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ORIGINAL PAPER

Genetic dissection of chromosome substitution lines of cotton to discover novel *Gossypium barbadense* L. alleles for improvement of agronomic traits

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Abstract We recently released a set of 17 chromosome substitution (CS-B) lines ($2n = 52$) that contain *Gossypium barbadense* L. doubled-haploid line '3-79' germplasm systematically introgressed into the Upland inbred 'TM-1' of *G. hirsutum* (L.). TM-1 yields much more than 3-79, but cotton from the latter has superior fiber properties. To explore the use of these quasi-isogenic lines in studying gene interactions, we created a partial diallel among six CS-B lines and the inbred TM-1, and characterized their descendents for lint percentage, boll weight, seedcotton yield and lint yield across four environments. Phenotypic data on the traits were analyzed according to the ADAA genetic model to detect significant additive, dominance, and additive-by-additive epistasis effects at the chromosome and chromosome-by-chromosome levels of CS-B lines. For example, line 3-79 had the lowest boll weight, seedcotton yield and lint yield, but CS-B22Lo homozygous dominance genetic effects on seedcotton and lint yield were nearly four times those of TM-1, and its hybrids with TM-1 had the highest additive-by-additive epistatic effects on seedcotton and lint yield. CS-B14sh, 17, 22Lo and 25 produced positive homozygous dominance effects on lint yield, whereas doubly heterozygous combinations of CS-B14sh with CS-B17, 22Lo and 25 produced negative dominance effects, suggesting that epistatic effects between genes in these chromosomes strongly affect lint yield. The results underscore the opportunities to systematically identify genomic regions harboring genes that impart agronomically significant effects via epistatic interactions. The chromosome-by-chromosome approach significantly complements other strategies to detect and quantify epistatic interaction effects, and the quasi-isogenic nature of families and lines from CS-B intermatings will facilitate high-resolution localization, development of markers for selection and map-assisted identification of genes involved in strong epistatic effects.

Introduction

Cotton is the primary source of non-synthetic textile fiber, as well as an important source of food, feed, fuel and other products. With a raw product value of ~\$6 billion year^{-1}, cotton has been an important element of the US economy and balance of trade (Gingle et al. 2006). It is a major crop in 13 states and grown in 17 states in USA on about 5 million hectares, more than all crops except maize, wheat or soybean, with a return of about \$6.5 billion annually for

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its fiber and seed byproducts (USDA-NASS 2002; Gingle et al. 2006). Worldwide, more than 100 million family units are involved in cotton production, and the value is estimated at $24 billion. A committee of public and private scientists organized by the National Cotton Council of USA suggested that US cotton yields peaked in 1992 and reached an alarming rate of declining of about 16.8 kg ha^{-1} $year^{-1}$ (3.3% annual rate) and year to year variations in yield were almost four times higher in the period from 1980 to 1998 than in 1960 to 1979 (Gingle et al. 2006).

Genetic diversity in Upland cotton cultivars in the USA is low (Bowman et al. 1996). Upland cotton breeding relies primarily on crossing a few elite lines of closely related genotypes with high yield and superior fiber quality as well as reselection within existing cultivars (Van Esbroeck and Bowman 1998; Gingle et al. 2006). Commercial breeding has been devoted largely to marker-assisted backcrossing to expedite development of transgenic lines that combine transgenic insect resistance and/or herbicides tolerance with desirable attributes of previously developed cultivars. Additional wide-cross introgression and interspecific breeding are needed to reduce genetic vulnerability of the crop, and to infuse more genetic diversity into adapted backgrounds.

Exotic species have contributed beneficial alleles for improving valuable traits in many plant species (Tanksley and McCough 1997). In many cases, “cryptic” and unexpectedly useful genetic variations from wild species have been used to improve tomato, canola and other crops (Osborn et al. 2008). Wild and unadapted species have been utilized in cotton mostly for the improvement of simply inherited traits such as disease and pest resistance, drought tolerance and cytoplasmic male sterility (Mergeai 2003; Robinson and Percival 1997). A number of primitive accessions of *Gossypium hirsutum* have been bred into improved germplasm, providing diversity that is useful to commercial cotton breeders for genetic improvement of agronomic and fiber traits (McCarty and Jenkins 2005, McCarty et al. 2007). Although it is widely recognized that exotic cotton germplasm contains potentially valuable genes, the exotic gene pools from species other than *G. hirsutum* remain largely untapped and underutilized. This may be due partly to the paucity of information about the beneficial alleles in these related species, and the difficulty, time and cost of interspecific introgression, which increase greatly with genetic distance between donor and recipient genomes.

Pima and Sea Island cottons (*Gossypium barbadense*) are well known for their exceptional fiber length, strength and fineness. Their fiber offers superior spinning and manufacturing performance, better textile products, and thus normally commands a 30–50% price advantage over fiber from high-yielding Upland cottons (*G. hirsutum*). Pima and Sea Island cottons require long growing seasons to produce profitable yield of high quality fiber and are thus primarily grown in Arizona, California, and New Mexico in USA. However, cotton farmers grow early maturing Upland cotton cultivars over 90% of the US cotton growing area because of their high yield, good agronomic qualities and wide adaptation.

Breeders have long aspired to combine the best attributes of *G. hirsutum* and *G. barbadense* (Lacape et al. 2005; He et al. 2008), but conventional methods of interspecific introgression using *G. barbadense* have fallen far short of being fully successful. This is predominantly due to complex interactions among traits, as well as numerous genomic incompatibilities between these two species. Indeed, interspecific crosses and introgression into cotton entail difficulties such as infertility, cytological abnormalities and distorted segregation (Reinisch et al. 1994; Ulloa et al. 2005). Alien gene retention and genetic recombination are often limited to non-random products from the conventional methods of interspecific introgression. Rhyne (1958) reported that the actual number of recombinants obtained were significantly fewer than the expected number in an interspecific backcross program of Upland cotton and Jiang et al. (2000) showed limited genetic transmission in advanced generation of the interspecific hybrids. A genetically distinct alternative to conventional introgression is to create interspecific chromosome substitution lines.

We developed and recently released a set of 17 disomic alien chromosome substitution (CS-B) lines through hypoaneuploid-based backcross chromosome substitution lines in a near-isogenic genetic background of TM-1 (Stelly et al. 2005). In each CS-B line, a pair of chromosomes (or chromosome arms) of *G. hirsutum* inbred TM-1 was replaced by the respective pair from *G. barbadense* doubled-haploid line 3-79. These disomic substitution lines are nearly isogenic to the common parent TM-1 for 25 chromosome pairs, as well as to each other, for 24 chromosome pairs. Given $n = 26$, each idealized CS-B chromosome substitution replaces about 4% of the *G. hirsutum* genome with a *G. barbadense* homoeolog and thereby reduces genetic “noise” from 96% of the genome.

Epistatic effects tend to be of paramount importance in wide crosses, so the CS-B lines presented an novel opportunity for studying potent epistatic interaction effects on a chromosome-by-chromosome basis. Previous studies based on the introgression of an individual or a pair of alien chromosome or single heterozygous combination for a specific substituted chromosome or chromosome arm demonstrated that the CS-B lines are unique research resources for chromosomally localizing genes that significantly affect important agronomic and fiber traits, and a powerful means of interspecific introgression for germplasm improvement (Saha et al. 2006; Jenkins et al. 2006, 2007). This study provided a unique opportunity to compare a double heterozygous combination versus a single heterozygous combination for any two specific substituted chromosome or chromosome arm and revealed chromosome based genetic maps showing non-additive genetic effects played a major role for most of the traits including seedcotton and lint yields. We explored this novel application by creating a partial diallel of CS-B lines and the recurrent parent TM-1. The specific objective was to detect the chromosomal effects, especially interaction effects, on four agronomic traits including lint percentage (LP), boll weight (BW), seedcotton yield (YLD) and lint yield (LY).

Materials and methods

Materials and experiment

Each CS-B line has a pair of chromosomes (Fig. 1) or arm segments of *G. hirsutum* inbred TM-1 replaced by the respective pair from *G. barbadense* doubled-haploid 3-79. CS-B designations for substitutions of terminal short-arm segments and long-arm segments bear "sh" and "Lo" suffixes, e.g., CS-B14sh, whereas whole-chromosome substitutions bear no suffice, e.g., CS-B16. A partial diallel cross among six CS-B lines (CS-B14sh, CS-B16, CS-B17, CS-B22sh, CS-B22Lo and CS-B25) and TM-1 (the recurrent parent) was made in the summer of 2003 at Mississippi State, USA. These CS-B lines were selected based on our previous reports on the potential to improve fiber and agronomic traits (Saha et al. 2006; Jenkins et al. 2006, 2007). The F_1 seeds were sent to Mexico in the fall of 2003 for F_2 seed development. The seven parents, including TM-1, were also sent there to make F_1 seeds. In 2004, 21 F_1 and F_2 hybrids and the parents, including 3-79 (the donor line), were grown in two locations (designated as environments 1 and 2) at Mississippi State, MS. Bulk samples from open bolls of F_2 plants in 2004 were used as F_3 seeds in 2005. In 2005, 21 F_2 hybrids and F_3 hybrids and the parents were grown in two locations (designated as environments 3 and 4). The hybrids and parental lines were planted in a randomized complete block design with four replications at two locations in 2004 and 2005.

Soil types of the two locations were very different, and included a Leeper silty clay loam (Fine, smectitic, nonacid, thermic Vertic Epiaquept, Environment 1 and 3) and Marietta loam (Fine-loamy, siliceous, active, fluvaquentic Eutrudepts, Environment 2 and 4). Our previous studies on the same farm revealed that the soil and environmental conditions of these two locations were very diverse with different potential for yield and other agronomic traits in cotton (Saha et al. 2006; Jenkins et al. 2007). Standard field practices were followed during the growing season for all environments. All experiments were conducted on the Plant Science Research Center, Mississippi State, MS (33.4°N 88.4°W).

Prior to machine harvest, 25-boll samples were "hand picked" for all plots in all four environments. Samples were used to determine boll weight (BW, g) and ginned to determine the lint percentage (LP, %). The seedcotton yield (YLD, kg/ha) was calculated from the plot weight obtained by a cotton picker and the lint yield (LY, kg/ha) was determined by multiplying seedcotton yield by mean lint percentage for each entry in each environment.

Genetic models and statistical methods

The genetic model including additive, dominance, additive × additive effects and their corresponding G × E interaction effects (ADAA model) was employed for the data analysis (Cockerham 1980; Zhu 1994; Wu et al. 2006a).

The mixed linear models were as follows:

$$\begin{aligned}\text{Parents}: y_{hiik(P)} &= \mu + E_h + 2A_i + D_{ii} + 4\mathrm{AA}_{ii} + 2\mathrm{AE}_{hi}\\ &\quad + \mathrm{DE}_{hii} + 4\mathrm{AAE}_{hii} + B_{k(h)} + e_{hiik} \qquad (1)\end{aligned}$$

$$\begin{aligned}\mathrm{F}_1: y_{hijk(F_1)} &= \mu + E_h + (A_i + A_j) + D_{ij}\\ &\quad + (\mathrm{AA}_{ii} + \mathrm{AA}_{jj} + 2\mathrm{AA}_{ij}) + (\mathrm{AE}_{hi} + \mathrm{AE}_{hj})\\ &\quad + \mathrm{DE}_{hii} + (\mathrm{AAE}_{hii} + \mathrm{AAE}_{hjj} + 2\mathrm{AAE}_{hij})\\ &\quad + B_{k(h)} + e_{hijk} \qquad (2)\end{aligned}$$

$$\begin{aligned}\mathrm{F}_2: y_{hijk(F_2)} &= \mu + E_h + (A_i + A_j) + \left(\frac{1}{4}D_{ii} + \frac{1}{4}D_{jj} + \frac{1}{2}D_{ij}\right)\\ &\quad + (\mathrm{AA}_{ii} + \mathrm{AA}_{jj} + 2\mathrm{AA}_{ij}) + (\mathrm{AE}_{hi} + \mathrm{AE}_{hj})\\ &\quad + \left(\frac{1}{4}\mathrm{DE}_{hii} + \frac{1}{4}\mathrm{DE}_{hjj} + \frac{1}{2}\mathrm{DE}_{hij}\right)\\ &\quad + (\mathrm{AAE}_{hii} + \mathrm{AAE}_{hjj}\\ &\quad + 2\mathrm{AAE}_{hij}) + B_{k(h)} + e_{hijk} \qquad (3)\end{aligned}$$

$$\begin{aligned}\mathrm{F}_3: y_{hijk(F_3)} &= \mu + E_h + (A_i + A_j) + \left(\frac{3}{8}D_{ii} + \frac{3}{8}D_{jj} + \frac{1}{4}D_{ij}\right)\\ &\quad + (\mathrm{AA}_{ii} + \mathrm{AA}_{jj} + 2\mathrm{AA}_{ij}) + (\mathrm{AE}_{hi} + \mathrm{AE}_{hj})\\ &\quad + \left(\frac{3}{8}\mathrm{DE}_{hii} + \frac{3}{8}\mathrm{DE}_{hjj} + \frac{1}{4}\mathrm{DE}_{hij}\right) + (\mathrm{AAE}_{hii}\\ &\quad + \mathrm{AAE}_{hjj} + 2\mathrm{AAE}_{hij}) + B_{k(h)} + e_{hijk} \qquad (4)\end{aligned}$$

where μ is the population mean, a fixed effect; E_h is the environment effect, either random or fixed (fixed in this study); A_i (or A_j) is additive effect from parent i (or j); D_{ii}, D_{jj} or D_{ij} is the dominance effect; AA_{ii}, AA_{jj}, or AA_{ij} is the additive × additive (AA) epistatic effect; AE_{hi} (or AE_{hj}) is additive by environment interaction effect; DE_{hii}, DE_{hjj} or DE_{hij} is the dominance by environment interaction effect; AAE_{hii}, AAE_{hjj}, or AAE_{hij} is the AA × environment

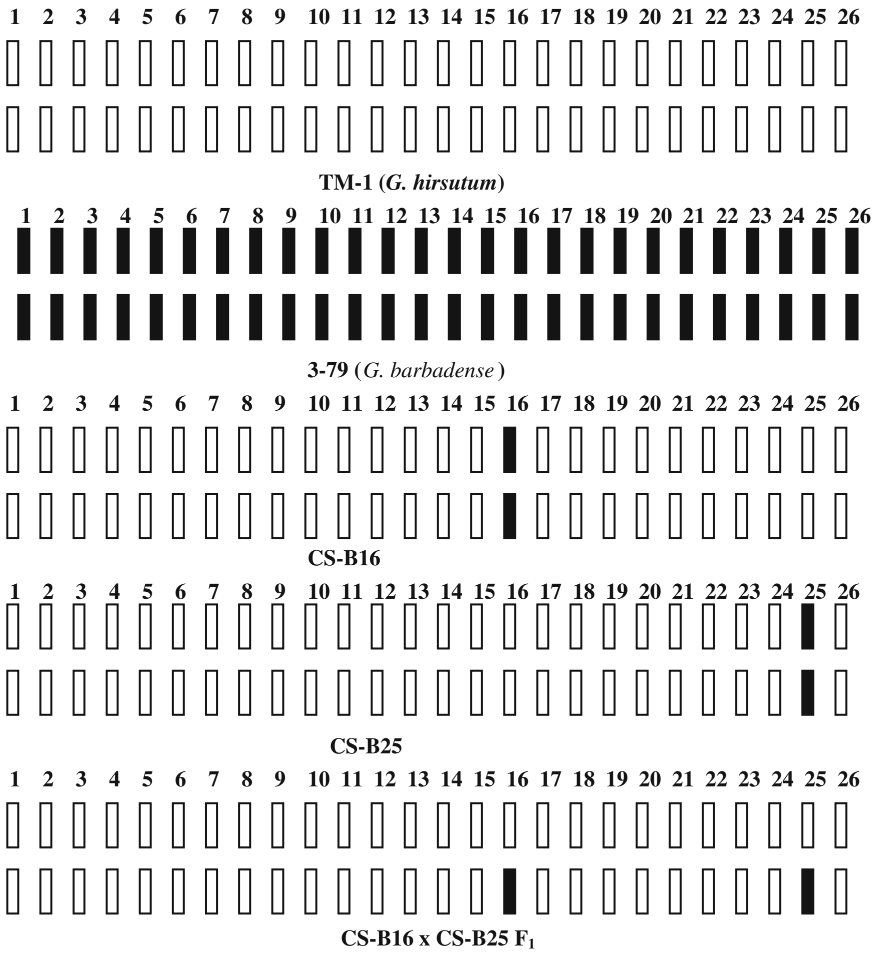

Fig. 1 Diagrammatic representation of CS-B lines and their crosses showing the substituted chromosome in *black color* from *G. barbadense* (3-79) in *G. hirsutum* genetic background. A comparative analysis of such unique lines provided opportunity to discern the chromosomal effects on agronomic traits

interaction effect; $B_{k(h)}$ is the block effect; e_{hijk} is the random error.

Variance components were estimated by MINQUE (1) in which all prior values were set as 1.0 (Zhu 1989). Random effects were predicted by the adjusted unbiased prediction (AUP) method (Zhu 1993). The phenotypic variance was partitioned into the variance components for additive ($V_{\mathrm{A}} = 2\sigma^2_{\mathrm{A}}$), dominance ($V_{\mathrm{D}} = \sigma^2_{\mathrm{D}}$), additive × additive ($V_{\mathrm{AA}} = 4\sigma^2_{\mathrm{AA}}$) additive × environment ($V_{\mathrm{AE}} = 2\sigma^2_{\mathrm{AE}}$), dominance by environment ($V_{\mathrm{DE}} = \sigma^2_{\mathrm{DE}}$), AA × environment ($V_{\mathrm{AAE}} = 4\sigma^2_{\mathrm{AAE}}$), residual ($V_{\mathrm{e}} = \sigma^2_{\mathrm{e}}$). The proportions of variance components to the phenotypic variance for each trait were calculated as well. Re-sampling (jackknife method) was applied to calculate the standard error (SE) for each parameter by removal of one replicate within each environment (Miller 1974). An approximate *t* test ($df = 15$) was used to detect the significance of each parameter. All data analyses were conducted by a program in C++ by the authors. This program is available upon request from Dr. Jixiang Wu (Jixiang.Wu@sdstate.edu).

The genetic effects were estimated based on the deviations from the respective population grand mean μ, not from TM-1. A two-tailed *t* test was used to detect the genetic effects significance from zero. Additive or homozygous dominance effects of the entire genome of the CS-B parent (25 chromosomes from TM-1 and one chromosome or chromosome arm from 3-79) were measured for each of the CS-B parents. In addition, a significant difference in additive or homozygous dominance effects between a specific CS-B line and TM-1 was considered to be a significant additive or homozygous dominance chromosome effect attributable to the specific substituted chromosome or chromosome arm from 3-79. Other significant differences among the lines were also attributed to the substituted chromosomes/arm segments, on the assumption that all other chromosomes were identical to TM-1.

As for any backcross-derived germplasm, the assumption of isogenicity would be only partially valid. Among CS-B lines, quasi-isogenicity would be expectedly for two reasons. First, the *G. hirsutum* hypaneuploids used as recurrent parents to create the CS-B line were themselves rendered quasi-isogenic by multiple backcrosses with TM-1, i.e., prior to using them as recurrent parents to create CS-B lines, so segments of non-TM-1 *G. hirsutum* genomes could remain in some of the *G. hirsutum* hypaneuploid recurrent parents. Secondly, each CS-B line was recovered after five or more backcrosses to the respective *G. hirsutum* hypoaneuploid, so residual *G. barbadense* L. segments could remain in other 25 chromosome pairs (Saha et al. 2006). Thus, CS-B line effects are likely due to the specific substituted chromosome, but could be due to remnant chromatin elsewhere in the CS-B line genome.

Results

Most of our results are concordant with our previous studies based on similar agronomic methods and experimental practices (Saha et al. 2006; Jenkins et al. 2006, 2007; Wu et al. 2006a) using CS-B lines. Differences among the lines were attributed to the contribution of the alien species substituted chromosome according to the simplifying assumption of isogenicity of non-substituted chromosomes.

Mean comparisons of the intercross of CS-B and parental lines

Line 3-79 had the lowest boll weight, seedcotton yield and lint yield among all parents (Table 1). TM-1 and 3-79, the ultimate recurrent and donor parents of the CS-B lines, differed significantly in the majority of agronomic traits as expected. TM-1 had 1.8% lower absolute lint percent, 53% higher boll weight, 131% more seedcotton and 120% more lint yield compared to 3-79 line. However, CS-B16 and CS-B22sh and CS-B22Lo had higher lint percentage than both donor and recurrent parents. The overall mean of lint percentage of the hybrids of CS-B lines ranged 34.2–36.7 (Table 2). The average boll weight, seedcotton yield and lint yield of the hybrids was smaller than TM-1, the recurrent parent. The mean boll weight of all CS-B lines ranged from 4.09 to 5.08 g (Table 1). The boll weight of the CS-B hybrids ranged from 4.53 to 5.56 g (Table 2).

Lint yield in cotton is determined by two major components: (1) the number of seeds and the weight of lint fiber produced on the seeds. The mean seedcotton yield was highest (1,917 kg ha^{-1}) in TM-1, relative to all of the parental CS-B lines, their hybrids and the donor line, 3-79. The mean seedcotton yield of CS-B lines ranged from 1,279 kg ha^{-1} (CS-B16) to 1,588 kg ha^{-1} (CS-B22sh) and in their hybrids from 1,695 kg ha^{-1} (CS-B16) to 1,805 kg ha^{-1} (CS-B17).

Variance analysis

Results showed that additive genetic effects had a significant role on lint percentage (54% of phenotypic variance, Table 3). The high additive and low residual variances for lint percentage among all the traits suggested that it is more stable than other traits across environments. In contrast, seedcotton and lint yields were affected more by the environments than the genetic components. Dominance and environment interaction were also major contributors to boll weight (57%), lint yield (34%), and seedcotton yield (25%).

Additive effects

Most of the CS-B lines exerted significant additive genetic effects on lint percentage and boll weight (Table 4). We detected additive genetic effect for higher lint percentage with CS-B16, CS-B22sh, and CS-B22Lo lines compared to TM-1. However, lines CS-B14sh and CS-B25 had significant negative additive effects for lint percentage compared to TM-1. TM-1 had lower lint percentage compared to line 3-79. Results suggested that genes for lint percentage were located on the alien chromosome associated with most of the CS-B lines.

CS-B16 and CS-B22sh resulted in significant positive additive effects, while CS-B14sh, CS-B22Lo and CS-B25 had significant negative additive effects on boll weight,

Table 1 Mean values of eight parents for four quantitative traits

	Lint percentage (%)	Boll weight (g)	Seedcotton yield (kg ha^{-1})	Lint yield (kg ha^{-1})
CS-B14sh	33.24*	4.09*	1,360*	452*
CS-B16	38.74*	5.08*	1,278*	495*
CS-B17	30.47*	5.02*	1,476*	449*
CS-B22sh	38.59*	4.71*	1,588*	610
CS-B22Lo	39.08*	4.27*	1,557*	607
CS-B25	32.30*	4.23*	1,455*	469*
TM-1[a]	**33.85**	**5.54**	**1,917**	**648**
3-79	**35.65**	**3.61**	**831**	**294**
LSD 0.05	0.50	0.19	237	86

Means calculated over four environments

* Significant from TM-1 at $P = 0.05$

[a] Parent lines are in bold font

Table 2 Mean values of crosses by three generations for four agronomic traits

CS-B crosses	Lint percentage (%)				Boll weight (g)				Seedcotton yield (kg ha^{-1})				Lint yield (kg ha^{-1})			
	F_1	F_2	F_3	Mean	F_1	F_2	F_3	Mean	F_1	F_2	F_3	Mean	F_1	F_2	F_3	Mean
CS-B14sh × CS-B16	35.80	35.18	34.98	35.32	5.35	4.79	4.92	5.02	1,351	1,615	1,931	1,632	483	568	675	575
CS-B14sh × CS-B17	32.48	32.50	33.93	32.97	5.28	4.96	4.92	5.05	1,350	1,818	2,225	1,798	440	589	754	594
CS-B14sh × CS-B22sh	36.77	36.05	36.40	34.41	5.21	4.66	4.91	4.92	1,444	1,628	2,089	1,720	531	586	760	626
CS-B14sh × CS-B22Lo	36.31	35.75	36.62	36.22	5.00	4.63	4.53	4.72	1,317	1,692	2,308	1,772	478	603	844	642
CS-B14sh × CS-B25	33.06	33.00	33.27	33.11	4.47	4.56	4.56	4.53	1,215	1,599	2,053	1,622	401	529	684	538
CS-B14sh × TM-1	33.61	33.31	34.45	33.79	5.29	4.95	4.80	5.01	1,439	1,607	2,377	1,808	484	535	824	614
CS-B16 × CS-B17	36.00	35.06	34.22	35.09	5.95	5.39	5.25	5.53	987	1,740	2,074	1,600	355	612	710	559
CS-B16 × CS-B22sh	39.91	38.35	35.78	38.01	5.58	5.37	4.83	5.26	1,395	1,625	2,296	1,772	557	621	822	666
CS-B16 × CS-B22Lo	39.06	38.15	38.20	38.47	5.07	4.80	5.44	5.10	1,299	1,681	1,941	1,640	508	640	741	630
CS-B16 × CS-B25	35.19	35.66	37.28	36.04	5.36	5.07	5.00	5.14	1,383	1,543	2,344	1,757	486	549	874	636
CS-B16 × TM-1	36.75	35.90	36.12	36.26	5.21	5.52	5.19	5.31	1,438	1,712	2,153	1,768	528	611	778	639
CS-B17 × CS-B22sh	35.68	35.12	34.89	35.23	5.54	5.31	5.11	5.32	1,410	1,751	2,359	1,840	504	613	823	647
CS-B17 × CS-B22Lo	35.30	35.24	36.60	35.71	5.19	5.00	5.03	5.07	1,294	1,705	2,376	1,792	457	601	869	642
CS-B17 × CS-B25	32.58	32.37	33.53	32.82	5.52	4.97	4.81	5.1	1,525	1,815	2,382	1,907	497	587	798	627
CS-B17 × TM-1	33.25	33.54	34.29	33.69	5.74	5.66	5.28	5.56	1,479	1,845	2,347	1,890	492	620	805	639
CS-B22sh × CS-B22Lo	38.93	38.42	37.00	38.12	4.86	4.72	4.98	4.85	1,146	1,699	2,293	1,713	446	654	846	649
CS-B22sh × CS-B25	35.72	35.87	35.63	35.74	4.99	4.73	4.75	4.82	1,567	1,576	2,204	1,782	561	566	784	637
CS-B22sh × TM-1	36.26	36.51	35.49	36.09	5.53	5.61	5.02	5.39	1,467	1,923	2,089	1,826	532	702	743	659
CS-B22Lo × CS-B25	35.76	35.39	35.88	35.68	4.63	4.54	4.64	4.60	1,343	1,590	2,352	1,762	480	564	842	629
CS-B22Lo × TM-1	36.78	36.04	35.67	36.16	5.21	5.03	5.01	5.08	1,378	1,860	2,475	1,904	506	670	884	686
CS-B25 × TM-1	32.96	33.24	33.84	33.35	5.27	4.96	4.88	5.04	1,233	1,776	2,479	1,830	407	590	840	612
LSD 0.05	0.64	0.54	0.89		0.26	0.19	0.29		266	272	468		94	96	165	

Table 3 Variance components expressed as proportions to the phenotypic variances for four traits

	Lint percentage	Boll weight	Seedcotton yield	Lint yield
V_A/V_P	0.536**	0.173**	0.000	0.000
V_D/V_P	0.096**	0.000	0.071**	0.058**
V_{AA}/V_P	0.078**	0.090**	0.065**	0.069**
V_{AE}/V_P	0.000	0.000	0.016**	0.005
V_{DE}/V_P	0.176**	0.570 **	0.253**	0.337**
V_{AAE}/V_P	0.000	0.000	0.012**	0.007*
V_e/V_P	0.115	0.167 **	0.583**	0.524**

* and ** 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_e error variance, V_P phenotypic variance, V_{AAE} additive by additive by environment variance

Table 4 Predicted additive effects (±SE) as deviations from the grand means for lint percentage and boll weight

	Lint percent (%) ± S.E.	Boll weight (g) ± S.E.
CS-B14sh	−0.972 ± 0.003*	−0.223 ± 0.002*
CS-B16	1.136 ± 0.005*	0.151 ± 0.001*
CS-B17	−1.263 ± 0.006*	0.206 ± 0.002
CS-B22sh	1.481 ± 0.006*	0.072 ± 0.002*
CS-B22Lo	1.295 ± 0.005*	−0.209 ± 0.002*
CS-B25	−1.110 ± 0.006*	−0.211 ± 0.002*
TM-1	−0.565 ± 0.006	0.214 ± 0.002

Grand means for lint percentage and boll weight are 35.40% and 5.58 g, respectively

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

suggesting genes associated with boll weight might be located on these chromosomes (Table 4). Results showed that the two arms of the substituted chromosome 22 carried genes with antagonistic additive genetic effects on boll weight suggesting some of the challenges associated with the improvement of this trait. None of the CS-B lines had greater additive effect on boll weight than TM-1.

Dominance effects

The dominance effects for lint percentage, seedcotton yield and lint yield varied among the CS-B lines and their crosses (Table 5). The dominance effects on average lint percentage ranged from −1.41% (CS-B14sh × CS-B17) to 1.35% (CS-B22sh × CS-B22Lo) among the lines. All of the lines except CS-B16 had opposite dominance effects on lint percentage in heterozygous versus homozygous conditions, which indicates these differences were due to the interactions of different alleles of the substituted chromosome in the same chromosome pair or alleles in other chromosome pair. Results showed that CS-B16, CS-B22sh and CS-B22Lo had negative dominance effects when carrying homozygous substituted chromosome pair, suggesting these alien chromosomes carry genes that affect lint percentage and could cause inbreeding depression in crosses with any of these lines. CS-B14sh, CS-B17 and CS-B25 did not have any significant dominance effect for lint percentage. However, all of the CS-B lines including CS-B14sh, CS-B17 and CS-B25 exhibited significant dominance effects on lint percentages in all crosses except CS-B22sh × CS-B25, suggesting lint percentages were subject to interaction effects of alleles when both of the substituted chromosomes were in heterozygous.

All of the CS-B lines had significant homozygous dominance effects on seedcotton yield ranging from −108 kg ha^{-1} (CS-B22sh) to 281 kg ha^{-1} (CS-B22Lo) (Table 5). Results showed that the two arms of chromosome 22 carry genes with opposing dominance effects on seedcotton yield. All of the lines, except CS-B17, had opposite dominance effects on seedcotton yield in heterozygous versus homozygous conditions specific to the substituted chromosomes, which suggests epistasis affected this trait.

All of the CS-B lines except CS-B17 had significant dominance effects on lint yield, which ranged from −28 kg ha^{-1} (CS-B16) to 91 kg ha^{-1} (CS-B22Lo) when carrying a substituted chromosome pair in homozygous condition (Table 5; Fig. 2). Similar to the results of seedcotton yield, all of the lines except CS-B17 had opposite dominance effects on lint yield in heterozygous versus homozygous condition of the substituted chromosome. CS-B22Lo had almost four times higher dominance genetic effect on seedcotton and lint yield compared to TM-1 when carrying the substituted chromosome as a homozygous pair suggesting the substituted chromosome of 3-79 carried some beneficial genes with potential to improve yield in TM-1. Although CS-B14sh, CS-B22Lo and CS-B25 had high positive dominance effects on lint yield when carrying substituted chromosome pair in homozygous condition, the hybrids of CS-B14sh with CS-B22Lo or CS-B25 had negative dominance effects on lint yield. The reduction of lint yield in the hybrids was likely due to the interactions between genes of the substituted chromosomes (Fig. 1).

Additive-by-additive epistatic effects

All of the CS-B lines including their hybrids had significant epistatic effects on lint percentage ranging from −0.83 (CS-B17) to 0.6% (CS-B16) (Table 6). CS-B16, CS-B22sh and CS-22Lo had higher epistatic effects on lint percentage compared to TM-1 when carrying the substituted chromosome pair in homozygous condition.

All of the CS-B lines had lower interaction effects ranging from −0.247 g (CS-B14sh) to −0.050 g (CS-B17)

Table 5 Predicted dominance effects as deviations from the grand means for lint percentage, seedcotton yield and lint yield

Name of the line	Lint percentage (%) ± S.E.	Seedcotton yield (kg ha^{-1}) ± S.E	Lint yield (kg ha^{-1}) ± S.E
CS-B14sh	0.433 ± 0.024	97 ± 7.9*	37 ± 2.9*
CS-B16	−0.742 ± 0.022*	−68 ± 6.5*	−28 ± 2.6*
CS-B17	0.354 ± 0.020	32 ± 5.1*	16 ± 1.8
CS-B22sh	−0.684 ± 0.023*	−108 ± 7.6*	−42 ± 3.0*
CS-B22Lo	−0.368 ± 0.017*	281 ± 15.9*	91 ± 5.9*
CS-B25	0.414 ± 0.023	143 ± 9.9*	48 ± 3.7*
TM-1	0.342 ± 0.025	64 ± 5.3	23 ± 1.9
CS-B14sh × CS-B16	0.892 ± 0.033*	62 ± 6.4	26 ± 2.5
CS-B14sh × CS-B17	−1.411 ± 0.033*	16 ± 7.0*	−7 ± 2.1*
CS-B14sh × CS-B22sh	−0.004 ± 0.025*	−34 ± 8.2*	−12 ± 2.7*
CS-B14sh × CS-B22Lo	−0.914 ± 0.028*	−71 ± 8.1*	−31 ± 3.1*
CS-B14sh × CS-B25	0.587 ± 0.021*	−54 ± 6.5*	−11 ± 2.1*
CS-B14sh × TM-1	−0.435 ± 0.036*	−127 ± 12.0*	−46 ± 4.3*
CS-B16 × CS-B17	1.674 ± 0.030*	−120 ± 10.8*	−24 ± 3.1*
CS-B16 × CS-B22sh	0.060 ± 0.023*	−0 ± 6.2*	0 ± 2.2*
CS-B16 × CS-B22Lo	0.858 ± 0.028*	68 ± 7.1	31 ± 2.7*
CS-B16 × CS-B25	−1.200 ± 0.037*	−95 ± 8.0*	−41 ± 3.3*
CS-B16 × TM-1	−0.309 ± 0.022*	202 ± 16.0*	62 ± 5.4*
TCS-B17 × CS-B22sh	−0.054 ± 0.022*	77 ± 9.5	24 ± 3.1
CS-B17 × CS-B22Lo	−0.614 ± 0.032*	−137 ± 9.6*	−51 ± 3.7*
CS-B17 × CS-B25	−0.573 ± 0.026*	23 ± 6.5*	0 ± 1.8*
CS-B17 × TM-1	−0.278 ± 0.019*	95 ± 5.6*	27 ± 1.8
CS-B22sh × CS-B22Lo	1.350 ± 0.035*	−168 ± 10.2	−44 ± 3.2*
CS-B22sh × CS-B25	0.442 ± 0.027	131 ± 9.3*	47 ± 3.3*
CS-B22sh × TM-1	0.215 ± 0.028*	203 ± 12.3*	71 ± 4.8*
CS-B22Lo × CS-B25	0.087 ± 0.020*	−33 ± 7.7*	−11 ± 2.6*
CS-B22Lo × TM-1	0.529 ± 0.032*	−216 ± 11.9*	−68 ± 4.3*
CS-B25 × TM-1	−0.651 ± 0.028*	−265 ± 18.1*	−87 ± 6.4*

Grand means for lint percentage, seedcotton yield, and lint yield are 35.40%, 1,666, and 588 kg ha^{-1}, respectively

e.g. CS-B14sh means the effect of the substituted chromosome 14sh in homozygous condition

CS-B14sh × CS-B16 means the substituted chromosomes 14sh and 16 are in heterozygous condition due to the cross between CS-B14sh and CS-B16

CS-B14sh × TM-1 means the substituted chromosome 14sh was in heterozygous condition due to the cross between CS-B14sh and TM-1, the recurrent parent

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

on average boll weight compared to TM-1 when carrying the substituted chromosomes in homozygous condition suggesting that genes associated with the substituted chromosomes most likely lower the boll weight. This is expected because 3-79, the donor line, has 35% lower boll weight than TM-1, the recurrent parent. All of the hybrids of CS-B lines except two (CS-B14sh × CS-B16 and CS-B22sh × CS-B25) had significant epistatic effects on boll weight. We also observed the majority of the hybrids had positive epistatic effects, indicating these epistatic effects were likely associated with heterosis. Hybrids of CS-B16 × CS-B22sh had the highest epistatic effect on boll weight among all others, thus the interaction of the genes located on these two substituted chromosome most likely caused this effect.

All of the CS-B lines had negative epistatic effect on seedcotton yield ranging from −141 kg ha^{-1} (CS-B22Lo) to −14 kg ha^{-1} (CS-B22sh) when carrying the substituted chromosomes in homozygous condition (Table 6). However, the majority of the hybrids had positive epistatic effects on seedcotton yield, implying heterotic performance resulted from significant interaction effects between alleles of the substituted chromosome(s) in heterozygous condition. Hybrids of CS-B22Lo and CS-B25 with TM-1 had the

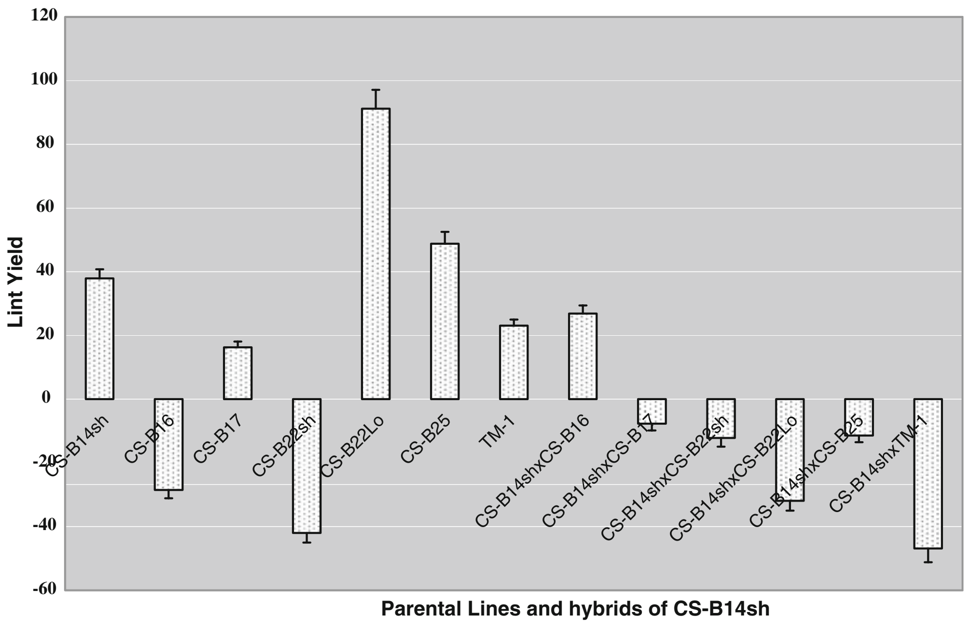

Fig. 2 Predicted dominance effects on lint yield (kg ha^{-1}) of CS-B lines, TM-1 and hybrids of CS-B14sh as a representative sample of the CS-B lines. Comparative results among the lines discern epistatic interaction effects for lint yield on a chromosome-by-chromosome basis

greatest additive-by-additive epistatic effect for seedcotton yield.

All CS-B lines in homozygous condition, except CS-B22sh, had negative additive-by-additive interaction effects on lint yield. This suggests that epistatic effects associated with the substituted chromosomes cause lint yield reduction (Table 6). Homozygous CS-B22sh had the highest additive-by-additive effects on lint yield among the lines, including TM-1, suggesting chromosome 22sh carry genes that most likely will be useful for improving lint yield. Most of the CS-B lines showed higher interaction effect on lint yield when carrying the substituted chromosomes in heterozygous condition indicating the interaction effect of the genes located on the substituted chromosome most likely caused the heterosis in the hybrids.

Discussion

The CS-B partial diallel revealed epistatic interactions for specific chromosome–chromosome combinations and demonstrated that this approach is particularly effective as a tool to dissect epistatic genetic effects. The study was facilitated by the ADAA model, which enabled genetic effects to be partitioned into additive, dominance, interaction effects for each of the CS-B lines (Wu et al. 2006b). To help resolve genetic effects, several CS-B lines were intermated with each other and the recurrent parent, and the progeny were used to define inter-chromosomal genetic effects, thus implying inter-locus interactions. The comparisons among CS-B lines and their crosses enabled the detection of significant alleles that were masked at the whole-genome level associated with various chromosomes in 3-79. The definition of cryptic effects, whether agriculturally desirable or not, is critical to advancing the development of new tools for breeding, e.g., marker-assisted and genome selection. Because epistasis is such a dominating force in wide-cross introgression and it is so difficult to analyze conventionally, such findings are expected to be especially beneficial to germplasm diversification efforts. The CS partial-diallel approach can be extended to include more CS lines and/or more rounds of CS inter-mating, e.g., double-crosses, ratcheting upwards the numbers of potentially interacting alleles. The isogenic nature of CS-B lines will expectedly facilitate finer localization of the epistatically interacting genes and advanced methods for molecular selection by enabling experiments with higher phenotypic and genetic resolution.

In their efforts to define gene networks, Li et al. (2005) used a much different experimental approach—selection and genome scanning of individuals with extreme phenotypes among many backcross-inbred families. It seems to have been very effective. In contrast to the CS approach to epistasis described here, the Li et al. (2005) approach was genome-wide, defined relatively complex (multi-factor) networks, required far more resources, and provided opportunities to discover variation among recurrent parents for differential interactions with the donors. On the other hand, CS lines can be subjected to topcross analyses to reveal important genotype-specific interactions between CS lines and other genotypes, e.g., specific combining ability (SCA) between CS lines and cultivars (Jenkins et al. 2006, 2007). With inclusion of the appropriate sets of families, epistasis can be identified (Wu et al. 2006b).

Overall, results from the partial diallel further confirmed the early findings that some of these CS-B lines carry some

Table 6 Predicted additive × additive epistatic effects as deviations from the respective grand mean for four agronomic traits

Name of the line	Lint percentage (%) ± S.E.	Boll weight (g) ± S.E.	Seedcotton yield (kg ha^{-1}) ± S.E.	Lint yield (kg ha^{-1}) ± S.E.
CS-B14sh	−0.356 ± 0.007*	−0.247 ± 0.004*	−115 ± 3.5*	−48 ± 1.3*
CS-B16	0.607 ± 0.005*	−0.034 ± 0.002*	−78 ± 2.9*	−21 ± 1.1*
CS-B17	−0.839 ± 0.007*	−0.050 ± 0.003*	−92 ± 2.5*	−47 ± 0.9*
CS-B22sh	0.518 ± 0.005*	−0.167 ± 0.002*	−14 ± 2.0*	3 ± 0.7*
CS-B22Lo	0.587 ± 0.007*	−0.218 ± 0.003*	−141 ± 2.8*	−44 ± 1.0*
CS-B25	−0.514 ± 0.006*	−0.211 ± 0.002*	−114 ± 2.8*	−49 ± 1.0*
TM-1	−0.281 ± 0.006	−0.010 ± 0.002	−17 ± 2.2	−12 ± 0.8
CS-B14sh × CS-B16	−0.371 ± 0.008*	0.003 ± 0.003	0 ± 2.4	−5 ± 0.9
CS-B14sh × CS-B17	0.075 ± 0.006*	0.059 ± 0.003*	56 ± 3.1*	19 ± 1.1*
CS-B14sh × CS-B22sh	0.182 ± 0.006*	0.021 ± 0.004*	19 ± 3.2*	10 ± 1.2*
CS-B14sh × CS-B22Lo	0.222 ± 0.007*	−0.002 ± 0.003*	55 ± 3.5*	24 ± 1.3*
CS-B14sh × CS-B25	−0.370 ± 0.006*	0.092 ± 0.003*	11 ± 3.4*	−2 ± 1.2*
CS-B14sh × TM-1	−0.161 ± 0.007*	−0.030 ± 0.004*	30 ± 4.1*	9 ± 1.5*
CS-B16 × CS-B17	−0.302 ± 0.004*	0.054 ± 0.004*	52 ± 2.4*	14 ± 0.9*
CS-B16 × CS-B22sh	0.404 ± 0.006*	0.166 ± 0.003*	2 ± 2.9*	8 ± 1.2*
CS-B16 × CS-B22Lo	0.025 ± 0.007*	−0.025 ± 0.003*	18 ± 3.5*	8 ± 1.4*
CS-B16 × CS-B25	0.256 ± 0.008*	0.035 ± 0.003*	53 ± 3.0*	25 ± 1.1*
CS-B16 × TM-1	0.103 ± 0.005*	0.074 ± 0.004*	−59 ± 3.1*	−19 ± 1.2*
CS-B17 × CS-B22sh	0.063 ± 0.008*	0.126 ± 0.004*	13 ± 2.9*	4 ± 1.1*
CS-B17 × CS-B22Lo	0.264 ± 0.009*	0.048 ± 0.003*	65 ± 3.1*	29 ± 1.2*
CS-B17 × CS-B25	−0.022 ± 0.007*	−0.004 ± 0.003*	67 ± 2.9*	22 ± 1.0*
CS-B17 × TM-1	0.124 ± 0.004*	0.144 ± 0.003*	25 ± 2.7*	10 ± 0.9*
CS-B22sh × CS-B22Lo	−0.036 ± 0.008*	0.045 ± 0.003*	50 ± 2.4*	19 ± 0.9*
CS-B22sh × CS-B25	0.027 ± 0.008*	−0.007 ± 0.003	−40 ± 3.8*	−14 ± 1.4*
CS-B22sh × TM-1	0.057 ± 0.006*	0.098 ± 0.004*	−50 ± 2.6*	−17 ± 1.0*
CS-B22Lo × CS-B25	−0.035 ± 0.006*	−0.030 ± 0.003*	13 ± 2.1*	5 ± 0.8*
CS-B22Lo × TM-1	−0.099 ± 0.008*	0.069 ± 0.002*	97 ± 2.8*	36 ± 1.0*
CS-B25 × TM-1	−0.124 ± 0.008*	0.003 ± 0.003*	92 ± 3.3*	29 ± 1.2*

Grand means for lint percentage, seedcotton yield, and lint yield are 35.40%, 1,666, and 588 kg ha^{-1}, respectively

e.g. CS-B14sh means the effect of the substituted chromosome 14sh in homozygous condition

CS-B14sh × CS-B16 means the substituted chromosomes 14sh and 16 are in heterozygous condition due to the cross between CS-B14sh and CS-B16

CS-B14sh × TM-1 means the substituted chromosome 14sh was in heterozygous condition due to the cross between CS-B14sh and TM-1, the recurrent parent

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

beneficial genes with potential to improve Upland cotton (Saha et al. 2006). The additive genetic effect estimates from this partial diallel provide an assessment of general combining ability due to the presence of specific alien chromosome or chromosome arm of 3-79 in TM-1 background. CS-B16, CS-B22sh and CS-B22Lo had high additive effects for lint percentage than TM-1. Thus, evaluating the additive effects for these CS-B lines may help cotton researchers to choose an appropriate CS-B line as a good general combiner in cultivar development.

Additive-by-additive epistasis effects are also important for selection of pure lines in a breeding program and transferable to the progenies (McCarty et al. 2004, 2007), and reflect cumulative effects of interactions among different loci. Dominance effects can be considered as the SCA of parents in specific hybrid combination, and reflect the cumulative effects of interactions between alleles. Both can broadly be divided into three categories of effects, based on different combinations associated with the substituted alien chromosome: (1) the difference of interaction effects between the homozygous substituted chromosome pair (e.g. CS-B14sh, Tables 5, 6) and the interaction effects between the respective pair of TM-1 chromosomes; (2) the difference of the interaction effects between the 3-79 and TM-1 alleles on the specific pair of the substituted chromosome (chromosome interaction effects in hybrids of the cross between a CS-B line and TM-1, e.g. CS-B14sh × TM-1, Tables 5, 6), from the interaction effects of the TM1 alleles on the same chromosome; and, 3) the difference of the interaction effects between the 3-79 and TM-1 alleles on the specific two pairs of the substituted chromosomes (chromosome interaction effects in bulk F_2 in the cross between two CS-B lines, e.g. CS-B14sh × CS-B16, Tables 5, 6) from the interaction effects of the TM1 alleles on the same two pair of the chromosomes (Fig. 1).

Complex traits of cotton and other crops involve genes that interact, directly or indirectly, as part of a network at the whole genome level. Linkage and pleiotropic effects on multiple traits can lead to conflicting results for various traits, some beneficial and others adverse (Ulloa 2006). Rong et al. (2004, 2007) detected over 400 QTLs controlling fiber and agronomic traits in Upland cotton. Strategies that reduce the "noise" level from other genes will facilitate delimitation of beneficial genes. Assuming the cotton genome ($n = 26$) has approximately 50,000 genes, then each substituted chromosome contains approximately 2,000 genes from *G. barbadense* L. Thus, the quasi-isogenic nature of CS-B lines provides much more detailed and precise quantitative genetic dissection of the complex agronomic traits, by reducing the noise of interacting genes at the whole genome level. Theoretically, the reduction in genetic complexities for single-locus effects would be approximately inversely proportional to the haploid chromosome number, $1/(n - 1)$ for whole chromosome substitutions. For multilocus interactions the reductions would be geometric with more extreme effect (Saha et al. 2006). This provided a unique opportunity to detect many of the cryptic alleles associated with the 3-79 substituted chromosomes in the CS-B lines.

Epistasis made a substantial contribution to each of the complex quantitative trait loci (QTLs). The importance of epistasis as the genetic basis for complex traits including flowering in cotton had been documented in our previous studies using CS-B lines (McCarty et al. 2006; Saha et al. 2006). Although the genetic phenomena of "epistasis", "transgressive segregation" and "adaptive peaks" were recognized long ago, recent molecular marker research has documented the advantage of interspecific introgression into tomato and other species using exotic germplasm as a source for beneficial alleles (Tanksley and McCough 1997). The results reported here document chromosome-specific "epistatic" effects on complex agronomic traits, showing the quantitative genetic effects of masking alleles at some loci by alleles at other loci under homozygous and heterozygous conditions (Tables 5, 6; Fig. 2). For example, TM-1, the recurrent parent, had 131% more seedcotton yield and 120% more lint yield compared to 3-79, the donor parent of the CS-B lines in this experiment. However, CS-B14sh, CS-B22Lo and CS-B25 lines had higher dominance effects on both seedcotton and lint yield under homozygous condition compared to TM-1. We detected in this research that interaction effects of alleles located on several *G. barbadense* 3-79 substituted chromosomes or chromosome arms have the potential to improve agronomic traits such as seedcotton and lint yield in *G. hirsutum* TM-1 (Tables 5, 6; Fig. 2).

The diallel data provided opportunities to compare effects of a single alien chromosome or chromosome pair versus two alien chromosomes or segregating chromosome pairs in the same genetic background. These provided a unique opportunity to detect epistatic interaction effects through comparisons of homozygous and heterozygous conditions on a chromosome-by-chromosome basis for individual agronomic traits. Assuming uniform genetic background of the CS-B lines, the comparative analysis of a double heterozygous combination versus a single heterozygous combination for any two specific substituted chromosome or chromosome arm (Tables 5, 6; Fig. 1) revealed that genetic effects were predominately non-additive for most of the traits including seedcotton and lint yields.

The results reported here document CS-B line agronomic attributes, but our previous studies showed that some of these CS-B lines have superior fiber quality traits. For example, alleles in CS-B25 decrease fiber micronaire, increase span length and fiber strength, all of which improve fiber quality (Saha et al. 2006; Jenkins et al. 2007). CS-B14sh had positive additive effect on 2.5% span length (Saha et al. 2006; Jenkins et al. 2007). Results from previous studies and this research suggested that some of these CS-B lines such as CS-B25 and CS-B14sh can be use to improve both fiber quality and agronomic traits.

Many breeders routinely select sources of high yield genes that are harbored by the limited number of high-yielding adapted cultivars in Upland cotton (Van Esbroeck and Bowman 1998). In effect, they tend to avoid incorporation of diverse sources of germplasm because doing so is likely to introduce unfavorable linkage groups that reduce yield (Robinson and Percival 1997). Recently, Bowman (1999) suggested that "the number one objective of the breeder—to increase lint yield—has been the ultimate deterrent to the introduction and maintenance of genetic diversity". Our results indeed indicate the cryptic presence of useful loci in *G. barbadense* with the potential to improve agronomic traits including seedcotton and lint yield in Upland cotton. For example, the heterozygous dominance effects for the substituted chromosome 16 (CS-B16 × TM-1) and 22sh (CS-B22sh × TM-1), respectively, showed significant positive dominance effects on seedcotton yield, suggesting that these CS-B lines harbor genes having the potential to improve seedcotton yield in the hybrids. This suggests, contrary to common assumption, that *G. barbadense* alleles could be used to improve yield and other agronomic traits, as well as fiber traits. Conventional methods of interspecific introgression are common plagued by hybrid breakdown due to incompatibility at the whole genome level between the two species (Beaseley and Brown 1942). By associating these effects with CS-B lines and, tentatively, specific chromosomes, this research provides a stepping stone towards understanding the role of epistasis and high-resolution chromosome-specific genetic dissection of complex agronomic traits in cotton. Our findings indicate additional genetic resolution is desirable for scientific and breeding purposes. In cases where epistatic interactions are the principal genetic effect (Jenkins et al. 2006, 2007; Saha et al. 2006), the CS-B lines can be used to determine which chromosome or chromosome arm was most likely to yield the desired sorts of information and genetic products.

The results here demonstrate another useful application of the cotton chromosome substitution lines. The CS-B lines are not only good candidates for introgressing specific chromosomal regions harboring useful traits in breeding program, as reported previously (Saha et al. 2006; Jenkins et al. 2006, 2007), but, as shown here, are also superb tools for dissecting genetic effects, including epistatic ones. These findings are highly relevant to both applied breeding and basic research. Epistatic interactions are especially important to the attainment of extreme phenotypes (Li et al. 2005), and exceptional phenotypes are highly desirable in both research and breeding. Having means to dissect and/or synthesize them are highly desirable. When assessed in unadapted germplasm and most early generation products of wide-cross introgression, alleles of potential value for complex traits are usually obscured from detection by overwhelmingly negative epistatic effects from other genes, or ignored, because they are negatively associated through linkages with other undesirable genes that epistatically undermine other traits, i.e., they occur in very undesirable types. Thus, CS-B lines and other chromosome substitution lines provide a means for bringing about chromosome specific introgression, and identifying means to establish knowledge and methods to better use the new germplasm.

In conclusion, the strength of this research derived from several perspectives including the: (1) documentation of chromosome-specific epistasis effect as the major factor for all of the agronomis traits; (2) identification on the cryptic presence of useful loci associated with *G. barbadense* chromosome or chromosome arm with the potential to improve agronomic traits including seedcotton and lint yield; and (3) discoveries of some new QTLs associated with the substituted chromosome or chromosome arm, not reported in our previous studies (Saha et al. 2006). Results suggested that CS-B lines can be used as complementary tools in conjunction with the conventional mapping methods to discover valuable genes and in wide-cross introgression with other traditional interspecific breeding methods for harboring useful traits.

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References

Beaseley JO, Brown MS (1942) Asynaptic *Gossypium* plants and their polyploids. J Agric Res 65:421–427

Bowman D (1999) Public cotton breeders-do we need them? J Cot Sci 3:139–152

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

Cockerham CC (1980) Random and fixed effect in plant genetics. Theor Appl Genet 56:119–131

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, Zhang YX, Li W, Nie YC, Guo XP (2008) Dissection of genetic variance in advanced generations from an interspecific cross of *Gossypium hirsutum* and *G. barbadense*. Plant Breed 127:286–294

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, McCarty JC, Wu J, 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 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

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

Li Z-K, Fu B-Y, Gao Y-M, Xu J-L, Ali J, Lafitte HR, Jiang Y-Z, Domingo RJ, Vijayakumar CHM, Maghirang R, Zheng T-Q, Zhu L-H (2005) Genome-wide introgression lines and their use in genetic and molecular dissection of complex phenotypes in rice (*Oryza sativa* L). Plant Mol Biol 59:33–52

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

McCarty JC, Jenkins JN, Wu J (2004) Primitive accession derived germplasm by cultivar crosses as sources for cotton improvement: I. Phenotypic values and variance components. Crop Sci 44:1226–1230

McCarty JC, Wu J, Saha S, Jenkins JN, Hayes R (2006) Effects of chromosome 5sh from *Gossypium barbadense* L. on flower production in *G. hirsutum* L. Euphytica 152:99–107

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

Mergeai G (2003) Forty years of genetic improvement of cotton through interspecific hybridization at Gembloux Agricultural University: achievement and prospects. In: Swanepol A (ed) Proceedings of the world cotton research conference, Cape Town, South Africa, pp 119–133

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

Osborn TC, Kramer C, Graham E, Braun CJ (2008) Insight and innovations from wide crosses: examples from Canola and Tomato. Crop Sci 47(S3):S229–S237

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

Rhyne CL (1958) Linkage studies in *Gossypium*. I. Altered recombination in allotetraploid *G. hirsutum* L. following linkage group transference from related diploid species. Genetics 43:822–834

Robinson FA, Percival AE (1997) Resistance to *Meloidogyne incognita* race 3 and *Rotylenchulus reniformis* in wild accessions of *Gossypium hirsutum* and *G. barbadense* from Mexico. J. Nematol 29:746–755

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, 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

Shurley D (2008) Cotton and the biofuels craze. Cotton Farm. August issue

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

Tanksley SD, McCough SR (1997) Seed banks and molecular maps: Unlocking genetic potential from the wild. Science 277:1063–1066

Ulloa M (2006) Heritability and correlations of agronomic and fiber traits in an okra leaf Upland cotton population. Crop Sci 46:1508–1514

Ulloa M, Saha S, Jenkins JN, Meredith WR, McCarty JC, Stelly DM (2005) Chromosomal assignment of RFLP linkage groups harboring important QTLs on an intraspecific cotton (*Gossypium hirsutum* L.) joinmap. J Hered 96:132–144

USDA-National Agricultural Statistics Service (2002) Census of agriculture. USDA-NASS, Washington, DC. http://www.nass.usda.gov/Census_of_Agriculture/index.asp. Accessed 16 Sept 2008

Van Esbroeck GA, Bowman DT (1998) Cotton germplasm diversity and its importance to cultivar development. J Cot Sci 2:121–129

Wu J, Jenkins JN, McCarty JC Jr, Saha S, Stelly DM (2006a) An additive-dominance model to determine chromosomal effects in chromosome substitution lines and other germplasms. Theor Appl Genet 112:391–399

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

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

Zhu J (1994) General genetic models and new analysis methods for quantitative traits. J Zhejiang Agric Univ 20:551–559