background (Mengistu et al., 2012). Chromosome substitution lines have also been used for intraspecific germplasm introgression in bread wheat and have also been effectively used for breeding as well as genetic analysis (Al-Qaudhy et al., 1988; Berke et al., 1992a,b; Campbell et al., 2003, 2004; Kaeppler, 1997; Law, 1966; Mansur et al., 1990; Shah et al., 1999, Yen and Baenziger, 1992; Yen et al., 1997, Zemetra and Morris 1968, Zemetra et al., 1986).

In our previous studies, three major approaches have been taken to genetically dissect the substituted chromosomal effects in the evaluation of the Pima cotton CS–B lines: (i) the CS–B have been crossed with the recurrent parent TM-1, (ii) the CS–B lines have been crossed with five elite Upland commercial cultivars from diverse breeding programs, and (iii) the CS–B lines have been intercrossed. From these approaches, genetic effects of individual CS–B lines have been estimated based on data of parents, F_2, and F_3 generations grown in field plots over multiple environments.

Based on our previous studies, we can conclude that CS–B02, CS–B06, CS–B16, CS–B18, CS–B5sh, and CS–B22sh showed additive effects for increased lint percentage greater than TM-1. CS–B16 additive effects increased fiber upper-half mean (UHM) fiber length. CS–B16 and CS–B11sh additive effects increased fiber strength. CS–B01 and CS–B16 additive effects reduced fiber micronaire, and CS–B18 reduced yield (Saha et al., 2004, 2006, 2008). Studies also suggested that significant epistatic effects are occurring between some CS–B chromosomes for selected fiber traits and for lint yield (Saha et al., 2010, 2011b, 2013).

A plant breeding approach was used to determine the genetic value of several CS–B lines using crosses of selected CS–B lines with five elite cultivars from diverse breeding programs (Jenkins et al., 2006). This research uncovered alleles in the CS–B lines that showed positive interaction with alleles in the elite germplasm. CS–B22Lo and CS–B22sh showed additive effects significantly greater than corresponding chromosomes of TM-1 for lint yield. CS–B02 and CS–B25 had the greatest additive effect (2.36 and 8.97 kN m kg^{-1}) among 13 CS–B lines for fiber strength. CS–B07 and CS–B18 exerted negative additive effects for fiber strength (Jenkins et al., 2006, 2007). Nine CS–B lines, including several with chromosome arms from two different chromosomes, were crossed with the same five cultivars, and additional CS–B chromosomes were discovered for fiber traits and lint percentage improvement as follows: CS–B10 and CS–B16-15 for lint percentage; CS–B01, CS–B11sh, and CS–B26Lo for fiber length; CS–B01, CS–B11sh, CS–B10, and CS–B17-11 for fiber length uniformity; CS–B01, CS–B11sh, CS–B12sh, CS–B26Lo, and CS–B17-11 for fiber strength; CS–B01, CS–B11sh, CS–B26Lo, CS–B10, and CS–B17-11 for fiber elongation; CS–B01, CS–B12sh, CS–B4-15, CS–B16-15, and CS–B17-11 for reduced micronaire; CS–B10, CS–B4–15, CS–B16-15, and CS–B17-11 for fibers with greater reflectance; and CS–B4-15 and CS–B17-11 for less yellow fibers (Jenkins et al., 2012). In a different study involving a set of diallele crosses among 11 diverse cultivars, fiber traits were mainly controlled by additive genetic effects with about equal additive and dominance effects for lint percentage and boll weight and primarily dominance effects for lint yield (Jenkins et al., 2009). These results suggested that biparental mating followed by random mating beginning with F_1 generations should be a good approach to combining several favorable alleles from these CS–B lines into one population (Jenkins et al., 2013).

Summarizing the favorable additive genetic effects shows several CS–B lines harboring useful additive alleles for specific traits, that is, lint yield (22sh and 22Lo), boll weight (04, 06, and 15sh), lint percentage (10, 16, 18, 22sh, and 22Lo), UHM fiber length (01, 04, 25, 11sh, 14sh, 15sh, and 26Lo), fiber strength (01, 02, 25, 11sh, 12sh, 15sh, and 26Lo), reduced fiber micronaire (01, 25,

and 12sh), fiber length uniformity (01, 10, and 11sh), and fiber elongation (01, 04, 10, 11sh, and 26Lo), (Jenkins et al., 2006, 2007, 2012, 2013).

The objective of the research reported here was to compare the genetic effects of chromosome substitution lines for chromosomes 1, 4, and 18, from Upland cotton, Pima cotton and Hawaiian cotton when topcrossed with five elite Upland cotton cultivars. An additive–dominance model was applied to analyze a data set including parents and their F_2 and F_3 hybrids, which were grown in multiple test environments. In this study, our focus was to estimate genetic variance components and predict genetic effects with a linear mixed model approach. These results should reveal more detailed and useful information that can be used for Upland cotton improvement through introgressing desirable chromosomes from other species by further use of these chromosome substitution lines.

MATERIALS AND METHODS
Materials and Field Experiments
Five elite cultivars of Upland cotton to be used as female parents were selected from the germplasm of major cotton seed breeding companies in the United States: 'Deltapine 90' (DP 90 PVP 8100143) developed by Delta and Pine Land Co., 'Sure-Grow 747' (SG 747 PVP 9800118) developed by Sure-Grow Co., 'Phytogen 355' (PSC 355 PI 612974) developed by Mississippi Agriculture and Forestry Experiment Station and licensed to Phytogen Seeds, 'Stoneville 474' (ST 474 PVP 9400152) developed by Stoneville Pedigreed Seeds, and 'Fibermax 966' (FM 966 PVP 200100209) developed in Australia where it was called 'Sicala 40' and marketed in the United States by Bayer Crop Science FiberMax division. These five parents were crossed with three CS-B lines (CS-B01, CS-B04, and CS-B18), three CS-T lines (CS-T01, CS-T04, and CS-T18), and TM-1, the recurrent parent of the chromosome substitution lines. The TM-1 crosses provide the comparisons for Upland cotton chromosomes 1, 4, and 18.

Entries (12 parents and 35 crosses) were grown in single-row plots 12 m long with rows spaced 97 cm and plants spaced 10 cm apart within rows (total 110 plants per row) and evaluated for yield and fiber quality. Planting pattern was two rows planted with one row skipped at Mississippi State, MS, and solid planted at Florence, SC. Experiments were conducted in three environments in 2010 and two environments in 2011. In 2010, F_2 seed and parents were planted, while in 2011, F_3 seed and parents were planted. Environments 1, 2, and 4 were on the plant science research farm at Mississippi State, MS (33.4° N, 88.8° W). Genotypes were planted in a Leeper silty clay loam (fine, smectic, nonacid thermic Vertic Epiaquepts) soil type for Environments 1 and 4 and in Marietta loam (fine-loamy, siliceous, active Fluvaquentic Eutrudepts) soil for Environment 2. Environments 3 and 5 were on the Clemson Pee Dee Research and Education Center near Florence, SC (34.1° N, 79.4° W) in a Norfolk loamy sand (fine-loamy, kaolinitic, thermic Typic Kandiudults) soil. Planting dates were 12 May 2010, 13 May 2010, and 16 May 2011 at Mississippi State, MS, and 18 May 2010 and 16 May 2011 at Florence, SC. A randomized complete block design with four replications was used in each environment.

Entries were grown using standard agronomic practices and insects were managed using University-recommended practices. Prior to machine harvest, a 25-boll random sample was hand collected in each plot to determine lint percentage, boll weight, and fiber quality. Plots were harvested with a commercial cotton picker modified for plot harvesting and weighing. Fiber samples were sent to STARLAB in Knoxville, TN, for high-volume instrument fiber measurements.

Data Analyses
The data were first analyzed by analysis of variance using SAS v. 9.4 (SAS Institute, 2013) PROC GLM to conduct multiple comparisons among parents and F_2 and F_3 genotypes. The data were also analyzed using an AD genetic model, where variance components and genetic effects were calculated per Jenkins et al. (2006, 2007), McCarty et al. (2004a,b, 2007), and Wu et al. (2010, 2014).

Although an AD model with additive × additive effects was analyzed with parents, F_2, and F_3 populations, we observed that additive × additive effects were small and insignificant for most of these traits and that the results appeared unstable because F_2 and F_3 populations were not repeated in all environments. Thus, we decided that an AD model without additive × additive effects would be employed in this study, and results are reported based on this genetic model. The AD model equations for parents, F_2, and F_3 populations were detailed in a previous report (Wu et al., 2010).

A linear mixed model approach, a minimum norm quadratic unbiased estimation approach, was used to estimate variance components (Rao, 1971; Zhu, 1989). Genetic effects, including additive and dominance effects, were predicted by the adjusted unbiased prediction method (Zhu, 1993). A randomized 10-group-based jackknife method was used to determine standard errors for all parameters (Wu et al., 2012, 2013). With standard errors and degrees of freedom of nine, we conducted significance tests for each parameter of interest based on calculated probability value and multiple comparisons among parameters based on confidence intervals of 95%. If confidence intervals overlap, the two means are not different. All genetic data analyses were conducted using an R statistical package, qgtools (Wu et al., 2014).

All genetic effects, including additive and dominance effects, were predicted as deviations from the population mean for each trait. Since there were two groups of CS lines (CS-B and CS-T) and TM-1 as the recurrent parent, all additive and homozygous dominance effects for male parents are also presented in figures as deviations from the TM-1 effects.

RESULTS
Variance components are presented as proportions of the phenotypic variance. Additive variances were the most important for lint percentage, fiber uniformity index (UI), fiber strength, and fiber elongation, whereas dominance variances were the most important for boll weight, lint yield, UHM fiber length, and fiber micronaire (Table 1).

Predicted additive effects are shown as deviations from the population grand mean and differences were observed among the five cultivars (Table 2). Lint percentage and lint

Table 1. Variance components for agronomic and fiber traits expressed as proportions of phenotypic variance derived from topcrossing chromosome substitution lines for chromosomes 1, 4, and 18 from three species of cotton with five cultivars.

Variance†	Lint percentage	Boll weight	Lint yield	Fiber length	Fiber uniformity	Fiber strength	Fiber elongation	Fiber micronaire
V_A	0.704**	0.203**	0.153**	0.095**	0.152**	0.438**	0.189**	0.200**
V_D	0.161**	0.307**	0.281**	0.345**	0.042	0.097**	0.102**	0.277**
V_{AE}	0.032**	0.000‡	0.010	0.001	0.021	0.011	0.005	0.047**
V_{DE}	0.001	0.202**	0.161*	0.133	0.041	0.010	0.160	0.119*
V_e	0.102	0.288**	0.395**	0.426**	0.744**	0.443**	0.543**	0.357**
Total V_p	8.405	0.345	109,930	1.010	6.997	605.78	0.209	0.163

*Significant at the 0.05 probability level.

**Significant at the 0.01 probability level.

† Phenotypic variance (V_P) was partitioned into additive (V_A), dominance (V_D), additive by environment (V_{AE}), dominance by environment (V_{DE}), and residual (V_e).

‡ Because of rounding, small contributions of some traits appear as 0.00 in this table.

Table 2. Predicted additive genetic effects for agronomic and fiber traits for five cotton cultivars, expressed as deviations from population grand mean, when topcrossed with chromosome substitution lines from chromosomes 1, 4, and 18 from three species of cotton.

Genotype	Lint percentage	Boll weight	Lint yield	Fiber length	Fiber uniformity	Fiber strength	Fiber elongation	Fiber micronaire
	%	g	kg ha⁻¹	mm	%	kN m⁻¹	%	
DP 90	0.85*	0.01ns	61*	0.23*	−0.06	6.97*	−0.06*	−0.10*
SG 747	2.06*	−0.05*	82*	−0.10*	0.22*	−11.72*	0.08*	−0.05*
PSC 355	1.66*	−0.15*	120*	−0.11*	0.33*	4.37*	0.36*	0.15*
ST 474	2.46*	−0.16*	66*	−0.27*	−0.04	−6.13*	−0.05*	−0.01
FM 966	2.05*	0.41*	109*	0.23*	0.25*	31.26*	−0.20*	0.13*
Population mean	38.19	5.22	1056	28.51	83.40	324	7.01	5.00

*Significant from population grand mean at the 0.05 probability level.

Table 3. Predicted homozygous dominance genetic effects for agronomic and fiber traits for five cotton cultivars, expressed as deviations from population grand mean, when topcrossed with chromosome substitution lines from chromosomes 1, 4, and 18 from three species of cotton.

Genotype	Lint percentage	Boll weight	Lint yield	Fiber length	Fiber uniformity	Fiber strength	Fiber elongation	Fiber micronaire
	%	g	kg ha⁻¹	mm	%	kN m⁻¹	%	
DP 90	−0.89*	−0.56*	−100	−1.45*	−0.27	−10.44*	0.12	0.20*
SG 747	1.73*	0.07	−8	−0.45*	0.05	−1.97	0.11*	0.23*
PSC 355	−0.38	−0.36*	−335*	−1.00*	−0.06	5.45*	0.12*	−0.09
ST 474	1.14*	−0.27*	−29	−0.54*	−0.14	−5.82	0.07	0.16*
FM 966	−1.03*	−0.82*	−259*	−0.77*	0.11	−8.52	0.03	−0.52*
Population mean	38.19	5.22	1056	28.51	73.40	324	7.01	5.00

*Significant from population grand mean at the 0.05 probability level.

yield were positive and significant for each of the cultivars. Additive effects for FM 966 were also positive for boll weight, UHM fiber length, UI, strength, and micronaire. DP 90 had positive additive effects for fiber length and strength. SG 747 had negative additive effects for fiber length, strength, and micronaire. PSC 355 had the largest lint yield additive effect with a small positive additive effect on fiber UI, strength, and elongation with negative effects on fiber length.

Predicted homozygous dominance effects are also of interest in cultivar development as these effects can also be fixed through breeding. Negative effects will lower the trait value, whereas positive effects will increase the trait value (Table 3) following self-pollination. There were significant negative homozygous dominance effects among

the cultivars for boll weight, lint yield, UHM fiber length, and fiber micronaire. PSC 355 and FM 966 had the largest homozygous negative dominance effects on lint yield with −335 and −259, respectively. DP 90 and PSC 355 showed negative homozygous dominance effects for UHM fiber length of −1.45 and −1.00 mm. Only FM 966 showed negative homozygous dominance effects for micronaire. Negative effects for micronaire are usually desired.

The population grand mean and predicted additive effects for the chromosome substitution lines as deviations from population mean are in Table 4. Figures 1 through 6 show the additive and homozygous dominance effects, with the upper and lower confidence interval bars at the 0.05 confidence level, graphed with TM-1 set as the zero line for

Table 4. Predicted additive genetic effects for agronomic and fiber traits for chromosomes 1, 4, and 18 chromosome substitution lines from three species of cotton, expressed as deviations from population grand mean, when topcrossed with five cultivars.

Parent	Lint percentage	Boll weight	Lint yield	Fiber length	Fiber uniformity	Fiber strength	Fiber elongation	Fiber micronaire
	%	g	kg ha^{-1}	mm	%	kN m kg^{-1}	%	
CS-T01	−0.81*	−0.16*	−34*	−0.44*	−0.29*	−4.02*	0.11*	−0.02
CS-B01	−1.70*	−0.05*	−48*	0.14*	0.13*	−5.43*	0.03	−0.29*
CS-T04	−2.20*	0.08*	−10	0.26*	0.35*	−1.10	−0.03	0.03
CS-B04	−0.59*	0.06*	−53*	0.14*	−0.21*	−13.68*	−0.10*	−0.03
CS-T18	−1.84*	−0.27*	−156*	0.08*	−0.14*	−0.86	−0.06*	0.03
CS-B18	−0.47*	0.07*	−141*	−0.13*	−0.55*	0.68	−0.01	−0.20
TM-1	−1.46*	0.22*	4	−0.02	0.02	−0.34	−0.08*	−0.02
Population mean	38.19	5.22	1056	28.51	83.40	324	7.01	5.00

*Significantly different from population mean at the 0.05 probability level.

each chromosome substitution line. The error bars on the zero line represent the confidence intervals for TM-1.

Chromosome 1

Additive effects for CS-B01 were significantly different from TM-1 for boll weight, fiber strength, elongation, and micronaire. CS-T01 had additive effects significantly different from TM-1 in lint percentage, boll weight, UHM fiber length, UI, and elongation. CS-B01 and CS-T01 had additive effects significantly different from one another for lint percentage, boll weight, fiber length, UI, and micronaire. However, CS-B01 had no positive additive effects greater than TM-1, except for elongation, and CS-T01 had positive additive effects greater than TM-1 for only two traits, lint percentage, and elongation (Table 4; Fig. 1).

Homozygous dominance effects for CS-B01 were negative and significantly different from TM-1 for lint percentage, boll weight, and micronaire. CS-T01 homozygous dominance effects were positive and significantly different from TM-1 only for lint percentage and micronaire and significantly negative and different from TM-1 for boll weight. Comparing CS-B01 and CS-T01, homozygous dominance effects were only different for lint percentage, with values of 0.68 and −2.47, respectively, and
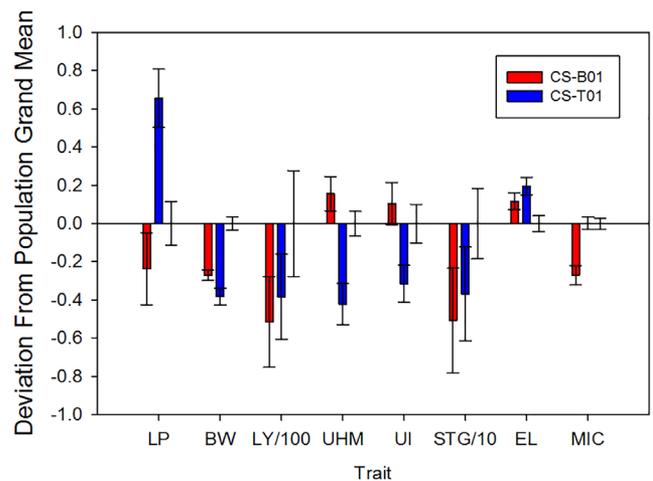

Fig. 1. Predicted additive genetic effects for chromosome 1 expressed as deviations from population mean and plotted with TM-1 values as zero. Error bars show 95% confidence intervals. LP, lint percentages; BW, boll weight; LY/100, lint yield/100; UHM, upper-half mean fiber length; UI, uniformity index; STG/10, fiber strength; EL, elongation; MIC, micronaire.

micronaire with values of −0.41 and 0.24, respectively (Table 5; Fig. 2).

Table 5. Predicted homozygous dominance genetic effects for agronomic and fiber traits for chromosomes 1, 4, and 18 chromosome substitution lines from three species of cotton, expressed as deviations from population grand mean, when topcrossed with five cultivars.

Parent	Lint percentage	Boll weight	Lint yield	Fiber length	Fiber uniformity	Fiber strength	Fiber elongation	Fiber micronaire
	%	g	kg ha^{-1}	mm	%	kN m kg^{-1}	mm	
CS-T01	0.68*	−0.57*	−153*	−1.03*	−0.24	−2.19	0.05	0.24
CS-B01	−2.47*	−0.65*	−351*	−0.47*	0.07	−6.58*	0.01	−0.41
CS-T04	−1.83*	−0.13*	−214*	−0.59*	−0.14	−4.36	0.06	−0.10
CS-B04	−2.38*	0.00†	−213*	−0.22	0.05	−11.73*	−0.05	−0.10
CS-T18	−1.11*	−0.09	−134*	−0.86*	−0.50	−5.44	−0.13*	−0.03*
CS-B18	−2.24*	−0.43*	−13	−0.73*	0.05	−2.31	0.35*	0.26*
TM-1	−0.96*	−0.15*	−225*	−0.29	0.06	−9.45*	0.07	−0.03
Population mean	38.19	5.22	1056	28.51	73.40	324	7.01	5.00

*Significantly different from population mean at the 0.05 probability level.

† Because of rounding, small contributions of some traits appear as 0.00 in this table.
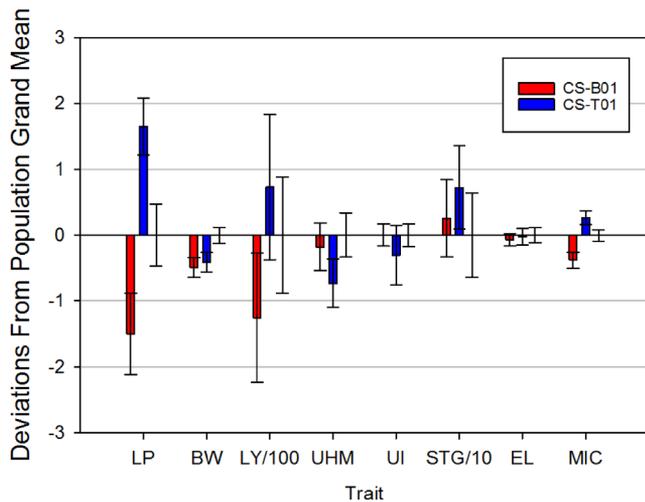
Fig. 2. Predicted homozygous dominance genetic effects for chromosome 1 expressed as deviations from population mean and plotted with TM-1 values as zero. Error bars show 95% confidence intervals. LP, lint percentages; BW, boll weight; LY/100, lint yield/100; UHM, upper-half mean fiber length; UI, uniformity index; STG/10, fiber strength; EL, elongation; MIC, micronaire.
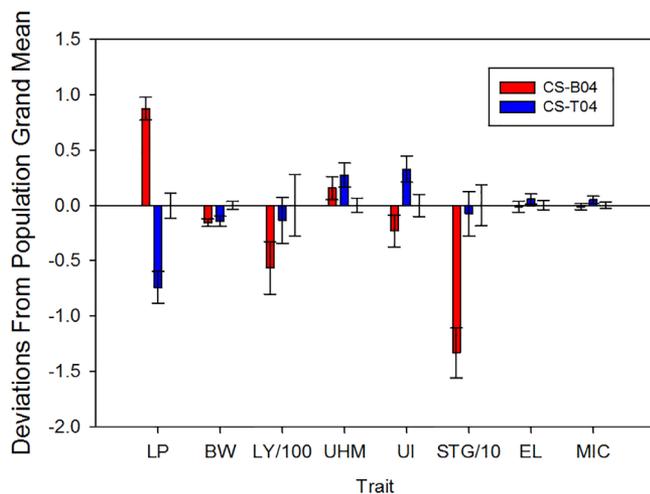

Fig. 3. Predicted additive genetic effects for chromosome 4 expressed as deviations from population mean and plotted with TM-1 values as zero. Error bars show 95% confidence intervals. LP, lint percentages; BW, boll weight; LY/100, lint yield/100; UHM, upper-half mean fiber length; UI, uniformity index; STG/10, fiber strength; EL, elongation; MIC, micronaire.

Chromosome 4

Additive effects for CS-B04 were significantly different than TM-1 for lint percentage, boll weight, lint yield, and fiber strength, but with a major positive difference for lint percentage and negative for fiber strength. CS-T04 had additive effects significantly different from TM-1 for lint percentage (negative) and fiber UI (positive) and slightly different for lint yield, boll weight, and fiber length. Additive effects for lint percentage were more positive for CS-B04 than
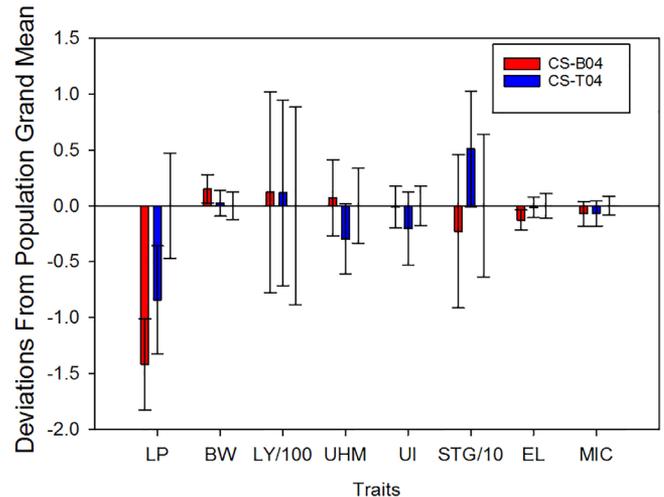

Fig. 4. Predicted homozygous dominance genetic effects for chromosome 4 expressed as deviations from population mean and plotted with TM-1 values as zero. Error bars show 95% confidence intervals. LP, lint percentages; BW, boll weight; LY/100, lint yield/100; UHM, upper-half mean fiber length; UI, uniformity index; STG/10, fiber strength; EL, elongation; MIC, micronaire.

for CS-T04; whereas CS-B04 was negative and CS-T04 was positive for UI compared with TM-1. CS-B04 had a major negative additive effect on fiber strength; whereas CS-T04 and TM-1 were not different from the population mean (Table 4; Fig. 3). Homozygous dominance effects were negative and large for lint percentage, lint yield, and fiber strength; however, the only major difference between CS-B04 and CS-T04 were for lint percentage with CS-B04 being more negative than CS-T04 (Table 5; Fig. 4).

Chromosome 18

Additive effects for CS-B18 and CS-T18 were significantly different from TM-1 for lint percentage, boll weight, and lint yield and for fiber uniformity in CS-B18. CS-B18 and CS-T18 were significantly different from each other for lint percentage, boll weight, and fiber uniformity (Table 4; Fig. 5). Homozygous dominance effects for CS-B18 were significantly different from TM-1 for lint percentage and lint yield only. CS-T18 was not significantly different from TM-1 for any trait. CS-B18 and CS-T18 were only different for lint percentage and elongation (Table 5; Fig. 6).

DISCUSSION

The six near isogenic TM-1 chromosome substitution lines used in these topcross experiments involve chromosome 1, 4, and 18 from two donor AD genome species, enabling contrasts with each other as well as their Upland cotton line TM-1 homologs, that is, among three species. Chromosome 18 is in the D subgenome, whereas chromosomes 1 and 4 are in the A subgenome in the tetraploid (AD) cotton species. All six chromosome substitution lines were developed in a TM-1 background. The results provide an opportunity
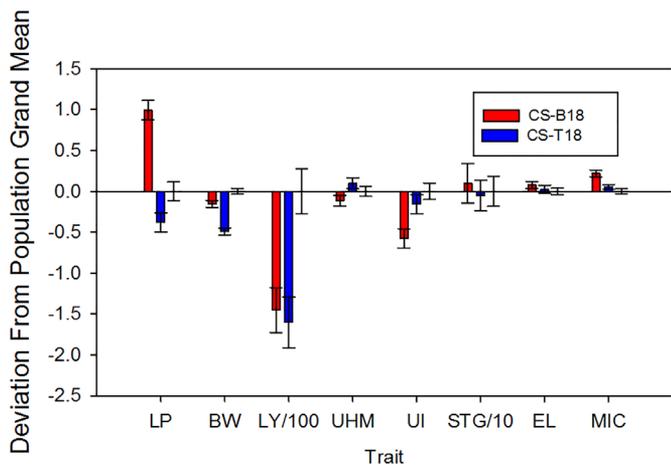
Fig. 5. Predicted additive genetic effects for chromosome 18 expressed as deviations from population mean and plotted with TM-1 values as zero. Error bars show 95% confidence intervals. LP, lint percentages; BW, boll weight; LY/100, lint yield/100; UHM, upper-half mean fiber length; UI, uniformity index; STG/10, fiber strength; EL, elongation; MIC, micronaire.
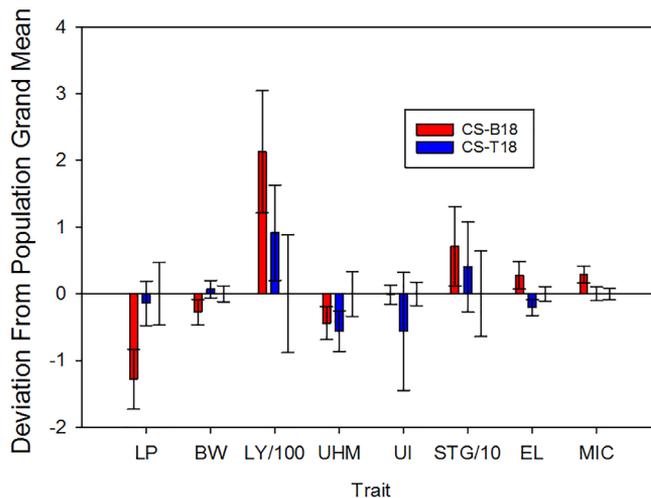

Fig. 6. Predicted homozygous dominance genetic effects for chromosome 18 expressed as deviations from population mean and plotted with TM-1 values as zero Error bars show 95% confidence interval. LP, lint percentages; BW, boll weight; LY/100, lint yield/100; UHM, upper-half mean fiber length; UI, uniformity index; STG/10, fiber strength; EL, elongation; MIC, micronaire.

to compare effects of the three individual chromosomes from three species. Relative to the overall experimental means, it should be noted that for TM-1, additive effects were negative for lint percentage, positive for boll weight, and more or less neutral for all other additive traits.

Additive effects on lint percentage by TM-1, T01, B04, and B18 were significantly lower than the cultivars, but the additive effects of these CSLs were higher than the corresponding TM-1 chromosomes (1, 4, and 18). This agrees with our previous studies (Jenkins et al., 2006, 2007). It is interesting that the corresponding three chromosomes from Pima cotton and Hawaiian cotton had opposite effects compared with TM-1 for lint percentage and for fiber length for chromosome 1. In addition, chromosome 1 from Pima cotton and Hawaiian cotton had opposite homozygous dominance effects for lint percentage and lint yield compared with TM-1. However, both the additive and dominance effects for the three chromosomes from all three species were negative for lint percentage and lint yield except that additive effects for lint yield for TM-1 was not different from the population mean.

Among the traits being investigated, narrow-sense heritability for lint percentage and fiber strength was relatively higher than for the other traits, suggesting QTL controlling these two traits could be more additive than dominant. It is also interesting to compare the CSLs in the TM-1 background where the results could reveal these chromosomes harboring QTL controlling these two traits in an additive manner. The results indicated that the chromosome 1 from Hawaiian cotton harbors a QTL with increased additive effect for lint percentage; whereas, chromosome 1 from TM-1 or Pima cotton harbors similar QTL with reduced additive effects. The results showed

that chromosomes 4 and 18 from Hawaiian cotton, TM-1, and Pima cotton may harbor different QTL controlling lint percentage. On the other hand, the results showed that chromosome 1 from Pima cotton showed a QTL with reduced additive effect for fiber strength compared with the corresponding chromosome from TM-1 but not different from Hawaiian cotton. Chromosome 4 from Pima cotton showed a QTL with reduced additive effect for strength compared with the corresponding chromosome from TM-1 and Hawaiian cotton. Chromosome 18 from Pima cotton, Hawaiian cotton, and TM-1 showed no difference in additive effect for fiber strength.

CS-B04 and CS-B18 increased lint percentage above Upland cotton; whereas, T01 increased lint percentage above Upland cotton. Bolls of TM-1 were significantly heavier than the cultivars and additive genetic effects for boll weight of chromosomes T01, B04, and B18 were significantly less than corresponding TM-1 chromosomes. Additive genetic effects of T18 and B18 reduced yield more than TM-1 chromosome 18. TM-1 and the three Hawaiian and Pima cotton chromosomes were similar to cultivars for UHM fiber length and genetic effects were evident; however, the positive additive effects were offset by negative homozygous dominance effects. No large major positive genetic effects were found for fiber UI. Fiber strength of CSL and TM-1 were close but lower than cultivars DP 90, PSC 355, and FM 966; no positive genetic effects were found for increased fiber strength among these CSLs; B04, however, exerted the largest significant negative genetic effect on fiber strength followed by B01 and T01. FM 966 had exceptionally high additive effect for strength (31.26 kN m kg^{-1}). Additive genetic

effects for B01 were significant and slightly positive for fiber elongation. Chromosome B01 exerted significant negative additive effects on micronaire, which is desirable; whereas B18 had a slightly positive effect on micronaire.

From a breeding perspective, CS-B01 and CS-T04 offer alleles for desirable additive effects for UHM fiber length and UI and CS-B04 for UHM fiber length. CS-B01 had a desirable additive effect on micronaire and homozygous dominance effects on elongation. However, B01 also had undesirable additive effects on lint percentage, boll weight, lint yield, and strength. The portfolio of opposing desirable and undesirable additive genetic effects is well exemplified by B01; the opposing effects would seem to underscore the importance of creating and analyzing advanced-generation, chromosome-specific recombinant inbred lines with advanced SNP technologies to isolate and identify nonpleiotropic additive genetic effects. This will render them highly amenable to marker-assisted selection (positive and negative) recombination and pyramiding. In addition, several heterozygous dominance effects could be expected in crosses of select CSL with specific cultivars. These cultivars were selected from major breeding programs across the United States and thus may act as surrogate for other elite breeding lines from individual US breeding program.

Acknowledgments

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