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BREEDING AND GENETICS

Effect of Chromosome Substitutions from *Gossypium barbadense* L. 3-79 into *G. hirsutum* L. TM-1 on Agronomic and Fiber Traits

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ABSTRACT

Pima cottons (*Gossypium barbadense L.*) possess fiber properties that are superior to the more widely grown Upland cottons (*G. hirsutum* L.). Incorporating the superior fiber properties from Pima into Upland cotton has generally not achieved stable introgression because of genome incompatibility. Using a set of stable lines (CS-B) containing chromosome or chromosome arm substitutions from *G. barbadense* (3-79) backcrossed into a *G. hirsutum* (TM-1) background, traits from the TM-1 parent that varied significantly could be attributed to genes in the substituted chromosome, to other residual 3-79 chromatin material, and/or their interaction with the other 25 chromosomes from TM-1. In 2002, seeds from 13 different CS-B lines, and the TM-1 and 3-79 parents, were planted in replicated tests at two locations in Mississippi and one location in Arizona for evaluation of agronomic and fiber properties. Compared with TM-1, the CS-B lines with substitutions for chromosomes 16, 18, 14sh and 22sh from 3-79 had reduced seed cotton yield and lint yield. The CS-B lines with alien chromosomes 2, 6, 16, 18, 5sh, 22Lo and 22sh from 3-79 had improved lint percentage. The CS-B line with substitution of chromosome 25 from 3-79 had reduced micronaire and increased fiber strength. All of the substituted chromosomes except 2, 4, and 6 had reduced boll weight. The CS-B lines 14sh, 15sh, and 25 had increased fiber length. The results provided information on the association of specific chromosomes with genes for agronomic and fiber traits. These new genomic resources will provide additional approaches for improvement of Upland cotton and will enable development of chromosome-specific recombinant inbred lines for higher resolution mapping.

Fiber quality traits, such as length, strength, micronaire, color, and trash content, affect the market price of cotton. The exceptional fiber length, strength, fineness, and manufacturing performance of Pima cotton (*G. barbadense*) provide a significant price advantage over the more widely grown Upland cotton (*G. hirsutum*), but Upland cotton produces higher lint yield. The need to improve fiber quality of Upland cotton requires innovative breeding approaches and a better understanding of the genetic basis for yield and fiber quality. Controlled interspecific introgression of genes from *G. barbadense* into *G. hirsutum* through chromosome substitution is one approach.

Historically, cotton breeders have faced many challenges in their attempts to introgress genes from *G. barbadense* into Upland cotton. Typically, breeders have worked at the whole genome level, leading to large amounts of unwanted DNA accompanying target genes during introgression. Since the improvement of one attribute may reduce another, correlations among traits of economic importance are also important considerations. For example, lint yield is positively correlated with micronaire, but negatively correlated with fiber length and fiber strength (Meredith, 1984). Such correlations pose difficulties in cotton breeding efforts, including efforts at interspecific introgression. Additional breeding challenges are posed by the multi-genic control, low heritability, and large environmental effects associated with some fiber quality traits (Meredith, 1984). Interspecific crosses and introgression efforts often lead to difficulties in infertility, cytological abnormalities, and distorted segregation. Rhyne (1958) reported that the actual number of recombinants obtained in an interspecific backcross program of Upland cotton were significantly fewer than expected. Breeders have

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recognized the excessive recovery of recurrent parent types in early backcross generations of introgression efforts. This has been substantiated by reports of strongly distorted segregation for factors underlying qualitative morphological traits and molecular markers (Reinisch et al., 1994; Mei et al., 2004). The preferential recovery of recurrent parent germplasm leads to highly nonrandom genome sampling, and has undoubtedly been among the factors that have hampered efforts to incorporate useful fiber quality traits from *G. barbadense* into Upland cotton through conventional backcross approaches.

Breeders typically rely on conventional whole-genome strategies in germplsam introgression. When applied to parents from different species, these strategies result in early backcross generations and/or inbreds that contain a large number of alien genes. Some of these genes are linked, and some are independently inherited. Detection of desirable genes in early generations is extremely difficult. In these situations, the effects of individual genes are camouflaged by the extreme genetic variation among plants, gene interactions, and the genetic instability across generations that arise from high levels of heterozygosity. In wide crosses, whole-genome F_2 derived from recombination inbreds also suffer from the high potential for extreme genetic variation and epistasis, in addition to the extensive loss of germplasm across sexual generations during the inbreeding process. The difficulty of detecting genes of interest is greatly exacerbated by potent epistatic interactions in wide crosses, such as in crossing *G. hirsutum* and *G. barbadense*. For example, the As_1 and As_2 loci, which affect meiotic synapses of homologous chromosomes, render plants completely sterile (i.e. zero yield) when doubly homozygous recessive, irrespective of the genotype of any other locus. The likelihood of such effects is maximized in whole-genome introgression efforts. Unfortunately, the usefulness of conventional backcrossing and backcross inbred development to dilute the genetic "noise" that camouflages genes of interest is offset by progressively nonrandom genome sampling that arises due to repeated preferential transmission across sexual generations.

To reduce the negative effects of interspecific incompatibilities during introgression, which are maximized by whole-genome introgression, backcrossed chromosome or chromosome arm substitution (CS-B) lines that carry a single pair of *G. barbadense* chromosomes or segments in an Upland cotton background were used. This strategy should allow high quality fiber traits from *G. barbadense* to be targeted for introgression into Upland cotton, while reducing negative effects of alien germplasm on various agronomic traits. Examples of transfer of genetic material from alien chromosomes have been well documented in wheat (*Triticum aestivum* (Knott, 1987), other crops (Skibinska et al., 2002), and cotton (Kohel et al., 1977; Ma and Kohel, 1983; Ren et al., 2002**;** Ren and Zhang, 2001).

In this study, the individual chromosomes from *G. hirsutum* (TM-1) were replaced with the corresponding chromosomes from 3-79 (*G. barbadense*) by hypoaneuploid-mediated backcross chromosome substitution. The agronomic and fiber trait performance of the euploid (2n = 52) chromosome substitution lines from three locations is reported. Measurement of different quantitative traits in a uniform genetic background enables detection of genetic effects from all genes on a specific chromosome or chromosome arm (Ren et al., 2002; Ren and Zhang, 2001; Shah et al., 1999). In this report, we focus on the chromosomal association of important agronomic and fiber traits based on comparative analysis of the CS-B lines in a TM-1 background with their parental lines.

MATERIALS AND METHODS

Thirteen backcrossed chromosome substitution lines, which differ in individual chromosome substitutions from *G. barbadense*, were used in this experiment (Stelly et al., 2003). These germplasm lines are near-isogenic (BC_5), with the exception of the replacement of a specific homologous pair of chromosomes or chromosome segments from 3-79 (*G. barbadense*) into TM-1, an Upland cotton (*G. hirsutum*). TM-1 is an inbred line derived from the commercial cultivar Deltapine 14 (Delta and Pine Land Co.; Scott, MS) and maintained over 40 generations by self pollination, as described by Kohel et al. (2001). Line 3-79 originated as a doubled-haploid from Pima germplasm.

BC_5S_1 seeds (selfed seeds of BC_5 plant) from euploid (2n = 52) CS-B lines specific to 13 different chromosomes (Stelly et al., 2003) and seeds from the parental lines, TM-1 and 3-79, were planted in a randomized complete block design with four replications at one location in Mississippi and Arizona in 2001, and with five replications at a second MS location in 2002.

The soil type at the Mississippi location used in both 2001 and 2002 was a Marietta loam (fine-loamy, siliceous, active, thermic fluvaquentic Eutrudepts), and the soil type at the site used in 2002 only was a Leeper silty clay loam (fine, smectitic, nonacid, thermic vertic Epiaquepts). The Maricopa, Arizona location was a low desert site and the soil was a Casa Grande fine sandy loam (fine-loamy, mixed, superactive, hyperthermic Typic Natragids).

Standard production practices were followed at all locations. In Arizona, a 50-boll sample from nodes 10 through 14 from each plot was hand-harvested for fiber analyses prior to machine harvesting for yield. A 50-boll, hand-harvested sample was collected at the Marietta loam site and a 25-boll, hand-harvested sample was collected from the Leeper loam site from each plot prior to machine harvest in Mississippi. Fiber analyses were performed by StarLab, Inc. in Knoxville, Tennessee.

A genotype with genotype × environment interaction model was used for the data analysis. The mixed linear model for genotype *i* in block *j* within environment *h* was as follows:

$$y_{hij} = \mu + E_h + G_i + GE_{hi} + B_{j(h)} + e_{hij} \qquad (1)$$

where μ is the fixed population (or grand) mean; E_h is the random environmental effect; G_i is the random genotype effect; GE_{hi} is the random $G \times E$ interaction effect; $B_{j(h)}$ is the random block effect; and e_{hij} is the random error.

The reason for considering the genotype effect as random is to evaluate both the genetic variation and the genetic effects. Variance components were estimated by the minimum norm quadratic unbiased estimation (MINQUE) procedure in which all initial values were set at 1.0 (Zhu, 1989). The phenotypic variance was defined as

$$V_p = V_G + V_{GE} + V_e \qquad (2)$$

where, V_p = phenotypic variation, V_G = genotypic variation, V_{GE} = genotypic by environment variation, and V_e = residual variation, and $V_G = \sigma^2_G$, $V_{GE} = \sigma^2_{GE}$, and $V_e = \sigma^2_e$.

Genetic effects were predicted by the adjusted unbiased prediction (AUP) approach (Zhu, 1993). A resampling (jackknifing) method was applied to calculate the standard error (SE) for each parameter by removal of one block at a time within environment (Miller, 1974). The *t*-test was used to detect the significance of the variance components. The primary interest was in comparing the genetic effect for a trait in each CS-B line with the TM-1 line. A statistically significant difference between the performance for a trait in a specific CS-B line and in the TM-1 line inferred that one or more genes affecting this trait were located on the respective chromosome or chromosome arm and were expressed in the TM-1 background of the other 25 chromosomes. Alternatively, we know that after five backcrosses a small amount of residual chromatin from *G. barbadense* is still present in the near isogenic CS-B lines. A 95% confidence interval (CI) was used to test the significance of the deviation from TM-1. All data analyses were conducted by a software program in C++ language.

RESULTS AND DISCUSSION

The phenotypic variance for each trait was partitioned into components and presented as proportions (Table 1). Genotype variances for each trait were higher than the genotype by environment variances, which indicates these CB-S lines were stable across the three environments. Residual variance accounted for less than 20% contribution to the phenotypic variance for all traits except elongation, which indicates that the genotypic effects or genotype by environment interaction effects for most traits could be precisely detected.

For any trait from the CS-B line that differs positively or negatively from TM-1, the effect is due to either genes on the specific substituted chromosome and/or epistasis between TM-1 genes and genes on the substituted chromosome, but since only the homozygous lines were grown, these two effects can-

Table 1. Proportions of estimated variance components for agronomic and fiber traits

Parameters	Agronomic and fiber trait [z]							
	Yield	Lint yield	Lint percentage	Boll weight	Micronaire	2.5% Span length	Elongation	Strength
V_G / V_P	0.686**	0.661**	0.820**	0.789**	0.830**	0.829**	0.530**	0.764**
V_{GE} / V_P	0.137**	0.141**	0.091**	0.066*	0.079	0.052**	0.132*	0.060**
V_e / V_P	0.177**	0.198**	0.089**	0.145*	0.091	0.119**	0.338**	0.176**

[z] Variance components designated with * and ** are significant at $P \leq 0.05$ and 0.01, respectively.

not be separated. Also, for any positive or negative changes in a trait in a CS-B line from 3-79 could be due to the genes on the TM-1 chromosomes other than the substituted chromosome, the absence of the TM-1 chromosome, and/or epistasis between TM-1 genes and genes on the substituted chromosome. There is probably a small amount of residual 3-79 chromatin in chromosomes other than the substituted chromosome or chromosome arm, which can affect some of these traits.

Line 3-79 produced significantly less seed and lint cotton, and had lower lint percentage, smaller bolls, lower micronaire, and longer and stronger fibers than TM-1 (Tables 2 and 3). Means with their standard errors were compared for significant differences with TM-1 and 3-79 using the 95% confidence interval (95% CI) (Table 3). The CS-B line with substituted chromosome 2 from 3-79 had higher lint percentage, micronaire, and fiber strength relative to TM-1. The CS-B line with substituted chromosome 4 had increased fiber elongation compared with TM-1. The CS-B line with alien chromosome 6 produced higher lint percentage relative to TM-1. Kohel et al. (1977) reported that this chromosome was also associated with late flowering, low micronaire and high lint percentage using a similar CS-B line. The CS-B line with substituted chromosome 7 of 3-79 had increased boll weight and micronaire compared with TM-1. The CS-B line with substitution for chromosome 16 had reduced seed yield, lint yield, and fiber length, but increased lint percentage and boll weight relative to TM-1. Ren et al. (2002) reported that chromosome 16 was associated with lint percentage, boll weight, fiber length, lint index, fiber elongation, and days to flowering. Meredith (1984) reported that lint percentage had a high positive correlation with lint yield. Chromosomes 16 and 18, and the short arm of chromosome 22 had a significant negative predicted genetic effect on lint yield, and a significant positive effect on lint percentage. The presence of either chromosome reduced seed cotton yield more than was offset by the increase in lint percentage, so lint yield is reduced even though there might be gene(s) for increased lint percentage associated with these chromosomes.

The CS-B line with substituted chromosome 17 had increased lint yield, boll weight, and fiber elongation, but reduced lint percentage, micronaire, and fiber length compared with TM-1. Kohel et al. (1977) reported short fiber length associated with chromosome 17. The CS-B line for substituted chromosome 18 had reduced seed yield, lint yield, and boll weight, but greater lint percentage, and micronaire relative to TM-1. The CS-B line with substitution for chromosome 25 had a significant association with all traits except seed cotton yield

Table 2. Phenotypic mean values for agronomic and fiber traits across the three locations

CS-B line	Yield (kg/ha)	Lint yield (kg/ha)	Lint (%)	Boll weight (g)	Micronaire	2.5% Span length (mm)	Elongation (%)	Strength (kNm/kg)
CS-B02	**2393**	**814**	**33.86**	**5.36**	**4.97**	**28.97**	**6.84**	**207**
CS-B04	**2387**	**780**	**32.36**	**5.53**	**4.70**	**29.67**	**9.18**	**195**
CS-B06	**2584**	**862**	**33.33**	**5.53**	**4.77**	**28.88**	**7.96**	**196**
CS-B07	**2379**	**789**	**33.01**	**5.21**	**4.96**	**29.26**	**8.18**	**196**
CS-B16	**1429**	**525**	**36.30**	**5.17**	**4.82**	**28.57**	**7.65**	**189**
CS-B17	**2420**	**714**	**29.30**	**4.92**	**4.20**	**28.39**	**9.06**	**196**
CS-B18	**1392**	**488**	**34.57**	**4.58**	**5.13**	**28.98**	**8.17**	**203**
CS-B25	**2358**	**719**	**30.33**	**4.93**	**3.73**	**30.37**	**7.19**	**218**
CS-B05sh	**2065**	**716**	**34.87**	**4.68**	**4.95**	**28.49**	**7.66**	**185**
CS-B14sh	**1765**	**578**	**32.74**	**4.31**	**4.57**	**30.35**	**7.41**	**200**
CS-B15sh	**2622**	**849**	**32.31**	**5.31**	**4.69**	**30.03**	**8.33**	**203**
CS-B22sh	**1686**	**626**	**37.00**	**5.03**	**5.12**	**27.40**	**6.96**	**191**
CS-B22Lo	**2204**	**847**	**38.41**	**4.42**	**5.29**	**28.34**	**7.17**	**195**
TM-1	**2519**	**827**	**32.76**	**5.62**	**4.74**	**29.35**	**8.13**	**196**
3-79	**540**	**180**	**30.74**	**2.75**	**3.32**	**33.97**	**8.62**	**272**

Table 3. Predicted genotypic effects of CS-B lines for agronomic and fiber traits expressed as deviations from the grand mean with the standard error

CS-B line	Agronomic and fiber traits [z]							
	Yield (kg/ha)	Lint yield (kg/ha)	Lint (%)	Boll weight (g)	Micronaire	2.5% Span length (mm)	Elongation (%)	Strength (kNm/kg)
CS-B02	332 ± 81^{+}	121 ± 26^{+}	0.30 ± 0.18^{*+}	0.46 ± 0.08^{+}	0.31 ± 0.05^{*+}	-0.39 ± 0.10^{+}	-1.05 ± 0.16^{+}	4.79 ± 2.59^{*+}
CS-B04	345 ± 71^{+}	94 ± 23^{+}	-1.18 ± 0.16	0.62 ± 0.05^{+}	0.02 ± 0.05^{+}	0.30 ± 0.10^{+}	1.24 ± 0.18*	-7.58 ± 2.10^{+}
CS-B06	526 ± 63^{+}	170 ± 21^{+}	-0.18 ± 0.09^{*+}	0.63 ± 0.05^{+}	0.10 ± 0.05^{+}	-0.49 ± 0.16^{+}	0.06 ± 0.17^{+}	-6.39 ± 2.00^{+}
CS-B07	326 ± 50^{+}	99 ± 16^{+}	-0.55 ± 0.07^{+}	0.31 ± 0.07^{*+}	0.29 ± 0.05^{*+}	-0.06 ± 0.10^{+}	0.29 ± 0.15	-6.59 ± 2.59^{+}
CS-B16	-623 ± 79^{*+}	-164 ± 28^{*+}	2.73 ± 0.41^{*+}	0.25 ± 0.09^{*+}	0.13 ± 0.06^{+}	-0.81 ± 0.19^{*+}	-0.24 ± 0.19^{+}	-14.07 ± 2.79^{+}
CS-B17	326 ± 89^{+}	13 ± 27^{*+}	-4.20 ± 0.09^{*+}	0.01 ± 0.06^{*+}	-0.48 ± 0.04^{*+}	-0.97 ± 0.14^{*+}	1.17 ± 0.23*	-6.49 ± 2.20^{+}
CS-B18	-681 ± 73^{*+}	-208 ± 25^{*+}	1.04 ± 0.14^{*+}	-0.32 ± 0.10^{*+}	0.45 ± 0.04^{*+}	-0.39 ± 0.13^{+}	0.30 ± 0.15	0.80 ± 1.70^{+}
CS-B25	280 ± 74^{+}	23 ± 21^{*+}	-3.13 ± 0.18^{*+}	0.01 ± 0.06^{*+}	-0.93 ± 0.04^{*+}	1.01 ± 0.18^{*+}	-0.70 ± 0.14^{*+}	16.57 ± 3.59^{*+}
CSB05sh	37 ± 87^{*+}	35 ± 29^{+}	1.31 ± 0.26^{*+}	-0.21 ± 0.10^{*+}	0.29 ± 0.05^{*+}	-0.87 ± 0.13^{*+}	-0.22 ± 0.11^{*+}	-17.27 ± 2.50^{*+}
CS-B14sh	-273 ± 85^{*+}	-107 ± 26^{*+}	-0.84 ± 0.43	-0.60 ± 0.12^{*+}	-0.09 ± 0.07^{+}	1.01 ± 0.21^{*+}	-0.49 ± 0.08^{*+}	-1.30 ± 2.99^{+}
CS-B15sh	548 ± 104^{+}	151 ± 34^{+}	-1.24 ± 0.12*	0.41 ± 0.08^{*+}	0.02 ± 0.03^{+}	0.65 ± 0.17^{*+}	0.38 ± 0.17	0.50 ± 2.50^{+}
CS-B22sh	-357 ± 63^{*+}	-59 ± 23^{*+}	3.54 ± 0.14^{*+}	0.11 ± 0.06^{*+}	0.46 ± 0.05^{*+}	-1.99 ± 0.11^{*+}	-0.94 ± 0.16^{*+}	-10.88 ± 2.40^{+}
CS-B22Lo	158 ± 100^{+}	158 ± 39^{+}	4.85 ± 0.13^{*+}	-0.49 ± 0.10^{*+}	0.62 ± 0.04^{*+}	-1.04 ± 0.13^{*+}	-0.71 ± 0.19^{*+}	-6.89 ± 2.40^{+}
TM1	464 ± 78	136 ± 27	-0.76 ± 0.11	0.71 ± 0.06	0.08 ± 0.04	-0.04 ± 0.14	0.20 ± 0.07	-6.29 ± 2.50
3-79	-1408 ± 73	-461 ± 24	-1.70 ± 0.36	-1.90 ± 0.07	-1.26 ± 0.05	4.07 ± 0.21	0.70 ± 0.15	60.78 ± 2.50

[z] **Values designated with * and + are different from TM-1 and 3-79, respectively at $P \leq 0.05$ based on confidence interval test.**

compared with TM-1. The CS-B line with substituted chromosome arm 5sh (short arm of chromosome 5) showed association with all traits except lint yield. The CS-B line with alien chromosome arm 14sh had reduced seed cotton yield, lint yield, boll weight, and fiber elongation, but increased fiber length compared with TM-1. The CS-B line for substituted chromosome arm 15sh produced lower lint percentage, but higher boll weight and fiber length. The CS-B line with alien chromosome arm 22sh showed association with all traits except fiber strength. The CS-B line with substituted chromosome arm 22Lo (long arm of chromosome 22) produced higher lint percentage and micronaire, but lower boll weight, fiber length, and elongation.

All of the CS-B lines produced significantly greater seed cotton yield and lint cotton yield than 3-79. Five of the substituted chromosomes or chromosome arms (16, 18, 5sh, 14sh, 22sh) produced significantly less seed cotton than TM-1. Six substituted chromosomes or arms (16, 17, 18, 25, 14sh, and 22sh) produced lower lint cotton yield than TM-1. Seven CS-B lines (2, 6, 16, 18, 5Sh, 22Lo, and 22sh) had greater lint percentage than both 3-79 and TM-1, but substituted chromosomes 17 and 25 produced lower lint percentage, and substituted chromosome 7 had higher lint percentage than 3-79. The results revealed both positive and negative transgressive segregation for lint percentage in CS-B lines. Lint percentage is often correlated with leaf pubescence, and it is interesting that sometimes the progeny of interspecific crosses show leaf and stem pubescence characteristics that are not observed in any of the parents (unpublished data). All of the CS-B lines produced larger bolls than 3-79, and ten substituted chromosomes or arms (7, 16, 17, 18, 25, 5sh, 14sh, 15sh, 22sh, 22Lo) had smaller bolls than TM-1. All of the CS-B lines had higher micronaire than 3-79, and six (2, 7, 18, 5sh, 22sh, and 22Lo) had higher micronaire than TM-1. The CS-B lines with alien chromosome 17 or 25 had significant reductions in micronaire relative to TM-1. Micronaire readings are an indicator of fiber fineness and maturity. Discount in cotton price begins for fiber having micronaire below 3.5 and above 4.9 (Silvertooth, 1999). All of the lines had weaker fiber strength than 3-79, but fibers in the CS-B lines with substituted chromosomes 2 or 25 were significantly stronger than TM-1. Kohel

et al. (2001) also reported the association of chromosome 25 with the fiber strength quantitative trait locus (QTL). All of the substituted lines had shorter fibers than 3-79. CS-B lines with alien chromosome 25, 14sh, or 15sh had longer fibers, and substituted chromosomes or chromosome arms of 16, 17, 5sh, 22sh, or 22Lo produced shorter fibers than TM-1. Substituted chromosome lines 4 and 17 had significantly greater fiber elongation than TM-1.

These results showed that both parents had negative deviations from the grand mean for lint percentage and positive deviations from the grand mean for elongation. The higher lint percentage and lower elongation of the CS-B lines may be due to some kind of epistatic effect. Several instances of negative transgressive segregation (i.e. significantly poorer quality than the TM-1 parent) for high micronaire, short fiber length, decreased elongation, and decreased strength in CS-B lines were also observed. Kohel et al. (2001) reported transgressive segregation in fiber qualities in the interspecific crosses between TM-1 and 3-79, and suggested (p. 171) "the occurrence of interspecific transgression might be due to induced mutation, gene complementation, and/or unlocking of the recessive genes". Substituted chromosome 5sh had significantly weaker fiber strength, length, and elongation than TM-1. This might be due to the effect of the substituted *G. barbadense* chromosome or chromosome arm harboring alleles for poor fiber quality genes or an epistatic effect.

Cytogenetic analyses have previously revealed that the cultivated tetraploid species *G. hirsutum* and *G. barbadense* contain 52 chromosomes and have the disomic tetraploid constitution AADD. The A-subgenome and D-subgenome chromosomes of *G. hirsutum* have been designated as chromosomes 1-13 and 14-26, respectively. Assuming that one gene on a substituted chromosome affects one quantitative trait, then, theoretically, the possible number of genotypic values detected for eight traits and the 13 chromosome substitution lines would be 104 (8 × 13). Across the 13 chromosome substitution lines, 56 significant values for genotypic effects that affect fiber were detected for the substituted chromosomes. In this study, data included the effect of five substitute chromosomes specific to the A-subgenome and eight substitute chromosomes specific to the D-subgenome of the CS-B lines. The A-subgenome genotypic values were significant 32.5% (13 of 40) of the time, but the D-subgenome genotypic values were significant 71.6% (43 of 64) of the time. Results suggested that on average, 2.8 traits per A-subgenome chromosome and 6.14 traits per D-subgenome chromosome were significant in comparison with TM-1. These results support those of Jiang et al. (1998) that most QTLs influencing fiber quality and yield were located on the "D" subgenome derived from an ancestor that does not produce spinnable fibers. They concluded (p. 4419) that "the merger of two genomes with different evolutionary histories in a common nucleus appeared to offer unique avenues for phenotypic response to selection" during polyploidy formation, and the domestication and breeding of tetraploid cottons resulted in superior fiber quality and yield in the D-subgenome compared to its ancestor. Rong et al. (2004) reported higher marker density on the D-subgenome compared to the A-subgenome in the tetraploid cotton.

The primary thrust of this research was to use germplasm with specific chromosomes or chromosome arms as an approach for germplasm enhancement of agronomic and fiber qualities that will benefit the cotton producers and industries. In recent years, lint quality has become a major issue because of 1) the technological changes in textile industries demanding high quality fibers, 2) the use of high volume instrument testing (HVI), and 3) the occurrence of discount prices due to unfavorable fiber characteristics. In this study, when only one pair of chromosomes from *G. barbadense* 3-79 was present with 25 pairs from *G. hirsutum* TM-1, we observed some negative effects from the alien chromosome between superior fiber traits and yield in many of the CS-B lines, which indicate the challenges in the introgression of *G. barbadense* traits in Upland cotton. The CS-B line with substituted chromosome 25 produced improved fiber strength, longer fibers, and lower micronaire relative to TM-1. This is important considering that micronaire and staple length are two essential fiber quality issues that influence price discounts in cotton market. Even though the results showed that while several backcrossed chromosome substitution lines had an overall negative effect on lint yield, the improved specific fiber quality traits in some of the CS-B lines demonstrate the potential of backcrossed chromosome substitution lines for improving fiber qualities in Upland cotton germplasm.

This is the first report on several newly developed backcrossed chromosome substitution lines.

The mode of development uses hemizygosity to preclude recombination during introgression, so all genes within the alien chromosome or chromosome segment are transferred into Upland cotton. Some of the cytologicaly aneuploid lines used in developing these CS-B lines were originally derived from different sources other than TM-1. Association for some of these traits might also be due to some background residual effect. There is also a possibility that the observed genetic effects could have been due to some unlinked residual effect of *G. barbadense* chromatin in other chromosomes and is independent of the homozygous condition of the substituted chromosome or arm from *G. barbadense*.

Even marker-assisted selection after conventional interspecific introgression, empowered by huge numbers of markers, could not guarantee transfer of all alien loci, especially in high recombination regions, which tend to be gene-rich, and, we surmise, subject to recombination, as well as gene conversion. Based on current dogma regarding ploidy and estimates of the number of genes in other plant genomes (Goff et al., 2002; Yu et al., 2002), one would estimate that each substituted chromosome contains at least 1000-2000 genes from *G. barbadense*. The CS-B line evaluation for QTL localization does not require segregating populations, so it differs from traditional QTL mapping and offers certain statistical advantages; however, the CS-B lines only provided an opportunity to associate some QTLs with a specific substituted chromosome (Nadeau et al., 2000). For precisely detecting the positions, the number, and the effects of QTLs on a specific substituted chromosome, recombinant substituted (RS) lines specific to a chromosome can be used by linkage with molecular markers (Kaeppler, 1997; Zeng, 1994; Shah et al., 1999). Efforts are underway to develop RS lines using these CS-B lines, so the number and the effects of QTLs could be more precisely dissected and detected. Once developed, these will offer a strong complement to ongoing conventional approaches of molecular mapping in other laboratories.

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