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ORIGINAL PAPER

Inheritance of long staple fiber quality traits of *Gossypium barbadense* in *G. hirsutum* background using CSILs

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Abstract *Gossypium hirsutum* is a high yield cotton species that exhibits only moderate performance in fiber qualities. A promising but challenging approach to improving its phenotypes is interspecific introgression, the transfer of valuable traits or genes from the germplasm of another species such as *G. barbadense,* an important cultivated extra long staple cotton species. One set of chromosome segment introgression lines (CSILs) was developed, where TM-1, the genetic standard in *G. hirsutum*, was used as the recipient parent and the long staple cotton *G. barbadense* Hai7124 was used as the donor parent by molecular marker-assisted selection (MAS) in BC_5S_{1-4} and BC_4S_{1-3} generations. After four rounds of MAS, the CSIL population was comprised of 174 lines containing 298 introgressed segments, of which 86 (49.4%) lines had single introgressed segments. The total introgressed segment length covered 2,948.7 cM with an average length of 16.7 cM and represented 83.3% of tetraploid cotton genome. The CSILs were highly varied in major fiber qualities. By integrated analysis of data collected in four environments, a total of 43 additive quantitative trait loci (QTL) and six epistatic QTL associated with fiber qualities were detected by QTL IciMapping 3.0 and multi-QTL joint analysis. Six stable QTL were detected in various environments. The CSILs developed and the analyses presented here will enhance the understanding of the genetics of fiber qualities in long staple *G. barbadense* and facilitate further molecular breeding to improve fiber quality in Upland cotton.

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Introduction

Cotton (*Gossypium* spp.) is one of the most important economic crops worldwide, being the leading natural fiber for the manufacture of textiles. The genus *Gossypium* includes approximately 45 diploid species ($2n = 26$) differentiated cytogenetically into eight genome groups (A–G and K) and five allotetraploid species ($2n = 52$) (Fryxell 1992). Four of these species, including two tetraploids *Gossypium hirsutum* L. $(AD)_1$ and *G. barbadense* L. $(AD)_2$, and two diploids *G. herbaceum* L. and *G. arboreum* L., were independently domesticated for fiber production. *G. hirsutum* is the most widely cultivated among the four cultivated *Gossypium* species and has been the subject of most genetic studies and breeding efforts. Several lines of evidence have demonstrated low levels of genetic diversity in *G. hirsutum*, especially among agriculturally elite types (Ulloa and Meredith 2000; Wendel et al. 1989). Increasing genetic diversity is, therefore, essential for genetic improvement efforts for this crop. *G. barbadense,* another important cultivated species, is characterized as an extra long staple cotton compared to Upland cotton (*G. hirsutum*), which exhibits high yield but only moderate performance in fiber qualities (Liu et al. 2000). Interspecific introgression can potentially be used to transfer genes and valuable alien traits, including fiber qualities, from the

G. barbadense germplasm for the improvement of the Upland cotton species (Lacape et al. 2005).

Fiber qualities including fiber length, strength and micronaire are inherited quantitatively, controlled by polygenes and easily affected by the environment. To date, more than 200 quantitative trait loci (QTL) related to various aspects of fiber qualities have been mapped using different populations, including F_2 (Jiang et al. 1998; Paterson et al. 2003; Mei et al. 2004; Lin et al. 2005) and advanced backcross populations (Lacape et al. 2005; Chee et al. 2005a, b; Draye et al. 2005). However, interspecific hybrid progeny of these two species have poor agronomic traits, distorted segregation, sterility, mote formation, limited recombination due to genome incompatibility, and the single plant based fiber scoring system in the F_2 population results in poor resolution QTL mapping in the interspecific hybrids (Reinisch et al. 1994). Therefore, the genetic dissection of long staple fiber qualities in *G. barbadense* remains to be explored using a new strategy.

A set of chromosome segment introgression lines (CSILs) that include near-isogenic lines covering the entire genome of a crop can be developed by crossing donor and recipient parents, backcrossing to the recipient parent and using molecular marker-assisted selection (MAS) (Eshed and Zamir 1994). One or a few homozygous chromosome segments are derived from the donor parent, but the rest of the genome is the same as that of the recipient parent. These lines provide ideal material for genomic research, particularly for QTL mapping. Fine mapping of QTL using CSILs has been reported for tomato, rape and rice. Paterson et al. (1990) constructed contiguous introgression lines using restriction fragment length polymorphisms (RFLPs) to perform fine mapping of QTL in tomato. Eshed and Zamir (1994) mapped six QTL for tomato quality using CSILs. Yamamoto et al. (1998) developed near-isogenic lines and finely mapped three QTL for heading date in rice. Meanwhile, Liu et al. (2003) localized 77 QTL for 18 agronomic traits using 12 single segment substitution lines in rice. Using CSILs, we can fine-map QTL and further clone fiber QTL using map-based cloning strategy as tomato and rice work (Frary et al. 2000; Fridman et al. 2000, 2004; Tian et al. 2006).

In this study, a CSIL population was developed and used for QTL mapping for fiber qualities such as fiber length, strength and micronaire. The objectives of this study were (1) to identify the additive and epistatic QTL of fiber length, strength and micronaire; (2) to identify stable QTL and their corresponding CSILs which can be further used in MAS for improving fiber quality in cotton varieties.

Materials and methods

Development of a set of cotton CSILs

Gossypium hirsutum cv. TM-1, the genetic standard for Upland cotton (Kohel et al. 1970) was obtained from the Southern Plains Agricultural Research Center, USDA-ARS, College Station/Texas, USA. *G. barbadense* cv. Hai7124, grown extensively in China, is the offspring of a selected individual in studies of inheritance of resistance to *Verticillium dahlia* (Pan et al. 1994; Yang et al. 2008). TM-1 exhibits moderate fiber quality performance, while Hai7124 is known for superior fiber quality (Table 1).

Table 1 Phenotypic variation of fiber quality traits in the four environments

Trait	Environment	TM-1	Hai7124	CSIL				
				Mean	SD	Min.	Max.	CV (%)
FL	E1	29.00	32.30	29.77	1.00	27.24	33.10	3.37
	E2	28.57	32.50	28.46	1.01	26.09	32.55	3.54
	E3	29.10	33.00	29.34	1.49	24.27	34.89	5.07
	E4	29.34	32.70	29.41	0.97	25.39	32.00	3.30
FS	E1	30.50	36.60	31.03	2.01	26.00	35.50	6.46
	E2	30.10	35.90	30.85	1.75	25.50	36.05	5.66
	E3	30.20	37.21	31.16	2.06	25.75	39.77	6.60
	E4	30.30	36.70	30.94	1.85	23.00	36.20	5.99
FM	E1	5.10	3.90	5.20	0.55	4.20	7.00	10.57
	E2	5.00	4.00	5.42	0.35	4.40	6.55	6.50
	E3	4.75	3.90	4.75	0.39	3.50	6.00	8.22
	E4	3.75	3.30	3.77	0.48	2.60	5.00	12.76

Environment: E1 was referred to as the planting season at JSBC/NAU in 2008, E2 at JSBC/NAU in 2009, E3 at Saya in 2009, E4 at Dezhou in 2009

FL fiber length, *FS* fiber strength, *FM* fiber micronaire, *CV* co-efficient of variation

The selection scheme for CSILs development is described in Figure S1. The F_1 was generated by a cross using TM-1 as the recipient and Hai7124 as the donor parent in the summer of 2001 at Jiangpu Cotton Breeding Station, Nanjing Agricultural University (JCBS/NAU). The (TM-1 × Hai7124)F_1 progeny were backcrossed to TM-1 to produce 114 BC_1 plants in the winter of 2001 at Sanya, Hainan province. Only 82 BC_1 individuals were backcrossed with TM-1 to generate BC_2 generation at Nanjing in 2002 due to interspecific hybrids characterized by its late flowering. Approximately 12–15 BC_{2-5} plants were usually planted in each backcrossed family. Each plant was selected to backcross with TM-1 to generate BC_3 and advanced generations up to BC_5 obtained in the winter at Sanya, Hainan province and in the summer at JCBS/NAU in 2002 and 2003. During the backcrossing process, one backcrossed boll was harvested from each plant, delinted and mixed as the next generation to be planted. A total of 803 plants of 82 BC_5 families were selfed and individually planted as the BC_5S_1 plant line in 2004 at Nanjing to initiate MAS screening of *G. barbadense* introgressed chromosome segments.

The remaining 32 BC_1 seeds were planted and backcrossed with TM-1 to produce BC_2 generation in the winter of 2002 at Sanya, Hainan province and the backcrosses were further systemically performed using the same strategy until the BC_4 generation. A total of 297 plants of 32 BC_4 families were selfed and individually planted as the BC_4S_1 plant line in 2004 at JCBS/NAU to initiate the same MAS screening procedure. Therefore, each BC_5S_1 and BC_4S_1 plant can be traced to a single BC_1 plant. There was no active selection from BC_1 to BC_5.

Simple sequence repeat markers (SSR) were used to identify the *G. barbadense* introgressed chromosome segments. For each BC_5S_1 and BC_4S_1 line, ten seeds were planted, and 8,030 BC_5S_1 plants and 2,970 BC_4S_1 plants were obtained. Two or three plants from each BC_5S_1 line were randomly selected to generate the BC_5S_2 generation, and the genomic DNA was extracted at Nanjing in 2005. In BC_5S_1, a total of 2,100 plants were genotyped. Two hundred and twenty individuals possessing 1–2 homozygous donor chromosome segments in TM-1 background were selected as the first group of candidate CSILs. The 200 BC_5S_2 individuals with heterozygous donor chromosome segments were self-pollinated to produce the BC_5S_3 generation in 2006. One plant from each BC_5S_3 line was randomly genotyped, and BC_5S_4 lines were produced in 2007. One hundred and ten BC_5S_3 plants having homozygous donor chromosome segments were selected as the second group of candidate CSILs in 2007. One plant from each BC_4S_1 line was randomly selected to generate the 297 BC_4S_2 lines in 2005. One hundred sixty lines were randomly selected to produce the 160 BC_4S_3 lines in 2006. From each BC_4S_3 line, ten seeds were planted, and one plant was randomly selected for genotyping in 2008. One hundred and forty-five individuals with homozygous donor chromosome segments in TM-1 background were selected as the third group of candidate CSILs. The total of 475 candidate CSILs were genotyped with polymorphic markers, and 169 homozygous CSILs were selected. To compensate the missing chromosome segments in the 169 homozygous CSILs, 90 BC_5S_4 lines were further planted in 2008 and one plant from each BC_5S_4 line was randomly genotyped in 2009. Five plants with homozygous donor chromosome segments were selected to be included in the final set of CSILs.

Estimation of the length of introgressed chromosome segment

Introgressed chromosome segment lengths in CSILs were estimated based on graphical genotypes (Young and Tanksley 1989; Hospital 2002). A chromosome segment flanked by two markers from the donor (DD) was considered a 100% donor type; a chromosome segment flanked by two markers from the recipient (RR) was considered a 0% donor type, and a chromosome segment flanked by one marker from the donor and another marker from the recipient (DR) was considered a 50% donor type. So, the length of DD plus that of 1/2 DR was the estimated length of an introgressed chromosome segment (Xi et al. 2006).

Based on our interspecific map and a new chromosome nomenclature for the 13 homeologous chromosome pairs, 330 anchored SSR markers with an average interval of 10 cM between two markers were selected (Han et al. 2006; Wang et al. 2006a). Chromosome (chr.) A5 had the largest number of markers (20 SSRs), while chr. A1, A2 and A8 had the least (eight SSRs). The shortest genetic distance between two markers was 3.00 cM, and the farthest was 25.00 cM. Then, to detect actual lengths of introgressed chromosome segments, 1,000 new SSR markers with an average interval of 5 cM between two markers were selected based on our enhanced map (Guo et al. 2008). Information of all primers used in this report can be downloaded at http://www.cottonmarker.org/projects.

Evaluation of traits

One hundred and sixty-six CSILs were planted in a randomized block design with two replicates at intervals of ten rows with one row of TM-1 for controls, and seedlings were transplanted in the field for phenotype scoring at JCBS/NAU, Yangtze River cotton growing region, in 2008

and 2009. One hundred and sixty-six CSILs were directly grown in the same design in winter of 2009 at Sanya, Hainan province, the Southern cotton growing region. In 2009, 163 CSILs were also cultivated in the same way at Dezhou, Shandong province, Yellow river cotton growing region. The row spacing and the space between two adjacent plants were 80 and 40 cm, respectively. Field management was conducted according to common practices in cotton production. Each environment was designated based on the specific location and year. Environment 1 (E1) was referred to as the planting season at JSBC/NAU in 2008, environment 2 (E2) at JSBC/NAU in 2009, environment 3 (E3) at Saya in 2009 and environment 4 (E4) at Dezhou in 2009. The fiber qualities were evaluated by HVI: 2.5% fiber span length (FL, mm), fiber strength (FS, cN/tex) and fiber micronaire (FM).

Data analysis and QTL mapping

ANOVA were conducted using SPSS v17.0 (SPSS, Chicago, Ill, America). The standard *t* test is not suitable for non-idealized CSILs carrying several introgressed segments from the donor parent. Wang et al. (2006b, 2007) proposed a likelihood ratio test based on stepwise regression (RSTEP-LRT) to detect QTL of non-idealized CSILs. QTL IciMapping 3.0 (http://www.isbreeding.net) was used to detect the effects of additive and epistatic QTL of non-idealized CSILs. The LOD threshold 3.0 was used to declare significant additive QTL and 5.0 to declare significant epistatic QTL. To find stable QTL, multi-QTL joint analysis program was used to detect main-effected QTL, epistatic QTL and environment effects from four environments (Zhang and Xu 2005; Dou et al. 2010; Xu et al. 2011). In the joint analysis, the average phenotypic value of quantitative trait for the *i*th CSIL family at the *j*th environment, y_{ij}, may be described by the following model:

$$y_{ij} = \mu + E_j + G_i + GE_{ij} + \varepsilon_{ij}$$

where, μ is the population mean; E_j environmental effect of *j*th environment; G_i genetic effect of *i*th CSIL family; GE_{ij} is environment-by-QTL interaction effect between the *j*th environment and the *i*th CSIL; and ε_{ij} is a residual error with an assumed N (0, σ^2) distribution.

DNA extraction, PCR amplification and electrophoresis

Cotton genomic DNA was isolated from each individual representing an introgression line as described by Paterson et al. (1993). SSR–PCR amplifications were performed using a Peltier Thermal Cycler-225 (MJ Research) and electrophoresis of PCR products was performed as described by Zhang et al. (2000, 2002).

Results

Distribution of the donor chromosomal segments in CSILs

The genotypes of target markers in 174 CSIL were graphed in Fig. 1. Each line contained a substituted segment of a particular chromosomal region and/or additional small segments in non-target regions. Among 174 lines, we found 298 introgressed segments, and 86 lines (49.4%) contained a single introgressed segment. The total length of the introgressed segments spanned 2,948.6 cM with an average length of 16.7 cM between segments. The introgressed segments in each line varied in length, ranging from the shortest one of 3.5 cM to the longest one of 49.6 cM (Fig. 2; Table S1). The average length of the introgressed segments per chromosome was 191.4 cM and ranged from 102.7 cM on chr. D13 to 417.7 cM on chr. A5 (Table 2). The introgressed segments covered an average of 113.3 cM per chromosome and ranged from 77.9 cM on chr. D4 to 184.1 cM on chr. A5 (Table 2). The average genome coverage was 83.3% and ranged from 64.2% on chr. A10 to 100% on chr. D7 (Table 2). The genome coverage on chr. A1, A5, A8, A12, D3, D7 and D8 was greater than 90% (Table 2).

Phenotypic variation of fiber quality traits in four environments

ANOVA indicated that variances among the genotypes (the CSILs), the four environments, and the G × E interactions were significant for all traits (Table 3). As expected, CSILs displayed a high degree of variability in all environments. CSILs also showed transgressive segregation for all fiber qualities. Variation among the CSILs was also considerable for all fiber qualities. Although the mean of CSILs values (intermediate between the two parents) was always closer to the TM-1 parent value than to the Hai7124 parent, there were always some individual CSILs displaying transgression on both sides of the distribution for all traits in some environments, as shown by the maximum and minimum values in Table 1 and Fig. 3. As shown in Table 1, the coefficient of variation (CV) of the traits was in the order: fiber micronaire > fiber strength > fiber length. The result suggested that fiber micronaire has the largest variation, and is more easily affected by environment than the other traits.

Additive QTL mapping for fiber quality traits

The position, LOD score, additive effects, target CSIL and percentages of the phenotypic variance (PV) of the additive QTL are given in Table 4. The position of additive QTL

Fig. 1 *Gossypium barbadense* chromosome segment *introgression lines* in TM-1 of *Gossypium hirsutum. Pink colour* the genotype of the introgressed segment, the number was the name of the CSILs, *grey colour* the genotype of the recurrent parent-TM-1 (color figure online)

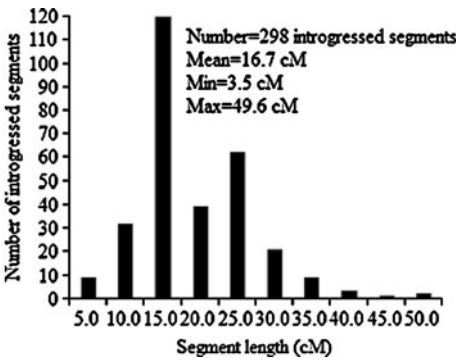

Fig. 2 Distribution of length of the introgressed chromosome segments in CSIL population

for fiber qualities in four environments (E1–E4) is presented in Fig. 4.

Fiber length

There were ten FL QTL based on values from four different environments. They were anchored on nine chromosomes including chr. A5, A7, A8, A11, A12, D5, D9, D11 and D12. Among them, there were seven QTL detected in one environment, two QTL in two environments and one QTL in all four environments. The additive effects (ranging from $A = 1.13$ to $A = 2.78$) of three QTL with LOD score of 3.23–9.21 increased the phenotypic value for fiber length, while the additive effects (ranging from $A = -2.06$ to $A = -0.56$) of remaining QTL with LOD score of 3.14–10.92 decreased it. The percentage of the phenotypic variance varied from 2.29 to 7.18%. *qFL-A8-1* detected by QTL IciMapping 3.0 and multi-QTL joint analysis had a positive effect and was supposed as a stable QTL.

Fiber strength

There were 16 QTL for FS based on values from four different environments. Eight QTL were anchored on chr. A7, A9, A11, A13, D1, D2, D7 and D11. There were two QTL detected on chr. A5, A8, A12 and D9, respectively. Among these 16 QTL, there were six QTL detected in one environment, six QTL in two environments and four QTL in all four environments. The additive effect of 11 QTL increased the phenotypic value for fiber strength (ranging from $A = 1.36$ to $A = 4.13$) and remaining five QTL decreased it (ranging from $A = -3.53$ to $A = -1.04$). The percentage of the phenotypic variance varied from 1.13 to 7.66%. Four QTL, *qFS-A8-1*, *qFS-A12-1*, *qFS-A12-2* and *qFS-D11-1*, were detected in all four environments. Therefore, these four QTL were stable QTL. The additive effects of *qFS-A8-1* and *qFS-A12-2* were positive, while those of *qFS-A12-1* and *qFS-D11-1* were negative. In

Table 2 Genome coverage of introgressed chromosome segments in CSILs

Chromosome	Length of introgressed segments (cM)[a]	Coverage of introgressed segments on genome (cM)[b]	Percentage of genome coverage (%)[c]
A01(Chr. 01)	162.8	95.6	93.1
A02(Chr. 02)	180.5	99.1	88.0
A03(Chr. 03)	162.8	120.4	82.9
A04(Chr. 04)	184.1	106.2	83.9
A05(Chr. 05)	417.7	184.1	91.5
A06(Chr. 06)	123.9	113.3	78.9
A07(Chr. 07)	113.3	85.0	87.4
A08(Chr. 08)	198.2	120.4	93.9
A09(Chr. 09)	215.9	113.3	83.2
A10(Chr. 10)	162.8	81.4	64.2
A11(Chr. 11)	244.2	123.9	83.2
A12(Chr. 12)	290.3	155.8	91.2
A13(Chr. 13)	191.1	113.3	82.0
Total	2,647.8	1,511.5	85.0
D01(Chr. 15)	194.7	99.1	80.4
D02(Chr. 14)	152.2	95.6	84.9
D03(Chr. 17)	205.3	95.6	96.8
D04(Chr. 22)	166.4	77.9	65.6
D05(Chr. 19)	251.3	159.3	83.0
D06(Chr. 25)	123.9	88.5	66.3
D07(Chr. 16)	198.2	138.1	100
D08(Chr. 24)	205.3	145.1	92.3
D09(Chr. 23)	145.1	116.8	75.4
D10(Chr. 20)	166.4	92.0	81.3
D11(Chr. 21)	261.9	148.7	83.9
D12(Chr. 26)	155.8	92.0	70.4
D13(Chr. 18)	102.7	85.0	70.3
Total	2,329.2	1,433.6	81.3

[a] The sum of length of all introgressed segments distributed on the chromosome

[b] The sum of length of all introgressed segments distributed on the chromosome but the length of overlapped segment was calculated only one time

[c] Percentage of genome coverage = coverage of introgressed segments on genome (cM)/genetic distance of tetraploid cotton (cM) × 100. Geneic distance of tertraploid cotton was 3,425.8 cM (Guo et al. 2008)

addition, *qFS-A8-1* was detected by multi-QTL joint analysis with positive effect.

Fiber micronaire

There were 17 QTL for FM based on values from four different environments. There was one QTL detected each on chr. A5, A12, D1, D4 and D5, respectively, two QTL on chr. A9, A11 and D11, respectively; three QTL on chr. A6 and D7, respectively. Among these 17 QTL, there were 14 QTL detected in one environment, two QTL in two environments, and one QTL in all four environments. The additive effects of 12 QTL increased the phenotypic values for fiber micronaire (ranging from $A = 0.34$ to $A = 0.95$), while remaining five QTL decreased it (ranging from $A = -0.64$ to $A = -0.29$). The percentage of the phenotypic variance varied from 1.25 to 5.83%. *qFM-A11-1* decreased the fiber micronaire value was detected in four environments, which suggested that *qFM-A11-1* is a stable QTL. There was no QTL detected by multi-QTL joint analysis.

Table 3 Joint analysis of variance for fiber quality traits in the CSILs population in four environments

Traits and source	DF	SS	MS	*F* value
FL				
CSILs (A)	162	1,675.37	10.34	22.25**
Environments (B)	3	401.93	133.98	293.65**
A × B	486	981.75	2.02	4.34**
FS				
CSILs (A)	162	4,404.29	27.19	26.87**
Environments (B)	3	24.26	8.09	8.14**
A × B	486	2,924.58	6.02	5.94**
FM				
CSILs (A)	162	156.82	0.97	11.82**
Environments (B)	3	744.09	248.03	3,086.24**
A × B	486	209.27	0.43	5.26**

Significance level: ** $p < 0.01$

The sub-genomic distributions and effects of additive QTL

The average additive effects and PV (%) of additive QTL on A_t sub-genome and D_t sub-genome are shown in Table 5. There were six QTL for fiber length, ten QTL for fiber strength and nine QTL for fiber micronaire detected on the A_t sub-genome, while there were four QTL for fiber length, six QTL for fiber strength and eight QTL for fiber micronaire distributed on D_t sub-genome. There is no significant difference in QTL numbers distributed on A_t and D_t sub-genome chromosomes although we detected 25 and 18 QTL for three fiber qualities on A_t and D_t sub-genome chromosomes, respectively (Table 5). Furthermore, for FL, average additive effects of additive QTL on A_t sub-genome were positive, but those on D_t sub-genome were negative. For FS and FM, average additive effect of additive QTL on A_t sub-genome and D_t sub-genome was all positive. For all fiber qualities, average additive value and percentage of the phenotypic variance of additive QTL on A_t sub-genome were approximately equivalent to that on D_t sub-genomes. Therefore, the contribution of the A_t

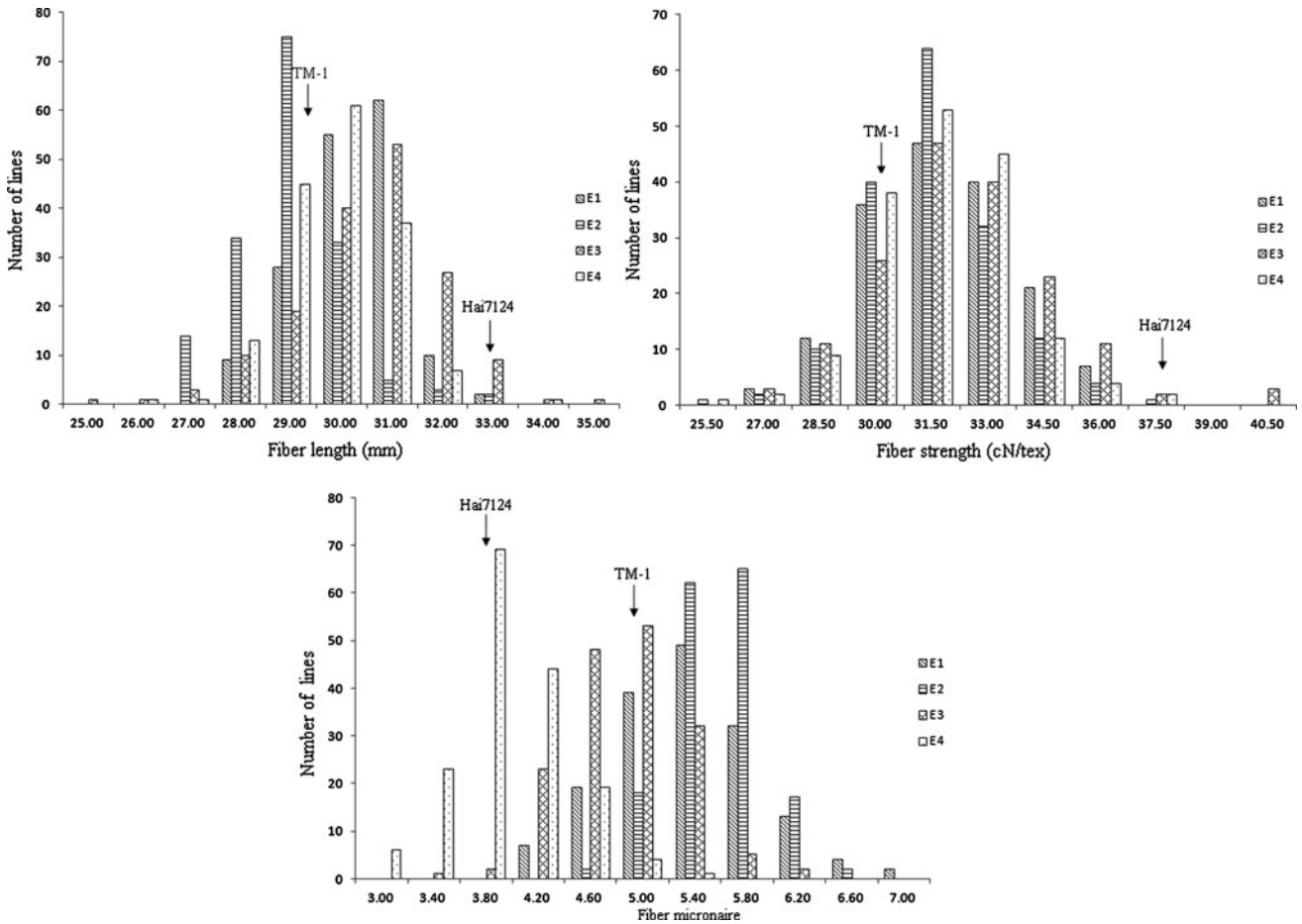

Fig. 3 Frequency distributions of fiber quality traits in CSIL population

sub-genome and the D_t sub-genomes for fiber length, strength and micronaire is approximately equivalent.

Epistatic QTL influencing fiber quality traits

In this study, a total of six pair-wise epistatic interaction QTL were detected for fiber length, strength and micronaire (Table 6) by QTL IciMapping 3.0 and multi-QTL joint analysis.

Fiber length

Two epistatic QTL (NAU845 × NAU1366 and NAU1366 × NAU998) were detected in E3 with LOD of 6.00–6.05 by QTL IciMapping 3.0 and involved three loci distributed on chr. A7, D2 and D11. The two epistatic QTL decreased the value of fiber length. The locus NAU1366 with negative effect was detected and played an important role because it was involved in multiple epistatic interactions. One more epistatic QTL (NAU845 × NAU429) was detected with LOD of 4.57 by multi-QTL joint analysis and involved two loci distributed on chr. A7 and A11. The epistatic QTL had negative effect for fiber length with PVE of 2.47%.

Fiber strength

Two epistatic QTL (NAU845 × NAU1366 and NAU1366 × NAU998) were detected in four environments with LOD of 7.32–22.54 by QTL IciMapping 3.0 and involved three loci distributed on chr. A7, D2 and D11. The two epistatic QTL had different effect in different environments that they increased the phenotypic value of fiber strength in E2 and decreased it in other environments. The locus NAU1366 with negative effect for fiber strength was detected and played an important role because it was involved in multiple epistatic interactions. Another epistatic QTL (NAU845 × NAU998) was detected in E4 with negative effect by QTL IciMapping 3.0. One more epistatic QTL (BNL4030 × BNL1694) was detected with LOD of 9.16 by multi-QTL joint analysis and involved two loci distributed on chr. A5 and D7. The epistatic QTL

Table 4 Additive QTLs for fiber quality traits based on values from four different environments detected by QTLIci Mapping 3.0 and multi-QTL joint analysis

QTL[a]	Marker name	Chromosome	Position	Target CSIL	LOD				*A*				PVE (%)			
					E1	E2	E3	E4	E1	E2	E3	E4	E1	E2	E3	E4
qFL-A7-1	NAU2995	A7	70.73	IL089-A7-4	4.97				−1.26				3.27			
qFL-D12-1	NAU4925	D12	17.02	IL162-D12-2	4.20				−1.17				2.81			
qFL-D5-1	NAU5489	D5	110.33	IL073-D5-9		3.14				−1.21				2.75		
qFL-A11-1	NAU429	A11	8.07	IL092-A11-2-1				3.25				1.13				2.29
				IL138-A11-2												
qFL-A12-1	NAU3109	A12	0.00	IL108-A12-1				10.92				−2.00				7.18
				IL047-A12-1-1												
				IL063-A12-1-2												
				IL155-A12-1-3												
qFL-A12-2	NAU1151	A12	99.06	IL147-A12-6				3.85				1.21				2.64
qFL-D9-1	NAU3967	D9	89.85	IL123-D9-7				4.85				−0.95				3.22
qFL-D11-1	NAU1366	D11	139.34	IL154-D11-8	3.71			4.00	−0.56			−0.62	2.53			2.73
qFL-A5-1	BNL3452	A5	26.14	IL052-A5-3		3.31	4.96			−1.24	−2.06			2.86	3.61	
qFL-A8-1	NAU3558	A8	37.06	IL104-A8-5	4.07	3.23	9.21	4.59	1.15	1.23	2.78	1.31	2.74	2.81	6.57	3.07
					10.64[a]				1.12[a]				5.87[a]			
qFS-A11-2	BNL3431	A11	119.17	IL144-A11-9	5.93				−2.37				3.12			
qFS-A9-1	NAU462	A9	117.54	IL117-A9-6		6.79				2.39				3.76		
qFS-A5-2	NAU3014	A5	88.00	IL056-A5-7			5.16				2.33				2.44	
qFS-A11-1	NAU1232	A11	16.85	IL139-A11-3			5.82				2.46				2.73	
qFS-A5-1	BNL3452	A5	26.14	IL052-A5-3				5.93				2.22				2.89
qFS-D9-1	NAU3967	D9	89.85	IL123-D9-7				6.84				−1.68				3.30
qFS-A8-2	NAU3324	A8	117.23	IL106-A8-9	5.75	3.28			−2.33	−1.73			3.03	1.96		
qFS-D7-1	NAU3608	D7	121.47	IL100-D7-11	3.87	3.11			1.96	1.69			2.13	1.89		
qFS-D9-2	MUSS151	D9	155.01	IL126-D9-11	3.76	3.31			1.93	1.74			2.08	1.98		
qFS-A7-1	NAU933	A7	0.00	IL086-A7-1	4.55		4.92		2.10		2.28		2.45		2.33	
qFS-D2-1	NAU2987	D2	62.16	IL024-D2-6		5.79		3.96		2.22		1.85		3.23		2.01
qFS-D1-1	BNL3090	D1	54.70	IL009-D1-3			5.08	3.83			2.31	1.82			2.40	1.95
qFS-A8-1	NAU3558	A8	37.06	IL104-A8-5	3.80	7.69	15.61	7.11	1.94	2.54	4.13	2.42	2.10	4.25	7.66	3.43
					11.17[a]				1.95[a]				7.76[a]			
qFS-A12-1	NAU3109	A12	0.00	IL108-A12-1	3.99	5.85	7.10	14.53	−1.93	−2.23	−2.71	−3.53	2.83	3.26	3.30	7.33
				IL047-A12-1-1												
				IL063-A12-1-2												
				IL155-A12-1-3												

Table 4 continued

QTL[a]	Marker name	Chromosome	Position	Target CSIL	LOD				*A*				PVE (%)			
					E1	E2	E3	E4	E1	E2	E3	E4	E1	E2	E3	E4
qFS-A12-2	NAU943	A12	84.93	IL158-A12-5 IL054-A12-5-1	4.61	3.61	3.52	4.42	1.36	1.88	1.41	1.52	2.07	2.76	2.36	1.13
qFS-D11-1	NAU1366	D11	139.34	IL154-D11-8	4.41	6.68	4.37	3.84	−1.04	−1.20	−1.09	−1.06	2.39	3.70	2.10	1.71
qFM-A6-1	NAU3677	A6	15.19	IL040-A6-1	5.99				0.64				2.66			
qFM-A11-2	BNL3431	A11	119.17	IL144-A11-9	6.15				0.65				2.73			
qFM-D7-1	NAU2626	D7	69.84	IL095-D7-5	12.86				0.95				5.83			
qFM-D11-1	NAU6530	D11	21.21	IL148-D11-2		4.04				0.40				2.51		
qFM-D7-2	NAU3608	D7	121.47	IL100-D7-11			9.06				0.55				3.43	
qFM-D11-2	NAU2950	D11	87.19	IL151-D11-5			4.77				−0.29				1.85	
qFM-A6-2	BNL2884	A6	41.62	IL077-A6-2				7.74				−0.51				2.80
qFM-A6-3	TMD02	A6	109.49	IL079-A6-5				5.74				0.44				2.09
qFM-A9-1	JESPR274	A9	42.80	IL114-A9-3				7.94				0.52				2.87
qFM-A9-2	NAU2354	A9	132.25	IL118-A9-7				12.00				0.64				4.43
qFM-D1-1	BNL3090	D1	54.70	IL009-D1-3				6.26				−0.46				2.28
qFM-D4-1	JESPR220	D4	102.49	IL048-D4-5				6.21				0.46				2.26
qFM-D5-1	CIR280	D5	103.09	IL039-D3-10				7.94				0.52				2.87
qFM-D5-2	NAU5489	D5	110.33	IL073-D5-9	11.26	6.45					0.61	0.47			4.31	2.34
qFM-A5-1	NAU1042	A5	46.74	IL053-A5-4		3.46		3.18		0.37		0.34		2.20		1.25
qFM-A11-1	NAU429	A11	8.07	IL092-A11-2-1	3.13	3.31	11.97	5.88	−0.48	−0.50	−0.64	−0.41	1.51	1.62	4.61	1.81

A: additive effect. A positive effect indicates the allele in Hai7124 increases the trait of interest, while a negative effect indicates the allele in Hai7124 decreases the trait value

FL fiber length, *FS* fiber strength, *FM* fiber micronaire, *PVE* percentage of phenotypic variation of the additive QTL

[a] The QTL detected by multi-QTL joint analysis

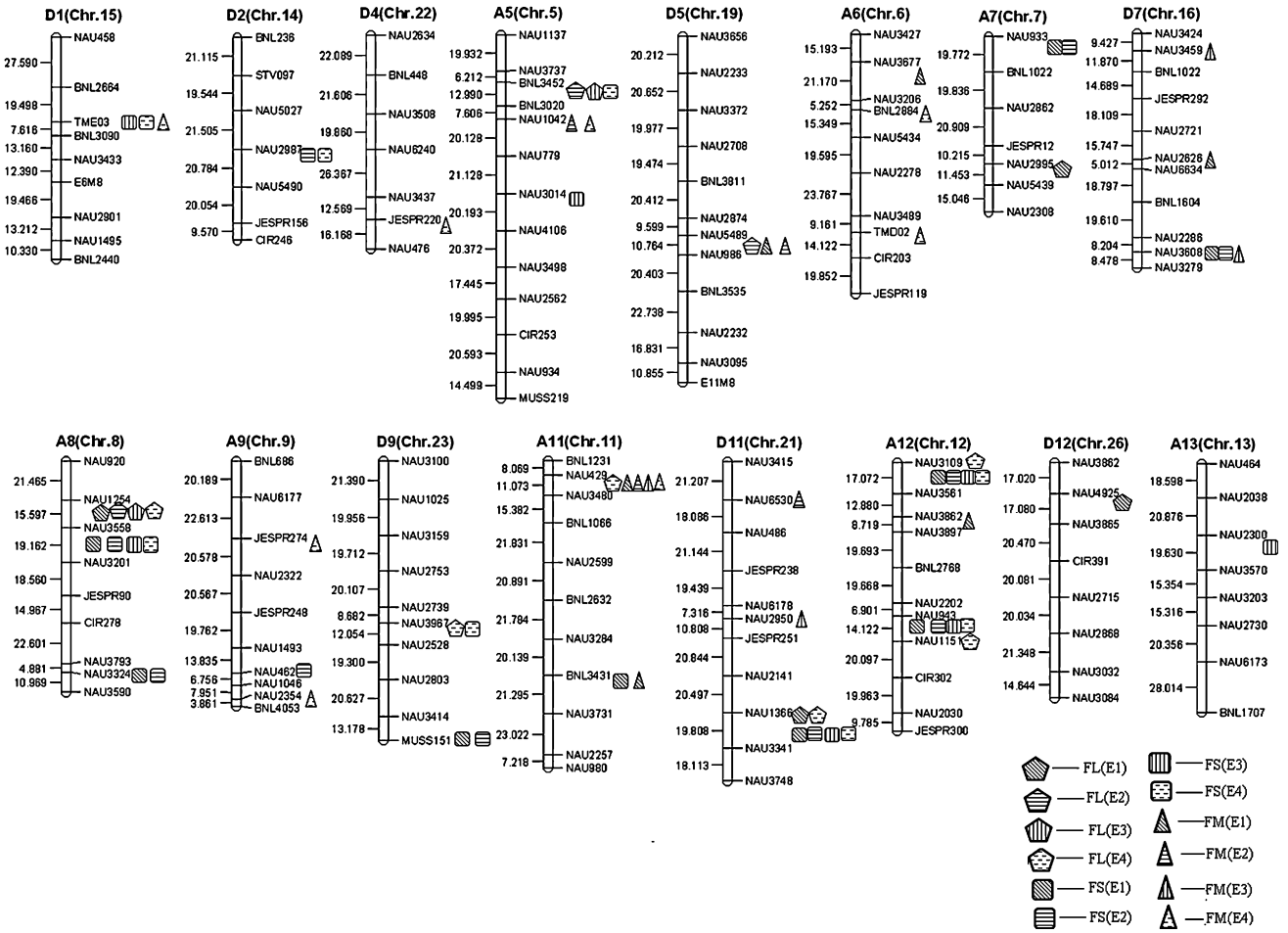

Fig. 4 Chromosomal locations of QTLs for fiber quality traits detected in four environments. *FL* fiber length, *FS* fiber strength, *FM* fiber micronaire, *E1* the location of Jiangpu Cotton Breeding Station, Nanjing Agriculture University in 2008, *E2* the location of Jiangpu Cotton Breeding Station, Nanjing Agriculture University in 2009, *E3* the location of Sanya, Hainan province in 2009, *E4* the location of Dezhou, Shandong province in 2009

Table 5 Average additive effect and PVE of additive QTLs on A_t sub-genome and D_t sub-genome

Trait	A_t sub-genome			D_t sub-genome			Goodness of fit to 1:1[a]
	Number	*A*	PVE (%)	Number	*A*	PVE (%)	
FL	6	0.23	3.7	4	−0.91	2.81	0.53
FS	10	0.67	3.21	6	0.72	2.37	0.32
FM	9	0.14	2.59	8	0.23	3.27	0.81
Total	25			18			0.29

A_t, D_t: Tetraploid chromosomes derived from A-genome and D-genome diploid progenitors, respectively

FL fiber length, *FS* fiber strength, *FM* fiber micronaire

[a] Goodness of fit to 1:1: *p* value of Chi-square

increased the phenotypic value of fiber strength with PVE of 5.68%.

Fiber micronaire

Three epistatic QTL (NAU845 × NAU1366, NAU1366 × NAU998 and NAU845 × NAU998) were detected in E1 with LOD of 7.40–9.09 by QTL IciMapping 3.0 and involved three loci distributed on chr. A7, D2 and D11. The two epistatic QTL (NAU845 × NAU1366, NAU1366 × NAU998) decreased the phenotypic value of fiber micronaire but the third epistatic QTL (NAU845 × NAU998) increased the phenotypic value of fiber micronaire. One more epistatic QTL (CIR097 × NAU429) was detected with LOD of 4.56

Table 6 Epistatic QTLs influencing the fiber quality traits based on values from four different environments

Trait	Marker1	Chr.	Marker2	Chr.	LOD				AA				PVE (%)			
					E1	E2	E3	E4	E1	E2	E3	E4	E1	E2	E3	E4
Fiber length	NAU845	A7	NAU1366	D11			6.00				−0.70				8.04	
	NAU1366	D11	NAU998	D2			6.05				−0.98				8.49	
	NAU845[a]	A7	NAU429[a]	A11	4.57				−0.57				2.47			
Fiber strength	NAU845	A7	NAU1366	D11	8.68	21.58	9.33	10.45	−0.94	0.14	−0.62	−0.34	6.18	15.02	7.04	7.69
	NAU1366	D11	NAU998	D2	8.20	22.54	7.42	7.32	−1.08	0.09	−0.85	−0.54	6.01	15.82	5.46	5.07
	NAU845	A7	NAU998	D2				8.55				−0.59				5.38
	BNL4030[a]	A5	BNL1694[a]	D7	9.16				2.14				5.68			
Fiber micronaire	NAU845	A7	NAU1366	D11	8.68				−0.16				8.03			
	NAU1366	D11	NAU998	D2	7.40				−0.03				7.77			
	NAU845	A7	NAU998	D2	9.09				0.05				8.95			
	CIR097[a]	D2	NAU429[a]	A11	4.56				0.25				0.80			

AA epistatic effect, *PVE* percentage of phenotypic variation of the additive QTLs

[a] Epistatic QTL detected by multi-QTL joint analysis

by multi-QTL joint analysis and involved two loci distributed on chr. A11 and D2. The epistatic QTL increased the phenotypic value of fiber micronaire with PVE of 0.80%.

Environmental effect and environment-by-QTL interaction

Significant environmental effects were observed for fiber length and micronaire. For fiber length, the environmental effect was 0.54, −0.77, 0.14, and 0.09 respectively, and the LOD score was 25.17. For fiber micronaire, the environmental effect was 0.40, 0.63, −0.04 and −0.99, respectively, and the LOD score was 162.24. These results suggested that the effect of environment for fiber strength was less than that for fiber length and fiber micronaire. There was no environment-by-QTL interaction detected by multi-QTL joint analysis.

Discussion

Genetic basis of long staple fiber quality traits in *G. barbadense*

Up to now, many populations used for mapping QTL in cotton are F_2 or RILs, which are derived from the crossing of two parents and self-crossing. The major shortcoming for using those populations is their complicated backgrounds. The lack of optimal genetic materials has limited our comprehensive understanding of quantitative traits (Ebitani et al. 2005). Other approaches have been considered to enhance the accuracy of mapping QTL, including the development of new statistical methods, enlargement of the population size and development of new mapping populations (Lin et al. 1995; Wu and Zeng 2001; Davasi and Soller 1995; Luo et al. 2002; Zhang et al. 2005; Zhang 2006). In this study, a set of interspecific CSILs in the genetic standard Upland cotton TM-1 was developed by backcrossing and MAS with *G. barbadense* Hai7124, the long staple cotton with resistance to *Verticillium wilt* as the donor parent. QTL mapping for fiber qualities was performed to identify stable QTL. The fact that 16 of 43 QTL were detected in more than one environment indicated that the CSIL population could enhance the accuracy of QTL mapping. Two important factors accounted for these results: (1) the clustered QTL were divided into different single QTL, because interactions between different QTL could decrease the accuracy of QTL mapping. The segments in the CSILs populations were broken into smaller pieces by backcrossing, and the clustered QTL were divided into single QTL. (2) The CSIL populations could easily be maintained in seed banks, which allowed for the analysis of different environmental influences on populations

and the study of multiple and even invasive or destructive traits. The statistical power of such analyses was increased, because replicate measurements of genetically identical individuals were conducted.

Additive QTL for fiber qualities reported here were consistent with previous reports in the literature. Of the 43 additive QTL, at least 30 QTL were reported to be localized on the same chromosome. In this study, we found that six QTL for fiber qualities were stable QTL that could be detected in various environments. The strong fiber strength QTL reported from an interspecific RIL by Lacape et al. (2010) localized on chr. A12, near locus NAU943, were corroborated by the stable QTL, *qFS-A12-2*, with peak LOD of 4.61 and greater fiber strength by the *G. barbadense* alleles. The strong fiber strength QTL reported from the A-genome diploid cotton intraspecific $F_{2:3}$ by Ma et al. (2008) localized on chr. A8, near locus NAU3558, were corroborated by the stable QTL, *qFS-A8-1*, with peak LOD of 15.61 and greater fiber strength by the *G. barbadense* alleles. Interestingly, the strong fiber strength QTL, qFS-D8-1, that could be detected in every environment and generation, was reported from the TM-1 × 7235 cross by Shen et al. (2007) localized on chr. D8. The stable fiber strength QTL, qFS-A8-1, that was detected in this research, may be a homoeologous QTL of qFS-D8-1 on chr. D8, because A8 and D8 are homologous chromosomes. The stable fiber length QTL (*qFL-A8-1*) which could be detected in all environments did not correspond with any previously reported fiber QTL in the literature. In other words, the *qFL-A8-1* was a new stable QTL. Therefore, the CSIL population present in this study could be very valuable genetic stocks for QTL mapping studies in cotton.

The chromosomal regions enriched in fiber QTL were compared with the chromosome regions statistically enriched in fiber-expressed genes reported by Xu et al. (2008). These authors used available mapping data for cotton EST unigenes from diverse libraries to assess their distribution among chromosomes. They identified a limited number of gene-rich regions: three fiber gene-rich islands on chr. A5, three islands on A10, one island on D1 and three islands on D2. We observed that only the island on chr. A10 did not contain the QTL by cross comparison of these regions.

Effect of A_t/D_t sub-genomes on the fiber quality QTL

It has been reported that more cotton fiber QTL are anchored on D_t sub-genome by meta-analysis (Rong et al. 2007), while another study observed that the fiber quality QTL numbers tagged on two sub-genomes are equivalent (Lacape et al. 2010). In this study, the number of additive QTL detected on A_t sub-genome was approximately equivalent to that on D_t sub-genome. The extant wild D-genome diploids, including the modern species *G. raimondii* recognized as the closest to the D-genome ancestor of polyploid cotton, only have very short and coarse non-spinnable trichomes on their seeds. Recent reports tend to confirm unequal homoeologous gene expression patterns in allopolyploid cottons (Flagel et al. 2008), leading to differential expression of duplicated genes during fiber development (Hovav et al. 2008) (1,500 A_t/D_t pairs of genes studied).

Our analysis of the average additive effect and percentage of phenotypic variation of QTL also yielded some interesting results. While the average additive effect of QTL for FL detected on A_t sub-genome increased the phenotypic value (i.e., the QTL were associated with longer fiber qualities), those for FL detected on D_t sub-genome decreased the phenotypic value (i.e., the QTL were associated with shorter fiber qualities). The average additive effect of QTL for FS and FM detected on A_t sub-genome and on D_t sub-genome increased the phenotypic value. For fiber length, strength and micronaire, the contribution of the A_t sub-genome and the D_t sub-genomes was approximately equivalent, because the QTL number and effects of two sub-genome were approximately equivalent.

Different types of QTL are used for molecular breeding in cotton via different breeding strategies

Among all 50 cotton species, *G. hirsutum* provides over 95% of the annual cotton crop worldwide and is characterized by its high yield, yet moderate performance in fiber qualities. On the other hand, *G. barbadense* exhibits low yield, but it has a finer and stronger fiber and serves as raw material for fine count yarn. Due to the many desirable traits in *G. barbadense*, fiber quality being primary among them, numerous efforts have been made in the past century to transfer these traits to Upland cotton through interspecific hybridization. Although there have been few successes achieved towards this difficult goal, molecular breeding may help to resolve the problem.

The development and evaluation of chromosome segment introgression lines are important for molecular breeding, and it have been successful in rice for which many CSILs have been developed (Ebitani et al. 2005; Wan 2006; Xi et al. 2006). Once favorable alleles in the genes/QTL on the introgressed segments have been identified, the CSILs become candidate lines for selection in the molecular breeding strategy (Fukuoka et al. 2010; Wang et al. 2007; Neeraja et al. 2007). In this study, a stable fiber length qFL-A8-1 with the peak LOD of 9.21 and contribution rate of 6.58% was detected in all environments, which could enable elongation of fibers. To achieve successful molecular breeding, Guo et al. 2005 proposed a modified backcrossing pyramiding breeding (MBPB)

scheme with MAS. The other stable QTL, *qFS-A8-1*, *qFS-A12-2* and *qFM-A11-2*, can also be used for molecular breeding. The varieties with high-yield, superior fiber quality and *Verticillium* resistance will be produced using various CSILs. Furthermore, by utilizing different CSILs and DNA markers, we may introduce genes/QTL derived from donor cultivars into elite cotton cultivars.

G. barbadense is characterized by fine, strong fibers. In the present study, the additive effect of 17 QTL decreased the fiber qualities of the Hai7124 line, suggesting that the phenotypes of *G. barbadense* could be enhanced by molecular breeding. Therefore, we can substitute the negative *G. barbadense* chromosome segments by MAS and MBPB methods to breed a variety with much finer and stronger fiber.

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