Theor Appl Genet (2011) 122:1351–1361
DOI 10.1007/s00122-011-1536-5

ORIGINAL PAPER

Delineation of interspecific epistasis on fiber quality traits in *Gossypium hirsutum* by ADAA analysis of intermated *G. barbadense* chromosome substitution lines

S. Saha · J. Wu · J. N. Jenkins · J. C. McCarty · R. Hayes · D. M. Stelly

Received: 7 September 2010 / Accepted: 6 January 2011 / Published online: 8 February 2011

Abstract Genetic diversity is the foundation of any crop improvement program, but the most cultivated Upland cotton [*Gossypium hirsutum* L., $2n = 52$, genomic formula $2(AD)_1$] has a very narrow gene pool resulting from its evolutionary origin and domestication history. Cultivars of this cotton species (*G. hirsutum* L.) are prized for their combination of exceptional yield, other agronomic traits, and good fiber properties, whereas the other cultivated 52-chromosome species, *G. barbadense* L. [$2n = 52$, genomic formula $2(AD)_2$], is widely regarded as having the opposite attributes. It has exceptionally good fiber qualities, but generally lower yield and less desirable agronomic traits. Breeders have long aspired to combine the best attributes of *G. hirsutum* and *G. barbadense*, but have had limited success. F_1 hybrids are readily created and largely fertile, so the limited success may be due to cryptic biological and technical challenges associated with the conventional methods of interspecific introgression. We have developed a complementary alternative approach for introgression based on chromosome substitution line, followed by increasingly sophisticated genetic analyses of chromosome-derived families to describe the inheritance and breeding values of the chromosome substitution lines. Here, we analyze fiber quality traits of progeny families from a partial diallel crossing scheme among selected chromosome substitution lines (CS-B lines). The results provide a more detailed and precise QTL dissection of fiber traits, and an opportunity to examine allelic interaction effects between two substituted chromosomes versus one substituted chromosome. This approach creates new germplasm based on pair wise combinations of quasi-isogenic chromosome substitutions. The relative genetic simplicity of two-chromosome interactions departs significantly from complex or RIL-based populations, in which huge numbers of loci are segregating in all 26 chromosome pairs. Data were analyzed according to the ADAA genetic model, which revealed significant additive, dominance, and additive-by-additive epistasis effects on all of the fiber quality traits associated with the substituted chromosome or chromosome arm of CS-B lines. Fiber of line 3-79, the donor parent for the substituted chromosomes, had the highest Upper Half Mean length (UHM), uniformity ratio, strength, elongation, and lowest micronaire among all parents and hybrids. CS-B16 and CS-B25 had significant additive effects for all fiber traits. Assuming a uniform genetic background of the CS-B lines, the comparative analysis of the double-heterozygous hybrid combinations (CS-B × CS-B) versus their respective single heterozygous combinations (CS-B × TM-1) demonstrated that

---

Communicated by B. Friebe.

S. Saha (✉) · J. N. Jenkins · J. C. McCarty · R. Hayes
United States Department of Agriculture-Agricultural Research Service, Crop Science Research Laboratory, 810 Highway 12 East, Mississippi State, MS 39762, USA
e-mail: Sukumar.saha@ars.usda.gov

J. Wu
Department of Plant and Soil Sciences, Mississippi State University, Mississippi State, MS 39762, USA

J. Wu
Plant Science Department, South Dakota State University, Brookings, SD, USA

D. M. Stelly
Department of Soil and Crop Sciences, Texas A&M University, College Station, TX, USA

interspecific epistatic effects between the genes in the chromosomes played a major role in most of the fiber quality traits. Results showed that fiber of several hybrids including CS-B16 × CS-B22Lo, CS-B16 × CS-B25 and CS-B16 × TM-1 had significantly greater dominance effects for elongation and hybrid CS-B16 × CS-B17 had higher fiber strength than their parental lines. Multiple antagonistic genetic effects were also present for fiber quality traits associated with most of the substituted chromosomes and chromosome arms. Results from this study highlight the vital importance of epistasis in fiber quality traits and detected novel effects of some cryptic beneficial alleles affecting fiber quality on the 3-79 chromosomes, whose effects were not detected in the 3-79 parental lines.

Introduction

Upland cotton is one of the most important cultivated crops in the US and in more than other 70 countries worldwide (Smith et al. 2009). It is planted on five million hectares in the US, greater than all other row crops except maize, wheat, and soybean, and contributes as a source of textile fiber about $6 billion per year (Gingle et al. 2006; USDA-NASS 2002).

Fiber quality has become a major issue in recent years because globalization and technological changes in textile industries have demanded higher quality fibers for maximum efficiency, quality, and market competitiveness. Previous studies showed that fiber quality traits are mostly associated with genetic components (e.g. moderate to high heritability, many genes); thus, there is great potential to improve fiber qualities through breeding (Zeng and Meredith 2009; Rong et al. 2007; He et al. 2007; Paterson et al. 2003; Jenkins et al. 2007; Saha et al. 2006). Cotton breeders would like to develop Upland cotton with elite fiber quality.

Gossypium hirsutum L., the most extensively cultivated cotton species, is characterized by improved agronomic traits including high yield, with good fiber properties, whereas, *G. barbadense* L. has exceptionally good fiber qualities, but agronomic traits are not as favorable as Upland cotton. Utilization of *G. barbadense* for *G. hirsutum* improvement at the whole-genome level has been less successful because of technical and biological challenges associated with the conventional methods of interspecific introgression (Stephens 1949; McKenzie 1970). Some of the problems in interspecific introgression between these two species have been poor agronomic qualities of progeny, sterility, mote formation, limited genetic recombination and distorted segregation and recovery.

Successful introgressive breeding involves difficult challenges that demand approaches that are different from and complementary to conventional methods of hybridization, optional backcrossing, and inbreeding, which entail many non-random effects and haphazard recovery of products. Interspecific introgression in *Gossypium* appears to be associated with a high level of epistasis (Saha et al. 2010; Paterson et al. 2004). A non-traditional method of interspecific cotton germplasm introgression is the use of alien chromosome substitution lines, where the entire genetic content of an individual chromosome or chromosome arm segment *G. hirsutum* is replaced by the corresponding alien chromosome or segment (Stelly et al. 2005). During hypoaneuploid-based chromosome or chromosome arm substitution, cytogenetic or marker-based selection of hemizygosity is used to preclude recombination, and selection of disomic euploid self-progeny is used to establish true-breeding homozygous disomic chromosome substitution lines. In previous reports, we described various chromosomal effects on fiber properties using chromosome substitution lines containing chromosomes and chromosome segments of *G. barbadense* line '3-79', i.e., CS-B lines (Saha et al. 2004, 2006; Jenkins et al. 2007).

This study was a continuation of our previous study of yield performance effects (Saha et al. 2010). In this study, we have focused on genetic variation for five important fiber quality traits. We used an ADAA model (Wu et al. 2006) to facilitate the analysis of multiple generations (F_1, F_2, F_3) among several carefully selected CS-B lines and TM-1. One of our aims has been to determine if such an analysis of chromosomal effects would reveal epistatic effects and thus more precisely define the genetic effects affecting the economically important fiber qualities of interspecific introgression products.

Materials and methods

Six CS-B lines (CS-B14sh, CS-B16, CS-B17, CS-B22sh, CS-B22Lo, and CS-B25) and TM-1 (the recurrent parent) were crossed in a half diallel mating design in the summer of 2003 at Mississippi State, MS. These CS-B lines were selected based on their potential to improve fiber traits (Saha et al. 2006; Jenkins et al. 2006, 2007).

The F_1 and parents seeds were selfed in Mexico in the fall/winter of 2003. The same crosses were also made in Mexico to provide additional F_1 seeds. In 2004, 21 F_1 and F_2 hybrids and their parents including 3-79 (the donor line) were planted in two locations (environments 1 and 2) at Mississippi State, MS. Bulk samples from open boll of F_2 plants in 2004 were open pollinated to produce F_3 seeds in 2005. In 2005, 21 F_2 and F_3 hybrids and the parents were grown in two locations (environments 3 and 4). The hybrids and their parental lines were planted in a randomized complete block design with four replications in each environment. Detailed information can be obtained by referring to our previous study (Saha et al. 2010). All experiments were conducted at the Plant Science Research Center, Mississippi State, MS (33.4°N 88.4°W).

Prior to machine harvest, a 25-boll hand-harvested sample was collected from the middle portion of the plants for each plot. Boll samples were ginned on a laboratory 10-saw gin to separate lint and seed. Lint samples were sent to STARLAB, Inc., Knoxville, TN, USA for determination of micronaire, elongation, fiber strength, UHM and uniformity ratio using high volume instrument (HVI) equipment.

Data analysis

The methods of data analysis are analogous to those detailed previously (McCarty et al. 2004a, b; Wu et al. 2006; Saha et al. 2010). First, fiber trait data were analyzed by the analysis of variance programs in SAS (SAS Institute 2001), and genotype means were separated using least significant difference (LSD) at the 0.05 level. An additive-dominance model with additive-by-additive epistatic effects (ADAA model) was used to estimate variance components and to predict genetic effects (Wu et al. 2006). Variance components were calculated by minimum norm quadratic unbiased estimation (MINQUE), in which, all prior values were set as 1.0 (Zhu 1989). Genetic effects were predicted by the adjusted unbiased prediction (AUP) method (Zhu 1993). The resampling (jackknife) method was used to calculate the standard error (SE) for each parameter by removal of one replicate within each environment (Miller 1974; Wu et al. 2008). Genetic effects were calculated as deviations from the respective grand mean μ, not from TM-1. Significance of the difference between the genetic effects for two lines were detected by the method of Patterson (1939) using the standard error of the difference between two effects. An approximate t test (df = 15) was used to test the significance of each parameter. A one-tailed t test was used to test the significance of variance components and a two-tailed t test for genetic effects. A significant difference in genetic effects between a specific CS-B line and TM-1 was considered to be a chromosome effect attributable to the specific substituted chromosome or chromosome arm from the donor parent.

Results

Mean comparisons of CS-B lines and their hybrids

TM-1 and 3-79 were used as the parents of CS-B line because TM-1 is considered as the genetic standard line in Upland cotton and 3-79 is a double haploid line. However, fiber trait means differed widely between the recurrent parent, TM-1, and donor parent, 3-79, further justifying the selection of these two parental lines (Table 1). As expected, line 3-79 had longer, stronger, more uniform fibers with more elongation and lower micronaire than TM-1, CS-B lines or any of the CS-B line hybrids (Tables 1, 2).

All six CS-B lines had significant effects on UHM, which indicates that each of the respectively substituted chromosomes contain alleles that affect UHM. The UHM among CS-B hybrids ranged from 28.12 to 30.39 mm (Table 2). CS-B14sh and CS-B25 had the highest UHM means, both significantly longer than TM-1 (Table 1). The average UHM was higher in the hybrids of CS-B17 × CS-B22sh and CS-B22sh × CS-B22Lo than their respective parents, which seems to indicate dominance effects of the alien allele(s) caused the hybrid vigor. In contrast, most (66%) of the CS-B line hybrids had shorter fibers than TM-1. The latter are especially interesting in the context of this study, in that they indicate the net effects on UHM by the TM-1 allele(s) in respective segments of chromosome are superior to those of 3-79, at least in a TM-1 genetic background. Given that 3-79 has a UHM greater than TM-1, 34.31 versus 29.42 mm, the simple expectation would be for alleles of 3-79 to be superior to those of TM-1 and for some chromosomes this proved to be the case.

Table 1 Mean of fiber quality values of eight parents over four environments

Entry	UHM (mm)	Uniformity ratio (UR)	Fiber strength (kN m kg^{-1})	Elongation (%)	Micronaire (Mic)
CS-B14sh	30.50*	84.51	291*	7.95	4.59
CS-B16	28.23*	82.82*	262*	7.95	4.99*
CS-B17	28.24*	83.71*	274*	8.38*	4.06*
CS-B22sh	26.57*	83.31*	285	8.01	5.31*
CS-B22Lo	27.73*	83.54*	280	8.15	5.32*
CS-B25	30.51*	85.00*	290	7.76*	4.32*
TM-1	**29.42**	**84.28**	**283**	**8.04**	**4.58**
3-79	**34.31***	**86.51***	**356***	**8.63***	**3.86***
LSD0.05	0.38	0.49	6.89	0.18	0.15

Parent lines of CS-B are in bold font

*Significance from TM-1 at $P \leq 0.05$

Table 2 Mean values of fiber quality traits from F_1, F_2, and F_3 generations

Cross	UHM (mm)	Uniformity ratio (UR)	Fiber strength (kN m kg^{-1})	Elongation (%)	Micronaire (Mic)
	Mean	Mean	Mean	Mean	Mean
CS-B14sh × CS-B16	29.91*	84.01	280	8.05	4.81*
CS-B14sh × CS-B17	29.73	84.45	279	8.19	4.58
CS-B14sh × CS-B22sh	29.14	84.21	287	8.07	5.03*
CS-B14sh × CS-B22Lo	28.98*	84.05	278	8.08	4.98*
CS-B14sh × CS-B25	30.39*	84.75	287	7.94	4.53
CS-B14sh × TM-1	29.76	84.52	283	8.04	4.70
CS-B16 × CS-B17	28.57*	83.54*	275*	8.27*	4.72
CS-B16 × CS-B22sh	28.32*	83.25*	272*	7.89	5.04*
CS-B16 × CS-B22Lo	28.12*	83.25*	274*	8.15	5.12
CS-B16 × CS-B25	29.29	83.90	277	8.01	4.80*
CS-B16 × TM-1	28.78*	83.39*	275*	8.04	4.79*
CS-B17 × CS-B22sh	28.48*	83.70*	275*	8.12	4.70
CS-B17 × CS-B22Lo	28.73*	84.08	276*	8.29*	4.82*
CS-B17 × CS-B25	29.92*	84.58	285	8.10	4.36*
CS-B17 × TM-1	29.24	84.27	276*	8.34*	4.62
CS-B22sh × CS-B22Lo	28.26*	83.81	281	8.08	5.16*
CS-B22sh × CS-B25	29.26	83.99	282	7.87	4.77*
CS-B22sh × TM-1	28.95*	83.99	282	7.92	4.81*
CS-B22Lo × CS-B25	29.25	84.09	282	8.01	4.89*
CS-B22Lo × TM-1	28.60*	83.95	281	8.23*	4.94*
CS-B25 × TM-1	29.87*	84.55	281	7.90	4.60
TM-1	29.42	84.28	283	8.04	4.58
LSD0.05	0.38	0.48	6.89	0.18	0.15

*Significance from TM-1 at $P \leq 0.05$

Uniformity ratios for five of the six CS-B lines were significantly different from the recurrent parent, TM-1 (Table 1); however, only the uniformity ratio of CS-B25 was significantly higher than TM-1, and it was still far short of the uniformity ratio of 3-79. Given that, the 3-79 uniformity ratio is considerably higher than TM-1, the observation of lower uniformity ratios than TM-1 in four CS-B lines was unexpected. Hybrids of CS-B14sh × TM-1, CS-B17 × CS-B22sh and CS-B22sh × CS-B22Lo had normally higher uniformity ratios than their parents except F_3 hybrids of CS-B17 × CS-B22sh with lower value, suggesting the possible effect of over dominance or transgressive segregation for fiber uniformity in a TM-1 genetic background.

Although fiber strength of the donor, 3-79, greatly exceeds that of the recurrent parent, TM-1, only one of the six substitution lines, CS-B14sh, had fiber significantly stronger than TM-1. In fact, two were significantly weaker than TM-1, i.e., CS-B16 and CS-B17. While these finding suggest the 3-79 segment in CS-B14sh carries one or more genes that collectively promote fiber strength in a TM-1 background, they also suggest that the alien alleles in CS-B16 and CS-B17 collectively caused a decrease in strength in a TM-1 background. Given that the means indicate a net negative effect, the data do not preclude the cryptic existence of beneficial 3-79 alleles in CS-B16 and CS-B17.

In terms of micronaire values, only two CS-B lines (CS-B17 and CS-B25) were within the range of the recurrent and donor parent values and three CS-B lines (CS-B16, CS-B22sh and CS-B22Lo) were significantly higher than TM-1. Though intermediate to both parents, the micronaire values of CS-B17 and CS-B25 were significantly lower than all other CS-B lines and TM-1, yet they remained significantly higher than 3-79. The F_1, F_2, and F_3 hybrids between these two lines, CS-B17 × CS-B25, also had exceptionally low micronaire relative to the hybrids of other CS-B lines, further suggesting the respective 3-79 chromosomes carry genes that reduce micronaire which is a positive breeding effect. Conversely, three CS line hybrids had micronaire values significantly greater than TM-1 and values beyond the range of parental phenotypes. Overall, findings suggest that CS-B related chromosomes of parents, 3-79 and TM-1, carry factors that can raise or lower micronaire values.

Genetic variance components

The estimated variance components are presented as proportions of the phenotypic variances (Table 3). Additive, dominance, and additive × additive epistatic effects were significant for all fiber traits, except that dominance effects for strength were not significant. Additive effect for UHM was highest among all variance components. Dominance was greater than additive variances only for elongation. Additive was greater than dominance for fiber length, strength, and micronaire. Additive and dominance effects were equal for uniformity. Dominance genetic effect-by-environment interactions were significant and large for length, strength, and micronaire. For all fiber traits, the experimental error effects were large and significant, ranging from 28 to 62% of the phenotype variances.

Additive effects

Additive genetic effects are equivalent to the general combining ability effects and the results are presented as deviations from the grand means (Table 4; Jenkins et al. 2007). CS-B16 had significantly greater negative additive effects than TM-1 for all fiber traits, except micronaire, indicating that the respective 3-79 chromosomes had genes negatively affecting these fiber traits in the TM-1 background. Significant and positive additive effects greater than TM-1 were shown for CS-B14sh and CS-B25 for fiber length, strength, and uniformity. Most other chromosomes had significant negative additive effects on most fiber properties and these were greater than TM-1 additive effects. CS-B17 had higher additive effects for elongation and lower additive effects for micronaire than TM-1. Results also revealed that the two arms of the substituted chromosome 22 had significant but opposite additive effects on fiber elongation.

Dominance effects

Dominance effects are equivalent to specific combining ability (Wu et al. 2006; Jenkins et al. 2007). Two types of dominance effects, homozygous and heterozygous, were predicted in this study (Table 5). The deviation from TM-1 of a homozygous dominance effect of a CS-B line measures the difference of dominance effects between the substituted pair of chromosomes and the respective pair of TM-1 chromosomes. The deviation of heterozygous dominance effects of the substituted chromosome/chromosomes (chromosome interaction effects in hybrids) from TM-1 measures the difference in the interaction effects between the 3-79 alleles on the heterozygous chromosome/chromosomes, from the interaction effects of the TM-1 alleles on the same chromosome/chromosomes (Jenkins et al. 2006, 2007; Saha et al. 2006, 2008a). Six CS-B lines had significant homozygous dominance genetic effects for uniformity ratio, elongation, and micronaire (Table 5). Homozygous dominance effects of TM-1 were negative for fiber length, uniformity, and elongation, but essentially zero for micronaire. Most CS-B lines (88%) had negative homozygous dominance effects for UHM, uniformity ratio, elongation, and micronaire. The homozygous dominance effects of CS-B lines and TM-1 were negative for most line/trait combinations. However, the homozygous dominance effects for CS-B lines were superior to TM-1 for all traits indicating that these CS-B lines can be used to improve some of these traits in Upland cotton. Note that the negative effects on micronaire of the CS-B lines are favorable, because lower micronaire is desirable in mature fibers.

Heterozygous dominance effects for UHM varied from -0.092 (CS-B14sh × CS-B25) to 0.118 (CS-B14sh × TM-1) among all crosses. Heterozygous dominance effect for uniformity ratio ranged from -0.829 (CS-B14sh × CS-B25) to 0.718 (CS-B14sh × TM-1) among the CS-B crosses. Heterozygous dominance effects varied from

Table 3 Estimated variance components expressed as proportions to the phenotypic variances for fiber quality traits

Variance Components	UHM	Uniformity Ratio	Fiber Strength	Elongation	Micronaire
V_A/V_P	0.444**	0.192**	0.022**	0.121**	0.330**
V_D/V_P	0.006*	0.193**	0.001	0.205**	0.062**
V_{AA}/V_P	0.066**	0.022**	0.098**	0.022**	0.050**
V_{AE}/V_P	0.000	0.003	0.006	0.065**	0.000
V_{DE}/V_P	0.206**	0.100**	0.253**	0.000	0.247**
V_{AAE}/V_P	0.000	0.000	0.000	0.018**	0.000
V_e/V_P	0.278**	0.489**	0.620**	0.569**	0.311**

*, **Variance component are significant at 0.05 and 0.01 respectively

V_A additive variance, V_D dominance variance, V_{AE} additive by environment variance, V_{DE} dominance by environment variance, V_{AAE} additive by additive interaction and environment variance, V_e error variance, V_P phenotypic variance

Table 4 Predicted additive effects (±SE) as deviated from the grand means for fiber quality traits

Entry	UHM (mm)	Uniformity ratio (%)	Fiber strength (kN m kg^{-1})	Elongation (%)	Micronaire (Mic)
CS-B14sh	0.608 ± 0.004*	0.358 ± 0.003*	1.795 ± 0.294*	−0.009 ± 0.001	−0.042 ± 0.001*
CS-B16	−0.345 ± 0.003*	−0.509 ± 0.004*	−1.942 ± 0.314*	−0.027 ± 0.001*	0.078 ± 0.001*
CS-B17	0.022 ± 0.003*	0.122 ± 0.004	−0.618 ± 0.098*	0.146 ± 0.003*	−0.215 ± 0.002*
CS-B22sh	−0.503 ± 0.003*	−0.232 ± 0.003*	−0.284 ± 0.049	−0.064 ± 0.001*	0.160 ± 0.001*
CS-B22Lo	−0.573 ± 0.003*	−0.144 ± 0.005*	−0.098 ± 0.029	0.079 ± 0.002*	0.223 ± 0.001*
CS-B25	0.734 ± 0.002*	0.311 ± 0.004*	1.265 ± 0.206*	−0.109 ± 0.002*	−0.153 ± 0.001*
TM-1	0.059 ± 0.004	0.100 ± 0.005	−0.108 ± 0.059	−0.015 ± 0.001	−0.051 ± 0.001

*Significance from TM-1 at $P \le 0.05$

Table 5 Predicted dominance effects for four fiber traits

Entry	UHM (mm)	Uniformity Ratio (%)	Elongation (%)	Micronaire (Mic)
Homozygous effects				
CS-B14sh	−0.043 ± 0.012*	−0.434 ± 0.018*	−0.164 ± 0.007*	−0.040 ± 0.004*
CS-B16	−0.002 ± 0.003*	−0.438 ± 0.019*	−0.183 ± 0.006*	−0.027 ± 0.003*
CS-B17	0.001 ± 0.003*	−0.133 ± 0.014*	−0.032 ± 0.007*	−0.100 ± 0.009*
CS-B22sh	−0.029 ± 0.010	−0.606 ± 0.019*	0.144 ± 0.009*	−0.045 ± 0.003*
CS-B22Lo	−0.021 ± 0.007*	−0.237 ± 0.016*	−0.055 ± 0.008*	−0.084 ± 0.007*
CS-B25	−0.074 ± 0.020	−0.552 ± 0.021*	−0.121 ± 0.005*	0.033 ± 0.005*
TM-1	−0.088 ± 0.024	−0.788 ± 0.021	−0.271 ± 0.008	0.009 ± 0.004
Heterozygous effects				
CS-B14sh × CS-B16	0.082 ± 0.022*	0.585 ± 0.020*	0.077 ± 0.005*	0.012 ± 0.005
CS-B14sh × CS-B17	0.026 ± 0.008*	0.052 ± 0.024*	−0.062 ± 0.006*	−0.145 ± 0.012*
CS-B14sh × CS-B22sh	0.012 ± 0.007*	0.206 ± 0.021*	0.039 ± 0.006*	0.135 ± 0.012*
CS-B14sh × CS-B22Lo	−0.016 ± 0.009*	0.294 ± 0.029*	0.109 ± 0.012*	−0.037 ± 0.004*
CS-B14sh × CS-B25	−0.092 ± 0.025	−0.829 ± 0.031	−0.068 ± 0.010*	0.121 ± 0.009*
CS-B14sh × TM-1	0.118 ± 0.031*	0.718 ± 0.023*	0.228 ± 0.012*	−0.017 ± 0.005*
CS-B16 × CS-B17	0.001 ± 0.003*	0.111 ± 0.018*	−0.066 ± 0.008*	0.094 ± 0.008*
CS-B16 × CS-B22sh	−0.072 ± 0.019	−0.411 ± 0.016*	−0.223 ± 0.010*	0.003 ± 0.005
CS-B16 × CS-B22Lo	−0.066 ± 0.019	−0.106 ± 0.018*	0.143 ± 0.010*	0.071 ± 0.006*
CS-B16 × CS-B25	0.081 ± 0.023*	0.541 ± 0.025*	0.211 ± 0.009*	−0.055 ± 0.006*
CS-B16 × TM-1	−0.048 ± 0.013	−0.067 ± 0.023*	0.211 ± 0.011*	−0.049 ± 0.005*
CS-B17 × CS-B22sh	−0.085 ± 0.025	0.253 ± 0.019*	0.115 ± 0.012*	0.140 ± 0.011*
CS-B17 × CS-B22Lo	0.026 ± 0.010*	−0.245 ± 0.021*	0.167 ± 0.014*	0.132 ± 0.012*
CS-B17 × CS-B25	0.030 ± 0.009*	0.296 ± 0.017*	0.070 ± 0.006*	−0.114 ± 0.009*
CS-B17 × TM-1	0.001 ± 0.003*	−0.147 ± 0.014*	−0.085 ± 0.006*	0.033 ± 0.006*
CS-B22sh × CS-B22Lo	−0.002 ± 0.006*	0.220 ± 0.020*	−0.312 ± 0.017	0.039 ± 0.009*
CS-B22sh × CS-B25	0.101 ± 0.027*	0.275 ± 0.021*	−0.152 ± 0.009*	−0.233 ± 0.018*
CS-B22sh × TM-1	0.068 ± 0.018*	0.568 ± 0.021*	0.212 ± 0.010*	0.051 ± 0.005*
CS-B22Lo × CS-B25	0.048 ± 0.013*	0.329 ± 0.029*	0.099 ± 0.008*	0.123 ± 0.010*
CS-B22Lo × TM-1	0.010 ± 0.004*	−0.081 ± 0.021*	−0.057 ± 0.011*	−0.099 ± 0.008*
CS-B25 × TM-1	0.033 ± 0.010*	0.628 ± 0.027*	0.026 ± 0.006*	0.049 ± 0.007*

*Significance from TM-1 at $P \le 0.05$

-0.312% (CS-B22sh × CS-B22Lo) to 0.228% (CS-B14sh × TM-1) for elongation and from -0.145 mc (CS-B14sh × CS-B17) to 0.140 mc (CS-B17 × CS-B22sh) for micronaire.

Results showed that some of the CS-B hybrids had positive heterosis effects in some fiber quality traits considering their parents.

Additive-by-additive interaction effects

Almost all (>98%) additive-by-additive effects on fiber traits by the CS-B lines and their crosses were significant (Table 6; Fig. 1). However, no CS-B line had a higher homozygous additive-by-additive effect on elongation percentage than TM-1. Among the lines, CS-B17 and CS-B25 had the most (-0.084 mic and -0.078 mic, respectively) beneficial (lowest values) homozygous additive-by-additive effects on micronaire. CS-B25 had the highest (0.200 mm, 0.164 and 3.805 kN m kg^{-1}) homozygous additive-by-additive effects on UHM, uniformity ratio and fiber strength.

The additive-by-additive interaction effects on UHM among the hybrids ranged from -0.122 mm (CS-B16 × CS-B22Lo) to 0.255 mm (CS-B14sh × CS-B25) (Table 6). Most of the hybrids of CS-B16, CS-B17, CS-B22sh and CS-B22Lo had higher additive-by-additive interaction effects for UHM than their respective CS-B parents carrying substituted chromosome or chromosome arm in homozygous condition. CS-B17 had negative epistatic effect on UHM when carrying the alien chromosome in homozygous form, but most (>80%) of its hybrids had positive epistatic effects when carrying the alien chromosome in heterozygous form. The heterotic performance of CS-B17 hybrids could have resulted from significant interaction between alleles of the substituted chromosome(s) in heterozygous condition. Additive-by-additive interaction effects for uniformity ratio were higher for most of the CS-B17 hybrids and lower for CS-B22sh hybrids

Table 6 Predicted additive × additive epistatic effects for five fiber traits

Entry	UHM (mm)	Uniformity Ratio (UR)	Fiber Strength (kN m kg^{-1})	Elongation (%)	Micronaire (Mic)
Homozygous effects					
CS-B14sh	0.185 ± 0.004*	0.085 ± 0.004*	2.550 ± 0.088	0.005 ± 0.001*	−0.027 ± 0.001*
CS-B16	−0.145 ± 0.003*	−0.038 ± 0.003*	−2.726 ± 0.098*	0.009 ± 0.001*	0.025 ± 0.001*
CS-B17	−0.196 ± 0.003*	−0.025 ± 0.003*	−0.520 ± 0.059*	0.025 ± 0.002	−0.084 ± 0.002*
CS-B22sh	−0.413 ± 0.005*	0.014 ± 0.003*	1.824 ± 0.059*	−0.015 ± 0.001*	0.077 ± 0.002*
CS-B22Lo	−0.195 ± 0.003*	−0.008 ± 0.002*	0.422 ± 0.069*	0.007 ± 0.001*	0.079 ± 0.002*
CS-B25	0.200 ± 0.004*	0.164 ± 0.006*	3.805 ± 0.108*	−0.011 ± 0.001*	−0.078 ± 0.002*
TM-1	0.104 ± 0.005	0.122 ± 0.006	2.236 ± 0.098	0.027 ± 0.002*	−0.039 ± 0.002*
Heterozygous effects					
CS-B14sh × CS-B16	0.103 ± 0.004	−0.037 ± 0.004*	−0.069 ± 0.098*	−0.005 ± 0.001*	−0.015 ± 0.002*
CS-B14sh × CS-B17	0.086 ± 0.004*	0.061 ± 0.005*	−0.461 ± 0.098*	0.011 ± 0.001*	0.038 ± 0.001*
CS-B14sh × CS-B22sh	0.023 ± 0.005*	−0.022 ± 0.003*	0.461 ± 0.118*	0.009 ± 0.001*	0.000 ± 0.002*
CS-B14sh × CS-B22Lo	−0.040 ± 0.004*	−0.024 ± 0.003*	−3.697 ± 0.147*	−0.016 ± 0.001*	0.039 ± 0.001*
CS-B14sh × CS-B25	0.255 ± 0.005*	0.188 ± 0.007*	3.501 ± 0.108*	0.012 ± 0.001*	−0.061 ± 0.002*
CS-B14sh × TM-1	−0.114 ± 0.006*	−0.047 ± 0.005*	0.510 ± 0.069*	−0.028 ± 0.002*	0.008 ± 0.001*
CS-B16 × CS-B17	−0.030 ± 0.003*	−0.013 ± 0.003*	2.628 ± 0.088*	0.036 ± 0.002*	−0.016 ± 0.001*
CS-B16 × CS-B22Sh	−0.012 ± 0.003*	−0.014 ± 0.003*	−1.991 ± 0.098*	0.004 ± 0.001*	0.043 ± 0.002*
CS-B16 × CS-B22Lo	−0.122 ± 0.005*	−0.078 ± 0.004*	3.560 ± 0.147*	0.002 ± 0.001*	0.014 ± 0.002*
CS-B16 × CS-B25	−0.003 ± 0.004*	−0.108 ± 0.006*	−1.579 ± 0.088*	−0.039 ± 0.002*	0.007 ± 0.002*
CS-B16 × TM-1	−0.031 ± 0.004*	−0.083 ± 0.005*	−2.932 ± 0.108*	−0.039 ± 0.003*	0.000 ± 0.002*
CS-B17 × CS-B22sh	0.168 ± 0.006*	−0.029 ± 0.003*	−1.667 ± 0.098*	−0.015 ± 0.001*	−0.070 ± 0.001*
CS-B17 × CS-B22Lo	0.005 ± 0.004*	0.067 ± 0.005*	−1.373 ± 0.069*	0.001 ± 0.002*	−0.022 ± 0.001*
CS-B17 × CS-B25	0.147 ± 0.004*	0.015 ± 0.002*	0.579 ± 0.069*	−0.006 ± 0.001*	−0.009 ± 0.002*
CS-B17 × TM-1	0.041 ± 0.003*	0.048 ± 0.003*	−0.539 ± 0.069*	0.047 ± 0.002*	0.014 ± 0.002*
CS-B22sh × CS-B22Lo	0.026 ± 0.005*	−0.023 ± 0.004*	0.696 ± 0.098*	0.038 ± 0.002*	0.009 ± 0.003*
CS-B22sh × CS-B25	0.026 ± 0.005*	−0.064 ± 0.004*	−2.334 ± 0.098*	−0.003 ± 0.001*	0.070 ± 0.002*
CS-B22sh × TM-1	0.031 ± 0.004*	−0.064 ± 0.005*	0.373 ± 0.108*	−0.058 ± 0.003*	−0.032 ± 0.002*
CS-B22Lo × CS-B25	−0.028 ± 0.004*	−0.066 ± 0.005*	−1.069 ± 0.088*	−0.009 ± 0.001*	−0.003 ± 0.001*
CS-B22Lo × TM-1	−0.095 ± 0.004*	0.024 ± 0.004*	0.765 ± 0.127*	0.037 ± 0.003*	0.048 ± 0.001*
CS-B25 × TM-1	0.026 ± 0.003*	−0.042 ± 0.005*	−2.961 ± 0.137*	−0.026 ± 0.002*	−0.015 ± 0.002*

*Significance from TM-1 at $P \leq 0.05$

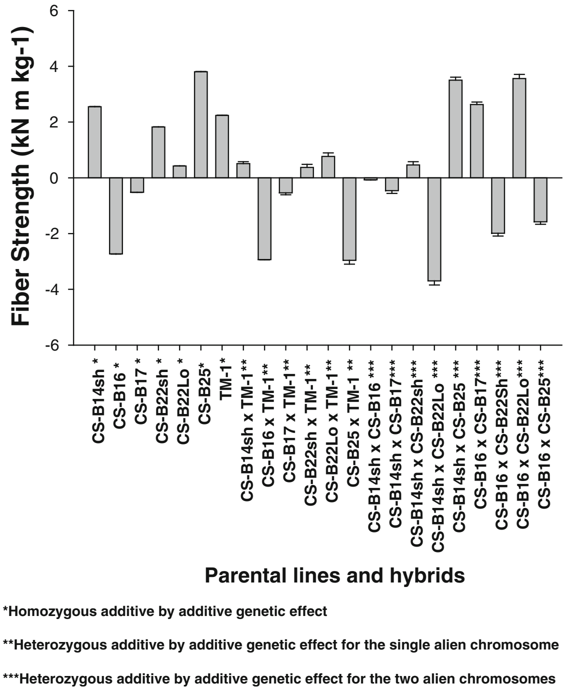

Fig. 1 Predicted additive-by-additive interaction effects on fiber strength of CS-B lines, TM-1 and the selected hybrids as representative samples of the CS-B lines. Note comparative results among the lines including single chromosome heterozygous versus two chromosomes heterozygous for the respective alien chromosome(s) and discern epistatic interaction effects for fiber strength on a chromosome-by-chromosome basis

than their respective CS-B parents, suggesting contrasting epistatic interaction between the alleles when carrying the alien chromosome in homozygous versus heterozygous condition for this trait. CS-B16 and CS-B17 had negative additive-by-additive interaction effects for fiber strength when carrying the alien chromosome in homozygous condition (−2.726, −0.520 kN m kg^{-1}, respectively) or heterozygous condition for the respective single alien chromosome (−2.932, −0.539 kN m kg^{-1}, respectively), however, CS-B16 × CS-B17 hybrid carrying both of the alien chromosomes in heterozygous condition had high positive (2.628 kN m kg^{-1}) additive-by additive interaction effect for fiber strength implying a clear example of epistatic interaction between the alleles in heterozygous condition of the two substituted chromosomes causing the increased genetic effect in fiber strength (Table 6; Fig. 1). CS-B14sh × CS-B22Lo and CS-B16 × CS-B22Lo had opposite additive-by-additive heterozygous interaction effects (−3.697 vs. 3.560 kN m kg^{-1}) for fiber strength suggesting the interaction effects of the alleles carried by the two alien chromosomes, chromosome 14sh and chromosome 16, had opposite genetic effects when heterozygous. Hybrids of CS-B22sh and CS-B22Lo had lower additive-by-additive interaction effects for micronaire than their parental CS-B lines, whereas hybrids of CS-B25 had higher additive-by-additive interaction effects for micronaire than the parental CS-B25 line, implying opposite genetic interaction effects for the alleles depending on the heterozygous or homozygous condition of the substituted chromosome(s).

Discussion

The near-isogenicity of BC_5S_n CS-B lines enables useful inferences. Each CS-B line is nearly isogenic with the recurrent parent, TM-1, for 25 chromosome pairs, and any two CS-B lines are nearly isogenic for 24 chromosome pairs. The reduction in “genetic noise” increases the detectability of net effects by the respective chromosome(s) and/or segment(s). While most CS-B line effects are reasonably ascribed to the substituted chromosome or segment on the assumption of near-isogenicity among the CS-B lines, the assumption expectedly only would be partially valid at the BC_5 or any other backcross generation. Thus, the CS-B effects are most likely due to the substituted chromosome or segment, but could be due to effects of residual chromatin elsewhere in the genome (Saha et al. 2010).

One of the major constraints on the improvement of Upland cotton fiber quality traits is that breeders must contend with the effects of several genetic bottlenecks in the origins of the commonly used germplasm. Wendel et al. (1989) reported that the first genetic bottleneck was a single interspecific hybridization event between an A- and D- genome diploid species during polyploidization that caused a very narrow gene pool in the origin of tetraploid cotton, estimated to have occurred just 1–2 million years ago, i.e., without significant time allowing extensive diversification. The second genetic constraint was the domestication of Upland cotton from a very small subset of wild genotypes. The third genetic bottleneck was that a few semi-domesticated progenies were brought into the USA and later dispersed to China, India, Australia, and other countries (Hutchinson et al. 1947), as the ancestors to the elite cultivated cotton gene pool.

Useful genetic diversity is the foundation for any crop improvement program. Increasing genetic diversity requires widening the germplasm base and one of the choices would be interspecific introgression from the primary gene pool. However, several biological and technical challenges are associated with interspecific introgression due to the incompatibility at the whole genome level between the species. Tapping the wild gene pool to introduce useful variation requires new and innovative approaches to discover the novel cryptic beneficial alleles in the unadapted species. Our previous reports showed that

CS-B lines could be used as a tool to introgress, unveil, and utilize the beneficial alleles for important fiber quality traits from *G. barbadense* (Saha et al. 2010; Saha et al. 2006; Jenkins et al. 2007). Our gross chromosomal assignments of CS-B line effects are in general congruent with the published QTL maps (Rong et al. 2004, 2007; Lacape et al. 2005; He et al. 2007).

We were able to identify systematically on a chromosome-by-chromosome basis the key elements of oligogenic epistasis related to fiber quality traits of interest. To test this, we followed the principles outlined by Wu et al. (2006) to extend the ADAA model to multiple generations (F_1, F_2 and F_3), so that we could dissect genetic effects into additive, dominance and interaction effects for each of the substituted chromosome or chromosome arm.

A study on the regional variety trials at Mississippi reported that the average of micronaire and fiber strength was 4.58 mic (range 3.63–5.14 mic) and 284.0 kN m kg^{-1} (range 246.94–286.36 kN m kg^{-1}), respectively, of the cotton varieties (Boykin 2006). The study also showed that the varieties had fiber length and uniformity ratio in the range of 25.4–30 mm and 80.7–84.0%, respectively, depending on the maturity. These CS-B lines were developed in the genetic background of TM-1, a line considered as the genetic standard for Upland cotton with insignificant breeding values for important traits. Accordingly, some of these significant genetic effects associated in the CS-B lines were numerically too small to have a major economic impact. Additional work should be conducted to detect genetic effects of CS-B lines in crosses with different elite cotton background, which could provide more valuable genetic information for a breeding program. Our previous reports on the top crosses of these lines with the elite USA cultivars suggested that some of these CS-B lines could be useful in improving important fiber traits in elite cotton lines (Jenkins et al. 2006, 2007). We demonstrated in this report that CS-B lines provide a means for chromosome specific identification and introgression of useful traits in Upland cotton.

Results showed that larger additive effects were present for CS-B14sh and CS-B25 regarding UHM, uniformity ratio and fiber strength compared to TM-1. CS-B17 had higher additive effects for elongation and lower additive effects for micronaire compared to TM-1. Additive effects are equivalent to the general combining ability and provide information for deciding desirable general combiner for improving traits of interest (Jenkins et al. 2009). Alleles that are broadly effective are clearly more important than alleles that provide desirable phenotype in only a limited number of genetic background (Osborn et al. 2007). This information could be used for incorporating beneficial alleles in improving inbred cotton lines (Jenkins et al. 2006, 2007).

The D subgenome from the non-fiber-producing wild ancestor played a major role in the genetic control of fiber growth and development in tetraploid cotton species (Rong et al. 2007; Lacape et al. 2005; Jiang et al. 1998). Jiang et al. (1998) reported that D-subgenome has some unique fitness advantages to mutations for important fiber traits and several paralogous loci for these favorable alleles in the A-subgenome might have been fixed during domestication of the tetraploid cotton species. They suggested that D-subgenome QTLs may partly explain the fact that domestication and breeding of tetraploid cottons has resulted in fiber with a higher quality than those achieved by parallel improvement of the A-genome diploid cottons which produce spinnable fibers. The merger of the A- and D-genomes in tetraploid cottons, with a different evolutionary history of these two subgenomes, may have offered unique avenues for phenotypic response to selection. In this study, we targeted several chromosomes from the *G. barbadense* D-subgenome to analyze their individual genetic effect on fiber quality traits using the selected six CS-B lines in the half diallel mating scheme. Results showed that the average distribution of QTL/chromosome (four dominance genetic effects except fiber strength, one additive genetic effect and four additive-by-additive interaction effects for all of the traits/chromosome) was almost same for all of the traits among the substituted chromosomes suggesting similar selection pressure across the D genome chromosome during evolution of tetraploid cottons provided each effect is considered as a single genetic event. Our previous study showed that the average distribution of the QTL was almost the same in the A (8.2 QTL/chromosome) and D (8.3 QTL/chromosome) genome, respectively, using CS-B lines and CS-B × TM-1 hybrids (Saha et al. 2006).

The partial diallel among CS-B lines and TM-1 used here enabled comparisons across chromosomes and across various genetic states, including various alien chromosome pairs in homozygous state (e.g., CS-B lines), single alien chromosomes (e.g., CS-B × TM-1 F_1 hybrids), pair-wise combinations of two single alien chromosomes (CS-B × CS-B F_1 hybrids), their inbred reproductive products (F_2 and F_3), after recombination, segregation and inheritance, all in a common, quasi-isogenic background. The approach provides unique opportunities to discover epistatic interaction effects through comparisons of homozygous and heterozygous conditions on a chromosome-by-chromosome basis for individual fiber traits. Assuming uniform genetic background of the CS-B lines, the comparative analysis of the double-heterozygote combinations (CS-B × CS-B F_1) versus their respective single heterozygotes (Tables 5, 6; Fig. 1) revealed that epistatic effects between the genes in the chromosomes strongly affected most of the fiber quality traits.

These analyses demonstrated that significant dominance and additive-by- additive interaction effects were associated with the substituted chromosome or chromosome arm for almost all of the fiber traits (Tables 5, 6; Fig. 1). CS-B14sh and CS-B17 had negative additive-by-additive epistatic effects for micronaire when the substituted chromosomes were in homozygous condition; however, the hybrid of CS-B14sh × CS-B17, carrying the same substituted chromosome in heterozygous condition, had positive additive-by-additive epistatic effects for micronaire implying significant epistatic interaction made a substantial contribution in heterotic performance for micronaire in the hybrid (Fig. 1). CS-B16 and CS-B17 both had negative additive-by-additive interaction effects in fiber strength when the substituted chromosome was homozygous or heterozygous for the single alien chromosome. However, the hybrid between CS-B16 and CS-B17, heterozygous for both of the substituted chromosomes, had higher positive additive-by-additive interaction effects for fiber strength than their parents, TM-1 and hybrids for the single substituted chromosome, suggesting the interaction effects of heterozygous loci of the two substituted chromosomes caused the increased additive-by-additive interaction effect for fiber strength in the CS-B16 × CS-B17 hybrid (Fig. 1). Results suggested that additional genetic resolution is desirable to understand the role of epistasis controlling complex fiber traits. Bowman and Gutierrez (2003) reported that 25% of Upland cultivars with improved fiber strength had unique gene combinations that were not expected based on the parent performance and could be attributed to transgressive segregation. He et al. (2008) reported significant digenic interaction effects for fiber strength in an interspecific cross of *G. hirsutum* and *G. barbadense*. In conventional wide crosses, the potential beneficial effects of alien alleles are usually overwhelmed by negative epistatic effects associated with linkage with undesirable genes. Paterson et al. (2004) reported that individual QTLs in combination with different unlinked introgressed alleles affect a phenotype to different degrees in cotton. They observed that in some cases, the same QTL in cotton was found to be statistically significant but with opposite effects in different genetic backgrounds (Paterson et al. 2004).

Jenkins et al. (2007) documented that different cultivars had different alleles of QTLs on different chromosomes and hybrids of the same CS-B line had different genetic effects for a trait with different cultivars. Accordingly, they suggested that CS-B lines could be used as a tester stocks to reveal different sources of beneficial alleles, thereby, providing a tool to combine beneficial alleles for improving a fiber quality trait.

Our results from this study and previous reports showed that most of the substituted chromosomes are associated with both beneficial and detrimental alleles for most of the important fiber traits (Saha et al. 2006, 2010; Jenkins et al. 2006, 2007). A number of previous reports on interrelationships between agronomic traits and fiber quality suggested lint yield was negatively correlated with fiber strength while positively correlated with lint percentage, micronaire and elongation (Zeng and Meredith 2009; Percy et al. 2006; Smith and Coyle 1997; McCarty et al. 1996; Meredith 1984). Many breeders avoid the exotic sources of germplasm pool, including *G. barbadense*, because they typically result in reduced yield and poor agronomic qualities (Rong et al. 2007; Lacape et al. 2005; Abdurakhmonov et al. 2008, 2009; Ulloa et al. 2002; Zheng et al. 2009). The need to improve fiber quality while maintaining improved agronomic properties including yield requires creative approaches and better understanding of the genetics of fiber traits. Our previous report from the same experiment showed that many of these CS-B lines carried cryptic beneficial alleles that have potential to improve agronomic traits including seed and lint yield (Saha et al. 2010). The collective results from this report and the previous study suggests that some of these CS-B lines and their hybrids carried alleles with the potential to simultaneously improve both agronomic and fiber quality in Upland cotton (Saha et al. 2006, 2010; Jenkins et al. 2006, 2007). This is contrary to the conventional assumption that *G. barbadense* alleles could only be useful to improve fiber quality traits.

The results highlight the paramount importance of epistasis in fiber quality traits and the value of CS-B lines in determining genetic contributions to these traits. Our findings indicate that additional genetic resolution is needed for the targeted exploitation of exotic germplasm to improve fiber quality in cotton breeding program.

Acknowledgments We thank Ms. Lillie Hendrix for helping in field research. We acknowledge partial support from the following sources: Cotton Inc., Texas State Support Committee, and Texas Dept. Agriculture Food & Fiber Research Grant Program. Joint publication of USDA/ARS, Mississippi Agricultural and Forestry Experiment Station, South Dakota State University, and Texas A & M University. Approved for publication as Journal Article No. J-11897 of the Mississippi Agricultural and Forestry Experiment Station.

References

Adams G (2006) Cotton's global market. In: Proceedings of Beltwide Cotton Conference, pp 2347–2350

Bowman DT, Gutierrez OA (2003) Sources of fiber strength in the U.S. Upland cotton from 1980 to 2000. J Cot Sci 7:164–169

Bowman DT, May OL, Calhoun DS (1996) Genetic base of upland cotton cultivars released between 1970 and 1990. Crop Sci 36:577–581

Boykin JC (2006) Gross monetary returns for conventionally processed cotton cultivars from Mississippi. J Cot Sci 10:284–289

Bradow JM, Davidonis GH (2000) Quantification of fiber quality and the cotton production–processing interface: a physiologist perspective. J Cot Sci 4:34–64

Gingle AR, Yang H, Chee PW, May OL, Rong J, Bowman DT, Lubbers EL, Day JL, Paterson AH (2006) An integrated web resource for cotton. Crop Sci 46:1998–2007

He DH, Lin ZX, Zhang XL, Nie YC, Guo XP, Zhang YX, Wu L (2007) QTL mapping for economic traits based on a dense genetic map of cotton with PCR-based markers using the interspecific cross of *Gossypium hirsutum* × *Gossypium barbadense*. Euphytica 153:181–197

He DH, Lin ZX, Zhang XL, Zhang YX, Li W, Nie YC, Guo XP (2008) Dissection of genetic variance in advanced generations from an interspecific cross of *Gossypium hirsut*um and *G. barbadense*. Plant Br 127:286–294

Hutchinson JB, Silow RA, Stephens SG (1947) The evolution of *Gossypium* and the differentiation of the cultivated cottons. Oxford University Press, London

Jenkins JN, Wu J, McCarty JC, Saha S, Gutierrez OA, Hayes R, Stelly DM (2006) Genetic effects of thirteen *Gossypium barbadense* L. chromosome substitution lines in topcrosses with Upland cotton cultivars: I. Yield and yield components. Crop Sci 46:1169–1178

Jenkins JN, Wu J, McCarty JC, Saha S, Gutierrez OA, Hayes R, Stelly DM (2007) Genetic effects of thirteen *Gossypium barbadense* L. chromosome substitution lines in topcrosses with Upland Cotton cultivars: II fiber quality traits. Crop Sci 47:561–570

Jiang CX, Wright RJ, El-Zik K, Paterson AH (1998) Polyploid formation created unique avenues for response to selection in *Gossypium* (cotton). Proc Natl Acad Sci USA 95:4419–4424

Jiang C, Wright RJ, Woo SS, DelMonte TA, Paterson AH (2000) QTL analysis of leaf morphology in tetraploid *Gossypium* (cotton). Theor Appl Genet 100:409–418

Kohel RJ, Richmond TR, Lewis CF (1970) Texas Marker-1. Description of a genetic standard for *Gossypium hirsutum* L. Crop Sci 10:670–671

Lacape JM, Nguyen TB, Courtois B, Belot JL, Giband M, Gourlot JP, Gawryziak G, Roques S, Hau B (2005) QTL analysis of cotton fiber quality using multiple *Gossypium hirsutum* × *Gossypium barbadense* backcross generations. Crop Sci 45:123–140

McCarty JC, Jenkins JN (2005) Registration of 14 primitive derived cotton germplasm lines with improved fiber strength. Crop Sci 45:2668–2669

McCarty JC Jr, Jenkins JN, Tang B, Watson CE (1996) Genetic analysis of primitive cotton germplasm accession. Crop Sci 36:581–585

McCarty JC Jr, Wu J, Jenkins JN (2007) Use of primitive derived cotton accessions from agronomic and fiber traits improvement: variance components and genetic effects. Crop Sci 47:100–110

McKenzie WH (1970) Fertility relationships among interspecific hybrid progenies of *Gossypium*. Crop Sci 10:571–574

Meredith WR (1984) Quantitative genetics. In: Kohel RJ, Lewis CF (eds) Cotton. ASA-CSSA-SSSA, Madison, pp 131–150

Miller RG (1974) The jackknife: a review. Biometrika 61:1–15

Osborn CT, Kramer C, Graham E, Braun CJ (2007) Insight and inoovations from wide crosses: examples from Canola and Tomato. Crop Sci 47(S3):S228–S237

Paterson AH, Saranga Y, Menz M, Jiang CX, Wright RJ (2003) QTL analysis of genotype X environment interactions affecting cotton fiber quality. Theor Appl Genet 106:384–396

Paterson AH, Boman RK, Brown SM, Chee PW, Gannaway JR, Gingle AR, May OL, Smith CW (2004) Reducing the genetic vulnerability in cotton. Crop Sci 44:1900–1901

Patterson DD (1939) Statistical technique in agricultural research. McGraw Hill, New York

Percy RG, Cantrell RG, Zhang J (2006) Genetic variation for agronomic and fiber properties in an introgressed recombinant inbred population of cotton. Crop Sci 46:1311–1317

Reinisch AJ, Dong J, Brubaker CL, Stelly DM, Wendel JF, Paterson AH (1994) A detailed RFLP map of cotton, *Gossypium hirsutum* × *Gossypium barbadense*: chromosome organization and evolution in a disomic polyploid genome. Genetics 138:829–847

Rong J, Abbey C, Bowers JE, Brubaker CL, Chang C, Chee PW, Delmonte TA, Ding X, Garza JJ, Marler BS, Park C, Pierce GJ, Rainey KM, Rastogi VK, Schulze SR, Trolinder NL, Wendel JF, Wilkins TA, Williams-Coplin TD, Wing RA, Wright RJ, Zhao X, Zhu L, Paterson AH (2004) A 3347-locus genetic recombination map of sequence-tagged sites reveals features of genome organization, transmission and evolution of cotton (*Gossypium*). Genetics 166:389–417

Rong J, Feltus FA, Waghmare VN, Pierce GJ, Chee PW, Draye X, Saranga Y, Wright RJ, Wilkins TA, May OL, Smith CW, Gunnway JR, Wendel JF, Paterson AH (2007) Meta-analysis of polyploidy cotton QTLs shows unequal contributions of subgenomes to a complex network of genes clusters implicated in lint fiber development. Genetics 176:2577–2588

Saha S, Wu J, Jenkins JN, McCarty JC Jr, Gutierrez OA, Stelly DM (2004) Effect of chromosome substitutions from *Gossypium barbadense* L. 3-79 into *G. hirsutum* L. TM-1 on agronomic and fiber traits. J Cot Sci 8:162–169

Saha S, Jenkins JN, Wu J, McCarty JC, Gutierrez OA, Percy RG, Cantrell RG, Stelly DM (2006) Effects of chromosome-specific introgression in Upland cotton on fiber and agronomic traits. Genetics 172:1927–1938

Saha S, Jenkins JN, Wu J, McCarty JC, Stelly DM (2008a) Genetic analysis of agronomic and fiber traits using four interspecific chromosome substitution lines in cotton. Plant Br 127:612–618

Saha S, Wu J, Jenkins JN, McCarty JC, Stelly DM (2008b) Chromosome substitution lines (CS-B) revealed the presence of cryptic beneficial alleles in *G. barbadense* with potential to increase lint and seedcotton yield in Upland cotton. In: Proceedings of Belt Cotton Conference, p 831

Saha S, Wu J, Jenkins JN, McCarty JC, Hayes R, Stelly DM (2010) Genetic dissection of chromosome substitution lines discovered novel alleles in *Gossypium barbadense* L. with potential for improving agronomic traits including yield. Theor Appl Genet 120:193–1205

SAS Institute (2001) SAS User's Guide, Version 8. SAS Institute, Cary

Smith CW, Coyle GG (1997) Association of fiber quality parameters and within boll yield components in Upland cotton. Crop Sci 37:1775–1779

Stelly DM, Saha S, Raska DA, Jenkins JN, McCarty JC, Gutierrez OA (2005) Registration of 17 Upland (*Gossypium hirsutum*) germplasm lines disomic for different *G. barbadense* chromosome or arm substitutions. Crop Sci 45:2663–2665

Stephens SG (1949) The cytogenetics of speciation in *Gossypium.* I. Selective elimination of the donor parent genotype in interspecific backcrosses. Genetics 34:627–637

Ulloa M, Meredith WR Jr, Shappley ZW, Kahler AL (2002) RFLP genetic linkage maps from four $F_{2.3}$ populations and a joinmap of *Gossypium hirsutum* L. Theor Appl Genet 104:200–208

USDA Economic Research Service (2009) Cotton: market outlook. http://www.ers.usda.gov/briefing/Cotton/2005baseline.htm

USDA-NASS (2002) 2002 Census of agriculture. USDA-National Agricultural Statistics Service, Washington. http://www.nass.usda.gov/Census_of_Agriculture/index.asp

Wendel JF, Olson PD, Stewart JM (1989) Genetic diversity, introgression, and independent domestication of Old World cultivated cottons. Am J Bot 76:1795–1806

Wu J, Jenkins JN, McCarty JC, Wu D (2006) Variance component estimation using the ADAA model when genotypes vary across environments. Crop Sci 46:174–179

Wu J, Jenkins JN, McCarty JC, Saha S, Percy R (2008) Genetic association of lint yield with its components in cotton chromosome substitution lines. Euphytica 164:199–207

Zeng L, Meredith WR Jr (2009) Association among lint yield components and fiber properties in an introgressed population of cotton. Crop Sci 49:1647–1654

Zhu J (1989) Estimation of genetic variance components in the general mixed model. Dissertation, North Carolina State University

Zhu J (1993) Methods of predicting genotype value and heterosis for offspring of hybrids (Chinese). J Biomath 8(1):32–44