Dissecting the genetic basis of fiber quality and yield traits in interspecific backcross populations of *Gossypium hirsutum* × *Gossypium barbadense*

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Received: 18 November 2018 / Accepted: 29 May 2019 / Published online: 14 June 2019
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Abstract

Fiber quality and yield are important traits of cotton. Quantitative trait locus (QTL) mapping is a prerequisite for marker-assisted selection (MAS) in cotton breeding. To identify QTLs for fiber quality and yield traits, 4 backcross-generation populations (BC₁F₁, BC₁S₁, BC₂F₁, and BC₃F₀) were developed from an interspecific cross between CCRI36 (*Gossypium hirsutum* L.) and Hai1 (*G. barbadense* L.). A total of 153 QTLs for fiber quality and yield traits were identified based on data from the BC₁F₁, BC₁S₁, BC₂F₁ and BC₃F₀ populations in the field and from the BC₂F₁ population in an artificial disease nursery using a high-density genetic linkage map with 2292 marker loci covering 5115.16 centimorgans (cM) from the BC₁F₁ population. These QTLs were located on 24 chromosomes, and each could explain 4.98–19.80% of the observed phenotypic variations. Among the 153 QTLs, 30 were consistent with those identified previously. Specifically, 23 QTLs were stably detected in 2 or 3 environments or generations, 6 of which were consistent with those identified previously and the other 17 of which were stable and novel. Ten QTL clusters for different traits were found and 9 of them were novel, which explained the significant correlations among some phenotypic traits in the populations. The results including these stable or consensus QTLs provide valuable information for marker-assisted selection (MAS) in cotton breeding and will help better understand the genetic basis of fiber quality and yield traits, which can then be used in QTL cloning.

Keywords Quantitative trait locus (QTL) · Fiber quality · Yield · Interspecific backcross populations · QTL cluster

Communicated by Stefan Hohmann.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00438-019-01582-8>) contains supplementary material, which is available to authorized users.

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Introduction

Cotton is an important economic crop worldwide that produces natural fibers used as raw materials in the textile industry. With the development of spinning technologies and mechanization of cotton harvesting, the demand for higher cotton fiber quality has increased. The current goal of cotton breeding is the development of new cultivars with higher fiber yield and superb fiber quality. *Gossypium barbadense* and *G. hirsutum* are the two most economically important tetraploid cultivated species. The former (including Egyptian cotton, Pima cotton and Sea-Island cotton) has longer, stronger and finer fibers; However, its disadvantages were a low yield and narrow adaptation. The latter (Upland cotton), has a high yield and is widely grown in many countries, accounting for approximately 95% of global cotton production (Chen et al. 2007); however, it has a relatively low fiber quality. Therefore, it is

of great significance to effectively transfer genes associated with high-quality traits from *G. barbadense* to *G. hirsutum* for synchronous genetic improvement of yield and fiber quality. No breakthrough has been reported in creating elite varieties with both high yield from *G. hirsutum* and high fiber quality from *G. barbadense* using traditional breeding methods (Zhang and Percy 2007). However, it was possible to transfer desirable genes from *G. barbadense* to *G. hirsutum* based on quantitative trait loci (QTL) mapping and new biotechnology.

Since the first cotton molecular genetic map was reported by Reinisch et al. (1994). More than 1000 QTLs for fiber quality and yield in cotton have been mapped using interspecific populations of *G. hirsutum* × *G. barbadense* and intraspecific populations of *G. hirsutum* (Fang et al. 2014; Jamshed et al. 2016; Keerio et al. 2018; Li et al. 2017a; Liu et al. 2017; Ma et al. 2017; Said et al. 2015a, b; Shang et al. 2016; Wang et al. 2015, 2016, 2017a, b; Yu et al. 2014; Zhai et al. 2016; Zhang et al. 2015b). The cotton genome draft sequences have laid a foundation for further QTL localization and molecular breeding at the genomic level (Li et al. 2014, 2015; Wang et al. 2012a; Zhang et al. 2015a). Many QTLs have been detected using natural populations, recombinant inbred or backcross inbred line populations or other populations based on single nucleotide polymorphism (SNP) markers (Ademe et al. 2017; Islam et al. 2016; Keerio et al. 2018; Li et al. 2016b; Ma et al. 2018; Sun et al. 2017; Zhang et al. 2016b). These studies provided important information for further study of QTLs/genes related to fiber quality and fiber yield and for marker-assisted selection (MAS) in breeding. However, only a few QTLs have been used in MAS (Cao et al. 2015). Most, if not all, linkage-based QTL mapping studies report results from only one mapping population.

To transfer desirable genes from *G. barbadense* to *G. hirsutum*, we developed different interspecific backcross populations and chromosome segment substitution line (CSSL) populations (Li et al. 2016a, 2017b; Lu et al. 2017; Song et al. 2017; Zhai et al. 2016; Lan et al. 2011; Liang et al. 2010; Kong et al. 2018) and constructed a high-density simple sequence repeat (SSR) genetic linkage map of the BC₁F₁ population, which comprised 2292 loci covering 5115.16 centimorgans (cM) of the cotton genome with an average distance of 2.23 cM between markers (Shi et al. 2015). This study reports the identification of QTLs related to fiber yield and fiber quality traits using a high-density map and 5 backcross populations from the same interspecific hybrid of the two cultivated tetraploid species. Consistent QTLs across different populations or environments were identified, which provides useful information to facilitate the understanding of the genetic basis of fiber quality and yield traits and lays a foundation for the simultaneous improvement of fiber quality and yield.

Materials and methods

Plant materials

Three backcross generations (BC₁F₁, BC₁S₁ and BC₂F₁) were derived from an interspecific cross between CCRI36 (*G. hirsutum* L.) and Hai1 (*G. barbadense* L.), of which CCRI36, the recipient parent, is a high yield cultivar bred by the Institute of Cotton Research (ICR), Chinese Academy of Agricultural Sciences (CAAS) and Hai1, the donor parent, is a cultivated cotton line of *G. barbadense* with superb fiber quality, and high resistance to Verticillium wilt (VW) and the dominant glandless trait (Shi et al. 2016).

The BC₁F₁ population included 135 individual plants, and the two parents were grown in the field (Anyang Experiment Farm, ICR, CAAS) in 2004. Each row was 8 m long and the rows were 0.8 m apart. The BC₂F₁ population (with 133 family lines), the BC₁S₁ population (with 120 family lines), and the two parents were planted in the field (Anyang Experiment Farm, ICR, CAAS) in 2005, with single-row plots for each family and two-row plots for the two parents. Each row was 8 m long and 0.8 m wide and included 32 plants. Additionally, 133 BC₂F₁ families were backcrossed with CCRI36, and the contemporary backcross bolls were named the BC₃F₀ population. The BC₂F₁ population (with 133 family lines) was planted in an artificial disease nursery (the BC₂F₁-DN population) in 2005 following a randomized complete block design with three replicates and one row (plot) for each family. Each row was 2.5 m long and contained 15 plants, and the rows were 0.6 m apart (Shi et al. 2016).

The glanded plants in the BC₁F₁, BC₂F₁ and BC₁S₁ population were removed at the seedling stage. Five populations (BC₁F₁, BC₂F₁, BC₁S₁, BC₂F₁-DN, and BC₃F₀) in 3 environments (the field in 2004, the artificial disease nursery in 2005, the field in 2005) were used to detect QTLs for fiber quality and yield traits in the present study.

Phenotypic evaluation

We harvested naturally opened self-pollinated bolls from each plant in the BC₁F₁ population in 2004, 30 naturally opened self-pollinated bolls from each plot for the BC₁S₁, BC₂F₁ and BC₂F₁-DN populations, and naturally opened backcrossed bolls (BC₃F₀) from each family in the BC₂F₁ population in the field in 2005 to evaluate fiber quality and yield traits. Three fiber quality traits and four yield components were analyzed, namely, boll weight (BW), lint percentage (LP), seed index (SI), lint index (LI), fiber

length (i.e., mean upper-half length, FL), fiber strength (FS), and fiber micronaire (FM).

The phenotypic data for each of the 5 populations (BC₁F₁, BC₂F₁, BC₁S₁, BC₂F₁-DN, and BC₃F₀) were independent.

Map construction

Cotton genomic DNA was extracted from young leaves of the 135 BC₁F₁ plants and the two parents as described by Paterson et al. (1993). Genotyping and genetic linkage map construction for the BC₁F₁ population were previously described (Shi et al. 2015). Briefly, the genetic map consists of 2292 marker loci on 26 chromosomes with a total length of 5115.16 cM and an average distance of 2.23 cM between markers. This high-density genetic linkage map served as a foundation for QTL analysis of the 5 populations (BC₁F₁, BC₁S₁, BC₂F₁, BC₂F₁-DN and BC₃F₀).

QTL analysis

The QTLs for fiber quality and yield traits were analyzed using the composite interval mapping method (Zeng 1994) and Windows QTL Cartographer 2.5 (Wang et al. 2006) with a walk speed of 1 cM, 5 control markers, and 1000 permutation tests (Shi et al. 2015). Positive additive effects indicated that Hai1 alleles decreased the phenotypic trait values, and negative scores indicated that Hai1 alleles increased the phenotypic trait values. The CCRI36 alleles had the opposite effects. The QTLs were named as follows: (q + trait abbreviation) + chromosome/linkage group + QTL number. For the same trait, QTL across different generations or environments were considered stable when their confidence intervals overlapped (Sun et al. 2012).

Results

Performance of fiber quality and yield traits of the populations and their parents

The CCRI36 and Hai1 parents differed in yield and fiber quality traits in that the former had a greater BW and LI, lower SI and intermediate fiber quality, while the latter had longer, stronger fibers, a lower BW and LI, and a higher SI (Table 1).

The mean values of FL and FS in the 5 populations were slightly higher than those of the recurrent parent (CCRI36), and the mean values of FM in the 5 populations were slightly lower or similar to those of the parent (CCRI36). The mean values of BW and LI in 4 populations were slightly higher than those of the parent Hai1. The mean values of SI were similar to that of the parent

Hai1. Large variation in all traits was observed among interspecific populations and transgressive segregation was detected in all the populations (Table 1; Fig. 1). FM exhibited more variation than the other fiber quality traits, and BW displayed more variation than SI. As expected, the earlier-generation populations exhibited more phenotypic variation than the later-generation populations. The FL, FS and FM in all 5 populations, SI and LI in 4 populations (BC₁S₁, BC₂F₁, BC₃F₀ and BC₂F₁-DN), and BW in 4 populations (BC₁F₁, BC₁S₁, BC₂F₁ and BC₂F₁-DN) exhibited a continuous and normal distribution (Fig. 1).

An overall description of the QTLs detected in the 5 populations

A total of 2292 marker loci distributed on 26 chromosomes (Shi et al. 2015) were used to map QTLs in the BC₁F₁, BC₁S₁, BC₂F₁, BC₂F₁-DN and BC₃F₀ populations. Two yield traits (SI and LI) were not measured in the BC₁F₁ population due to a low seed number for individual plants, and BW was not measured for the BC₃F₀ population because of artificial-hybridization.

In the 2004 BC₁F₁ population, a total of 22 QTLs were detected, including 4 for FL, 6 for FS, 7 for FM, and 5 for BW. In the 2005 BC₁S₁ population, 37 QTLs were detected, including 10 for FL, 5 for FS, 6 for FM, 5 for SI, 8 for LI, and 3 for BW, which showed that the number of QTLs detected for FL was the largest and the number of QTLs detected for BW was the smallest. In the 2005 BC₂F₁ population, more QTLs (44) were detected, including 7 for FL, 7 for FS, 7 for FM, 10 for SI, 6 for LI, and 7 for BW. In the 2005 BC₂F₁-DN population, a total of 37 QTLs were detected, including 7 for FL, 6 for FS, 5 for FM, 5 for SI, 8 for LI, and 6 for BW. In the 2005 BC₃F₀ population, 39 QTLs were detected, including 8 for FL, 5 for FS, 9 for FM, 11 for SI and 6 for LI. Most QTLs were detected in the BC₂F₁ population, the fewest QTLs in the BC₁F₁ population, and similar numbers of QTLs were identified in the BC₁S₁, BC₂F₁-DN, and BC₃F₀ populations.

QTL mapping of fiber quality traits in interspecific backcross populations

A total of 80 QTLs controlling fiber quality traits were identified in all 5 interspecific backcross populations: 33 for FL, 24 for FS, and 23 for FM. These QTLs were distributed on 19 chromosomes and explained 5.17–19.80% of the total phenotypic variation. Of these QTLs, 16 were stable, i.e., detected in 2 or 3 populations: 3 of them for FL, 5 for FS, and 8 for FM (Table 2; Fig. 2).

Table 1 Performance of fiber quality and yield traits for interspecific populations and their parents

Trait	Interspecific backcross populations				Parents		Year
	Generation (population)	Mean	Range	CV (%)	Hai1	CCRI36	
FL (mm)	BC ₁ F ₁	30.83	26.1–34.8	6.76	32.72	29.38	2004
	BC ₁ S ₁	28.54	24.6–33	5.49	33.66	28.40	2005
	BC ₂ F ₁	29.21	26.8–33.6	4.14			
	BC ₂ F ₁ -DN	29.04	26.3–32.5	4.12			
	BC ₃ F ₀	29.13	26.8–31.7	3.62			
FS (cN/tex)	BC ₁ F ₁	32.04	26.6–38.3	9.28	40.77	28.65	2004
	BC ₁ S ₁	29.31	24.21–34.89	7.30	39.82	28.71	2005
	BC ₂ F ₁	30.12	26.07–33.81	5.29			
	BC ₂ F ₁	30.62	27.34–34.69	5.44			
	BC ₃ F ₀	30.71	26.26–35.57	5.51			
FM (unit)	BC ₁ F ₁	3.66	2–5	14.38	4.18	4.10	2004
	BC ₁ S ₁	3.87	2.96–5.47	11.80	4.17	4.25	2005
	BC ₂ F ₁	4.11	3.16–5.08	7.06			
	BC ₂ F ₁ -DN	4.27	3.53–5.18	7.36			
	BC ₃ F ₀	4.00	3.2–4.89	7.12			
BW (g)	BC ₁ F ₁	3.55	1.88–5.73	22.95	3.10	4.50	2004
	BC ₁ S ₁	3.12	1.71–4.38	16.01	2.78	4.94	2005
	BC ₂ F ₁	4.49	3.67–5.51	8.88			
	BC ₂ F ₁ -DN	4.26	3.13–5.54	10.34			
	BC ₃ F ₀	–	–	–			
SI (g)	BC ₁ F ₁	–	–	–	–	–	2004
	BC ₁ S ₁	11.59	8.4–15.7	11.39	12.37	10.71	2005
	BC ₂ F ₁	12.00	10.1–14.1	7.25			
	BC ₂ F ₁ -DN	12.15	9.8–14.5	7.43			
	BC ₃ F ₀	12.83	10.3–14.8	7.24			
LI (g)	BC ₁ F ₁	–	–	–	–	–	2004
	BC ₁ S ₁	6.23	4.44–9.17	13.73	6.00	6.70	2005
	BC ₂ F ₁	6.73	4.74–8.53	8.27			
	BC ₂ F ₁ -DN	6.93	4.68–8.74	8.89			
	BC ₃ F ₀	8.47	4.47–11.59	13.42			

Fiber length

A total of 33 QTLs for FL were identified in the 5 populations (BC₁F₁, BC₁S₁, BC₂F₁, BC₂F₁-DN and BC₃F₀), each with a phenotypic variation explained (PVE) value of 5.67–19.80%; the QTLs were distributed on 14 chromosomes: 6 on C16, 4 each on C2, C10 and C11, 3 each on C4 and C8, 2 on C21, and only 1 on C3, C9, C12, C15, C20, C23 and C25. Thus, the QTLs for FL were clustered on C16, C2, C10 and C11.

Twenty-five of the 33 QTLs had positive additive effects, in which CCRI36 alleles increased FL by about 0.51–1.66 mm, whereas 8 QTLs had negative additive effects, in which Hai1 alleles increased FL by about 0.56–1.13 mm.

Notably, three of them could be stable: qFL-C16-4 was detected in both the BC₁S₁ and BC₃F₀ populations, with a

PVE of 13.63% and 16.15%, respectively, and qFL-C16-5 was detected in both the BC₂F₁ and BC₃F₀ populations, with a PVE of 7.25% and 18.25%, respectively. The QTL qFL-C20-1 was detected in both the BC₂F₁-DN and BC₃F₀ populations, with a PVE of 5.95% and 11.80%, respectively. CCRI36 alleles increased FL by approximately 0.52–1.17 mm.

Fiber strength

In total 24 QTLs for FS were detected in the 5 populations (BC₁F₁, BC₁S₁, BC₂F₁, BC₂F₁-DN and BC₃F₀), each with PVE 6.13–14.05%, and located on 10 chromosomes, 5 QTLs on C21, 4 each on C11 and C16, 3 each on C5 and C10, and only 1 on C4, C9, C12, C13 and C20, respectively. It showed that C21, C11 and C16 contained more QTL for FS. Thirteen

Fig. 1 Frequency distribution of 6 traits of fiber quality and yield in the interspecific backcross populations of *Gossypium hirsutum* × *Gossypium barbadense*

of the 24 QTLs had negative additive effects, in which Hai1 alleles increased FS about 0.85–1.99 cN/tex.

Importantly, 5 of them could be stable: 2 (qFS-C11-1 and qFS-C11-2) were detected in both the BC₁S₁ and BC₃F₀, with PVE 7.98–11.29%, and 2 (qFS-C11-3 and qFS-C11-4) were detected in both the BC₂F₁ and BC₁F₁-DN, explaining the phenotypic variations by 6.86–8.41%. Hai1 alleles increased FS by approximately 0.85–1.43 cN/tex. One of them was mapped on C16, qFS-C16-1 was detected in both the BC₁S₁ and BC₃F₀, explaining the phenotypic variations

by 6.28% and 10.46%. CCRI36 alleles increased FS by approximately 0.91–1.44 cN/tex.

Fiber micronaire

In total, 23 QTLs for FM were identified in the 5 populations, each with a PVE of 5.17–13.75%; the QTLs were distributed on 8 chromosomes: 7 on C21, 4 on C15, 5 on C10, 3 on C24, and only 1 on C1, C5, C11 and C25. Therefore, C21, C15, C10 and C24 contained most QTLs for FM. Hai1

Table 2 Results of QTL mapping of three fiber quality traits in the 5 interspecific populations

Trait	QTL	Gen	Env	C	Position (cM)	Nearest marker	Interval (cM)	LOD	Add	PVE (%)
FL	qFL-C2-1	BC ₁ F ₁	2004AY	C2	69.4	CICR0239	67.4–72.2	5.40	1.66	15.15
	qFL-C2-2	BC ₁ F ₁	2004AY	C2	79.3	NAU3875	78.3–89.7	2.67	1.26	8.37
	qFL-C2-3	BC ₁ S ₁	2005AY	C2	100.1	HAU2132	96.6–110.2	3.05	0.84	7.00
	qFL-C2-4	BC ₂ F ₁	2005AY	C2	146.6	HAU2690	137.5–158.4	3.32	0.67	7.27
	qFL-C3-1	BC ₂ F ₁	2005DN	C3	146.6	HAU0292	145.9–150.8	2.94	−0.63	6.19
	qFL-C4-1	BC ₃ F ₀	2005AY	C4	61.6	DPL0107a	57.4–63.4	4.04	0.64	9.13
	qFL-C4-2	BC ₃ F ₀	2005AY	C4	65.5	HAU1300	64.4–66.7	2.73	0.53	6.23
	qFL-C4-3	BC ₃ F ₀	2005AY	C4	70.1	HAU1215	66.7–73.8	2.51	0.51	5.74
	qFL-C8-1	BC ₁ S ₁	2005AY	C8	175.2	JESPR092	168.1–184.8	4.25	1.06	11.31
	qFL-C8-2	BC ₁ S ₁	2005AY	C8	187.0	NAU2407	184.8–187.8	3.36	0.90	8.01
	qFL-C8-3	BC ₁ S ₁	2005AY	C8	189.8	CGR5130	187.8–195.5	3.33	0.90	7.96
	qFL-C9-1	BC ₁ F ₁	2004AY	C9	131.5	HAU0361	122.6–140.2	2.78	1.33	7.31
	qFL-C10-1	BC ₁ S ₁	2005AY	C10	167.5	CIR166	164.3–169.9	3.41	1.15	11.13
	qFL-C10-2	BC ₁ S ₁	2005AY	C10	178.4	HAU0949	176.5–179.9	5.38	1.15	12.94
	qFL-C10-3	BC ₁ S ₁	2005AY	C10	185.5	NAU2911	183.5–188.3	3.28	1.02	10.08
	qFL-C10-4	BC ₁ S ₁	2005AY	C10	191.3	NAU2991	188.3–194.7	2.71	0.97	9.28
	qFL-C11-1	BC ₃ F ₀	2005AY	C11	58.3	MUSS281	41.4–65.1	2.55	−0.56	6.75
	qFL-C11-2	BC ₂ F ₁	2005AY	C11	77.2	BNL3442	75.7–79.2	4.70	−0.80	6.75
	qFL-C11-3	BC ₂ F ₁	2005AY	C11	89.7	HAU0848	86.5–95.2	2.82	−0.65	7.23
	qFL-C11-4	BC ₂ F ₁	2005AY	C11	175.2	TMB0064	172.3–180.6	3.42	−0.66	5.90
	qFL-C12-1	BC ₂ F ₁	2005DN	C12	31.5	CGR6698a	29–31.8	2.81	0.62	5.90
	qFL-C15-1	BC ₂ F ₁	2005DN	C15	123.1	NAU3486	119–130.8	2.55	−0.60	5.67
	qFL-C16-1	BC ₂ F ₁	2005DN	C16	146.8	DPL0048	144.3–149	5.04	0.89	12.12
	qFL-C16-2	BC ₂ F ₁	2005DN	C16	152.0	PGML00820	150.4–158.1	3.62	0.71	7.87
	qFL-C16-3	BC ₁ S ₁	2005AY	C16	160.3	BNL1604	159–165.4	3.52	1.08	11.00
	qFL-C16-4	BC ₁ S ₁	2005AY	C16	170.4	HAU1559	167–174.7	4.96	1.17	13.63
		BC ₃ F ₀	2005AY	C16	172.9	NAU2733	171.5–174.1	6.67	0.86	16.15
	qFL-C16-5	BC ₂ F ₁	2005AY	C16	179.7	DPL0283	174.1–182.5	3.25	0.66	7.25
		BC ₃ F ₀	2005AY	C16	175.7	NAU2556	174.1–176.7	7.66	0.92	18.25
	qFL-C16-6	BC ₃ F ₀	2005AY	C16	186.5	CGR6680	182.5–187.5	4.46	0.77	13.08
	qFL-C20-1	BC ₂ F ₁	2005DN	C20	12.3	CGR5565a	8.4–14.7	5.38	0.87	11.80
		BC ₃ F ₀	2005AY	C20	12.3	CGR5565a	5.9–15.4	2.77	0.52	5.95
	qFL-C21-1	BC ₁ F ₁	2004AY	C21	75.6	NAU3381	69.7–76	4.38	1.48	12.03
	qFL-C21-3	BC ₂ F ₁	2005AY	C21	98.4	PGML04104	93.5–102	3.75	0.73	8.70
	qFL-C23-1	BC ₂ F ₁	2005DN	C23	51.2	CICR0425	45.2–56.2	6.17	−1.13	19.80
	qFL-C25-1	BC ₂ F ₁	2005AY	C25	104.1	MUSS275	97.1–108.4	4.16	−0.73	8.89
FS	qFS-C4-1	BC ₃ F ₀	2005AY	C4	71.1	HAU1215	69.3–73.9	3.30	0.99	8.45
	qFS-C5-1	BC ₁ F ₁	2004AY	C5	50.2	CGR6247	49.5–51.6	3.51	1.88	9.59
	qFS-C5-2	BC ₁ F ₁	2004AY	C5	52.6	CICR0065b	51.6–57.4	2.75	1.83	8.81
	qFS-C5-3	BC ₃ F ₀	2005AY	C5	102.5	BNL3992	99.7–105.5	3.50	−0.95	7.77
	qFS-C9-1	BC ₂ F ₁	2005DN	C9	73.6	Gh112	63.1–83.7	3.36	−1.14	10.35
	qFS-C10-1	BC ₂ F ₁	2005AY	C10	122.1	HAU2009	121.3–125.6	3.00	−0.88	7.10
	qFS-C10-2	BC ₂ F ₁	2005AY	C10	133.2	DPL0116a	128.6–139.9	5.55	−1.22	14.05
	qFS-C10-3	BC ₂ F ₁	2005DN	C10	215.6	CGR5040	213.7–221.3	3.36	1.05	8.40
	qFS-C11-1	BC ₁ S ₁	2005AY	C11	77.0	BNL3442	74–79.2	4.00	−1.43	10.45
		BC ₃ F ₀	2005AY	C11	76.0	BNL3442	74.6–79.6	4.48	−1.16	11.29
	qFS-C11-2	BC ₁ S ₁	2005AY	C11	89.7	HAU0848	85.5–92.2	2.92	−1.23	7.98
		BC ₃ F ₀	2005AY	C11	88.7	HAU0848	85.5–92.3	3.73	−1.03	8.76

Table 2 (continued)

Trait	QTL	Gen	Env	C	Position (cM)	Nearest marker	Interval (cM)	LOD	Add	PVE (%)
FM	qFS-C11-3	BC ₂ F ₁	2005AY	C11	166.1	BNL0625	162.2–166.9	3.37	−0.88	7.33
		BC ₂ F ₁	2005DN	C11	160.7	CGR6862	157.2–166.9	3.31	−0.99	8.41
	qFS-C11-4	BC ₂ F ₁	2005AY	C11	167.6	DC40196	166.9–173.2	3.14	−0.85	6.86
		BC ₂ F ₁	2005DN	C11	169.7	SHIN-0601	168.6–174.1	3.38	−0.94	7.84
	qFS-C12-1	BC ₁ F ₁	2004AY	C12	81.7	DPL0303	80–83.7	3.10	−1.77	8.41
	qFS-C13-1	BC ₂ F ₁	2005AY	C13	179.6	PGML04131a	173.8–184.3	4.12	−0.98	9.10
	qFS-C16-1	BC ₁ S ₁	2005AY	C16	160.3	BNL1604	158.2–165.4	3.25	1.44	10.46
		BC ₃ F ₀	2005AY	C16	154.1	CGR5018	152–163.5	2.87	0.91	6.28
	qFS-C16-2	BC ₁ S ₁	2005AY	C16	171.4	HAU1559	167.6–172.9	4.08	1.43	10.54
	qFS-C16-3	BC ₁ S ₁	2005AY	C16	174.1	CICR0452	172.9–181.7	2.79	1.17	7.26
	qFS-C16-4	BC ₁ F ₁	2004AY	C16	190.1	HAU2060	188.3–191.4	2.57	1.53	6.20
	qFS-C20-1	BC ₂ F ₁	2005DN	C20	19.1	NAU5307	15.4–26	2.72	0.84	6.13
	qFS-C21-1	BC ₁ F ₁	2004AY	C21	31.5	CGR5747b	24.9–33.1	3.36	−1.99	9.16
	qFS-C21-2	BC ₁ F ₁	2004AY	C21	33.8	SHIN-1579	33.1–39.5	2.61	−1.85	7.22
	qFS-C21-3	BC ₂ F ₁	2005AY	C21	52.4	NAU4003	48.6–54.1	2.62	0.85	6.75
	qFS-C21-4	BC ₂ F ₁	2005AY	C21	60.0	DPL0582	58.2–65.1	4.46	1.02	9.89
	qFS-C21-5	BC ₂ F ₁	2005DN	C21	235.1	CICR0383	225.2–239.3	3.67	−1.03	8.56
	qFM-C1-1	BC ₁ F ₁	2004AY	C1	16.8	CGR5995	14–22.1	5.33	0.40	12.73
		BC ₃ F ₀	2005AY	C1	16.8	CGR5995	14.1–23.7	3.56	0.16	7.18
	qFM-C5-1	BC ₁ F ₁	2004AY	C5	25.6	DPL0247a	20–33.8	2.55	0.24	5.17
	qFM-C10-1	BC ₁ S ₁	2005AY	C10	59.7	NAU1066b	52.1–64.6	2.65	0.32	10.43
	qFM-C10-2	BC ₁ S ₁	2005AY	C10	67.6	NAU1066b	64.6–73	2.67	0.34	9.67
	qFM-C10-3	BC ₁ F ₁	2004AY	C10	181.8	NAU4008	178.4–183	2.91	−0.28	6.80
	qFM-C10-4	BC ₁ F ₁	2004AY	C10	186.5	NAU2911	183–188.3	3.93	−0.34	10.34
	qFM-C10-5	BC ₁ S ₁	2005AY	C10	189.3	NAU2991	186.1–194.9	2.57	−0.24	6.93
		BC ₁ F ₁	2004AY	C10	190.3	NAU2991	188.3–198.9	4.16	−0.36	11.34
	qFM-C11-1	BC ₂ F ₁	2005AY	C11	203.6	SWU0470	201.1–206.2	4.33	0.18	9.67
	qFM-C15-1	BC ₁ S ₁	2005AY	C15	74.9	CGR5236	73.3–76.6	5.16	0.33	13.10
	qFM-C15-2	BC ₂ F ₁	2005AY	C15	143.6	C2-0022C	142.2–145	4.70	0.19	10.79
	qFM-C15-3	BC ₂ F ₁	2005AY	C15	145.7	TMB1660	145–147.8	4.69	0.19	10.77
		BC ₂ F ₁	2005DN	C15	145.5	NAU3736	143.5–145.7	3.82	0.17	8.03
		BC ₃ F ₀	2005AY	C15	145.7	TMB1660	143.6–147.8	2.80	0.14	5.82
	qFM-C15-4	BC ₂ F ₁	2005AY	C15	151.5	TMB1664	149.7–153.5	5.36	0.20	12.22
		BC ₃ F ₀	2005AY	C15	151.5	TMB1664	149.4–153.5	3.95	0.17	8.06
		BC ₂ F ₁	2005DN	C15	154.5	PGML02824b	151.5–158.7	4.91	0.20	10.27
	qFM-C21-1	BC ₂ F ₁	2005DN	C21	68.8	NAU3156	63.4–74.5	5.83	−0.23	13.75
		BC ₃ F ₀	2005AY	C21	70.8	NAU3156	66.4–75.6	4.41	−0.19	11.24
	qFM-C21-2	BC ₂ F ₁	2005AY	C21	83.3	BNL3147	75.8–85	3.65	−0.17	8.10
		BC ₂ F ₁	2005DN	C21	80.6	BNL3147	77.5–82.6	5.41	−0.23	13.74
		BC ₃ F ₀	2005AY	C21	82.6	BNL3147	76.2–85	5.44	−0.20	11.88
	qFM-C21-3	BC ₂ F ₁	2005AY	C21	86.6	HAU0423	85–90.1	3.83	−0.17	8.47
		BC ₃ F ₀	2005AY	C21	86.0	BNL3449	85–90.1	4.99	−0.20	11.51
	qFM-C21-4	BC ₂ F ₁	2005AY	C21	94.1	PGML04105b	90.1–96.1	2.75	−0.16	7.34
		BC ₃ F ₀	2005AY	C21	94.1	PGML04105b	90.1–96.3	4.13	−0.19	10.15
	qFM-C21-5	BC ₁ F ₁	2004AY	C21	97.4	PGML04104	92.7–102.7	3.91	−0.33	9.06
	qFM-C21-6	BC ₃ F ₀	2005AY	C21	164.1	DC40025	153.4–178.1	3.27	0.15	6.70
	qFM-C21-7	BC ₂ F ₁	2005DN	C21	258.6	NAU6520	246.7–268.2	2.84	0.14	5.63

Table 2 (continued)

Trait	QTL	Gen	Env	C	Position (cM)	Nearest marker	Interval (cM)	LOD	Add	PVE (%)
	qFM-C24-1	BC ₃ F ₀	2005AY	C24	26.6	MUSS021	24.9–30.7	2.69	−0.13	5.36
	qFM-C24-2	BC ₁ S ₁	2005AY	C24	133.9	DPL0214b	131.2–136	4.66	−0.32	11.75
	qFM-C24-3	BC ₁ S ₁	2005AY	C24	138.9	HAU2738	137.4–142.9	2.53	−0.24	6.61
	qFM-C25-1	BC ₁ F ₁	2004AY	C25	129.2	CGR6799b	127.8–131.9	5.35	0.38	12.79

C chromosome, Gen generation, Env environment, AY Anyang Experiment Farm, DN artificial disease nursery, PVE phenotypic variation explained

alleles decreased FM by approximately 0.14–0.40 units for 12 of the 23 QTLs, whereas CCRI36 alleles decreased FM by approximately 0.13–0.36 units for the other 11 QTLs.

Notably, 8 of the QTLs were stable: qFM-C21-1 was detected in both the BC₁F₁-DN and BC₃F₀ populations, with a PVE of 11.24% and 13.75%, respectively, qFM-C21-2 was detected in 3 populations (BC₂F₁, BC₁F₁-DN and BC₃F₀), with a PVE of 8.10–13.74%, and qFM-C21-3 and qFM-C21-4 were detected in both the BC₂F₁ and BC₃F₀ populations, with a PVE of 7.34–11.51%. CCRI36 alleles decreased FM by approximately 0.16–0.23 units. The QTL qFM-C15-3 and qFM-C15-4 were simultaneously detected in the BC₂F₁, BC₂F₁-DN and BC₃F₀ populations, with a PVE of 5.82–10.77% and 8.06–12.22%, respectively. Hai1 alleles at the 2 QTLs decreased FM by approximately 0.14–0.19 units and 0.17–0.20 units, respectively. The QTL qFM-C10-5 was detected in both the BC₁S₁ and BC₁F₁ populations, with a PVE of 6.93% and 11.34%, respectively. Hai1 alleles increased FM by approximately 0.24–0.36 units. The QTL qFM-C1-2 was detected in both the BC₁F₁ and BC₃F₀ populations, with a PVE of 7.18% and 12.73%, respectively. Hai1 alleles decreased FM by approximately 0.16–0.40 units.

QTL mapping of yield traits in interspecific backcross populations

A total of 73 QTLs for 3 fiber yield traits were detected on 20 chromosomes in 4 of the 5 interspecific backcross populations. The PVE of each QTL was 4.98–18.92%. Seven of the QTLs were stable, i.e., detected in 2 or 3 populations simultaneously: 4 for SI and 3 for LI (Table 3; Fig. 2).

Boll weight

In total, 21 QTLs for BW were identified in the 4 populations (BC₁F₁, BC₁S₁, BC₂F₁, and BC₁F₁-DN), each with a PVE of 5.87–16.58%. Among the QTLs for BW, 5, 3, 7 and 6 QTLs were detected in the BC₁F₁, BC₁S₁, BC₂F₁ and BC₁F₁-DN populations, respectively. The QTLs were found on 12 chromosomes: 4 each on C18 and C21, 2 each on C10,

C14 and C17, and only 1 on C2, C3, C4, C11, C15, C19 and C20. Six QTLs (qBW-C10-1, qBW-C10-2, qBW-C11-1, qBW-C17-1, qBW-C17-2, and qBW-C21-1) for BW on C10, C11, C17 and C21 had negative additive effects, in which Hai1 alleles increased BW from 0.34 to −0.57 g. The other 15 QTLs had positive additive effects, in which the CCRI36 alleles increased BW from 0.20 to 0.57 g.

However, no stable QTLs were detected in 2 or more populations, generations or environments.

Seed index

A total of 27 QTLs for SI were identified in the 4 populations (BC₁S₁, BC₂F₁, BC₁F₁-DN and BC₃F₀), each with a PVE of 4.98–18.92%; the QTLs were distributed on 12 chromosomes: 5 on C3, 4 each on C14, C17 and C20, 3 on C22, and only 1 on C6, C8, C9, C10, C18, C21 and C25. Hai1 alleles increased SI by approximately 0.31–1.97 g for 15 of the 27 QTLs and decreased SI by approximately 0.29–1.55 g for the other 12 QTLs.

Notably, 4 of these QTLs were stable, and 2 that were detected in both the BC₂F₁ and BC₂F₁-DN populations mapped to C14 (qSI-C14-1) and C17 (qSI-C17-2), with a PVE of 7.00–7.35% and 15.75–18.92%, respectively. Hai1 alleles at the 2 QTLs increased SI by approximately 0.47–0.49 g and 0.70–0.81 g, respectively. Two QTLs were detected in both the BC₂F₁ and BC₃F₀ populations were mapped to C20 (qSI-C20-1 and qSI-C20-2), with a PVE of 9.48–9.60% and 6.18–8.93%, respectively. Hai1 alleles at the 2 QTLs decreased SI by approximately 0.54–0.59 g and 0.47–0.52 g, respectively.

Lint index

In total, 25 QTLs for LI were identified in 4 populations (BC₁S₁, BC₂F₁, BC₁F₁-DN and BC₃F₀), each with a PVE of 6.01–14.85%; the QTLs were found on 10 chromosomes: 7 on C16, 4 on C6, 3 each on C8 and C17, 2 each on C11 and C21, and only 1 on C12, C14, C23 and C25. Hai1 alleles increased LI by approximately 0.29–1.55 g for 14 of the 25 QTLs and decreased LI by approximately 0.31–1.97 g for the other 11 QTLs.

Fig. 2 Chromosomal locations of QTLs for 6 traits of fiber quality and yield in the interspecific backcross populations of *Gossypium hirsutum* × *Gossypium barbadense*. Asterisk, stable QTL; the number of asterisk, the number of environments in which the QTL was detected

Importantly, 3 of the QTLs were stable. One detected in both the BC₂F₁ and BC₁S₁ populations mapped to C14 (qLI-C14-1), with a PVE of 8.34–12.29%. Hai1 alleles increased LI by 0.33–0.65 g. Two QTLs (qLI-C16-1 and qLI-C16-2) detected in both the BC₂F₁ and BC₃F₀ populations were mapped to C16, with a PVE of 10.93–13.23% and 9.60–12.30%, respectively. Hai1 alleles increased LI by approximately 0.42–1.95 g and 0.40–1.83 g, respectively.

QTL clusters

Using the same linkage map from the BC₁F₁ population, a total of 179 QTLs for fiber quality and yield traits (7 traits: FL, FS, FM, BW, LP, SI, LI) were identified, of which 26 QTLs for LP were identified on 9 chromosomes with phenotype data related to the BC₁F₁ population (Shi et al. 2015).

Through comprehensive analysis, we found that 10 QTL clusters, including 71 QTLs, were related to 2 or more traits,

Fig. 2 (continued)

which is a common phenomenon in cotton (Rong et al. 2007; Lacape et al. 2010; Shen et al. 2007; Said et al. 2013, 2015b; Li et al. 2016b; Keerio et al. 2018). Two QTL clusters were detected on C16, C17 and C21, and one was detected on C4, C6, C10 and C11 (Table 4; Table S1).

There were 6 QTL clusters related to both fiber quality and yield traits, namely, C16-Cluster-1, C16-Cluster-2, C21-Cluster-1, C21-Cluster-2, C10-Cluster-1 and C4-Cluster-1. Thirteen QTLs were in C16-Cluster-1 on C16 (137–161 cM), including 3 for FL (qFL-C16-1, qFL-C16-2, and qFL-C16-3) and 1 for FS (qFS-C16-1) with positive additive effects and 5 for LP (qLP-C16-1, qLP-C16-2, qLP-C16-3, qLP-C16-4, and qLP-C16-5) and 4 for LI

(qLI-C16-1, qLI-C16-2, qLI-C16-3, and qLI-C16-4) with negative additive effects. The same results were observed for C16-Cluster-2 on C16 (169–193 cM), which harbored 12 QTLs, including 3 for FL (qFL-C16-4, qFL-C16-5, and qFL-C16-6) and 3 for FS (qFS-C16-2, qFS-C16-3, and qFS-C16-4) with positive additive effects and 3 for LP (qLP-C16-6, qLP-C16-7, and qLP-C16-8) and 3 for LI (qLI-C16-5, qLI-C16-6, and qLI-C16-7) with negative additive effects. C21-Cluster-1, in a region (60–76 cM) on C21, contained 4 QTLs, namely, qFL-C21-1 for FL and qFS-C21-4 for FS with positive additive effects, and qFM-C21-1 for FM and qLP-C21-1 for LP with negative additive effects. C10-Cluster-1, in a region (167–192 cM) on C10, harbored 9 QTLs,

Table 3 Results of QTL mapping for 3 fiber yield traits

Trait	QTL	Gen	Env	C	Position (cM)	Nearest marker	Interval (cM)	LOD	Add	PVE (%)
BW	qBW-C2-1	BC ₂ F ₁	2005DN	C2	171.3	NAU1246	165.9–176.6	2.91	0.24	7.17
	qBW-C3-1	BC ₂ F ₁	2005AY	C3	58.8	CICR0222	57.6–66.5	3.17	0.21	6.91
	qBW-C4-1	BC ₂ F ₁	2005DN	C4	85.8	MUCS570	82.3–89.8	2.67	0.23	6.53
	qBW-C10-1	BC ₁ F ₁	2004AY	C10	182.3	NAU2082	177.9–182.7	2.98	−0.45	7.16
	qBW-C10-2	BC ₁ F ₁	2004AY	C10	187.5	NAU2991	184.1–192.8	4.42	−0.57	11.31
	qBW-C11-1	BC ₁ F ₁	2004AY	C11	136.7	CICR0433	135.3–138.7	2.57	−0.42	5.87
	qBW-C14-1	BC ₂ F ₁	2005AY	C14	40.0	NAU3648	35.4–45.2	5.47	0.29	13.15
	qBW-C14-2	BC ₂ F ₁	2005AY	C14	48.5	PGML03232	47.1–50.6	3.41	0.23	7.98
	qBW-C15-1	BC ₁ S ₁	2005AY	C15	6.1	NAU3102	0.9–12.6	4.35	0.45	14.31
	qBW-C17-1	BC ₁ S ₁	2005AY	C17	112.5	NAU4052	109.2–114.6	4.42	−0.39	15.25
	qBW-C17-2	BC ₁ S ₁	2005AY	C17	119.4	CGR6185	117.7–122.6	4.30	−0.34	11.44
	qBW-C18-1	BC ₂ F ₁	2005DN	C18	42.6	CGR6787	28.9–44.3	2.64	0.23	6.57
	qBW-C18-2	BC ₂ F ₁	2005DN	C18	47.5	PGML01649	44.3–50	3.06	0.25	7.56
	qBW-C18-3	BC ₂ F ₁	2005DN	C18	51.1	BNL1079	50–51.8	2.77	0.23	6.88
	qBW-C18-4	BC ₂ F ₁	2005DN	C18	52.1	NAU3816a	51.8–53.8	2.54	0.22	6.33
	qBW-C19-1	BC ₂ F ₁	2005AY	C19	89.3	PGML03375	88.2–91.6	2.82	0.20	6.14
	qBW-C20-1	BC ₁ F ₁	2004AY	C20	113.7	HAU1491b	107.5–121.5	3.89	0.57	9.09
	qBW-C21-1	BC ₁ F ₁	2004AY	C21	48.8	CGR5097	45–57.2	2.84	−0.43	6.51
	qBW-C21-2	BC ₂ F ₁	2005AY	C21	137.1	DPL0867	133.7–140.9	3.47	0.24	8.77
	qBW-C21-3	BC ₂ F ₁	2005AY	C21	147.0	CGR5233	145.6–147.8	7.10	0.52	16.58
	qBW-C21-4	BC ₂ F ₁	2005AY	C21	155.7	TMB1976	153.8–157.7	5.32	0.40	15.36
SI	qSI-C3-1	BC ₃ F ₀	2005AY	C3	97.0	BNL3441	96.2–99.8	2.72	−0.46	5.67
	qSI-C3-2	BC ₃ F ₀	2005AY	C3	106.3	BNL2443	105–107.2	3.25	−0.57	6.64
	qSI-C3-3	BC ₃ F ₀	2005AY	C3	109.6	CICR0034	108.6–112.4	4.06	−0.58	9.13
	qSI-C3-4	BC ₃ F ₀	2005AY	C3	114.4	HAU0195b	112.9–114.8	4.48	−0.57	8.94
	qSI-C3-5	BC ₃ F ₀	2005AY	C3	116.1	CGR6528	114.8–118.1	4.24	−0.59	9.62
	qSI-C6-1	BC ₂ F ₁	2005DN	C6	58.6	CICR0461b	55.2–61.7	3.22	0.54	8.55
	qSI-C8-1	BC ₁ S ₁	2005AY	C8	77.7	CER0152c	71.1–87.3	2.52	0.71	5.38
	qSI-C9-1	BC ₂ F ₁	2005DN	C9	111.9	BNL1672	106.2–114.5	2.81	−0.47	6.52
	qSI-C10-1	BC ₃ F ₀	2005AY	C10	41.9	DPL0485	41.1–49.8	2.51	0.43	4.98
	qSI-C14-1	BC ₂ F ₁	2005AY	C14	150.4	NAU3913	148.5–154.6	3.52	−0.47	7.35
		BC ₂ F ₁	2005DN	C14	147.5	PGML01521	143.1–150.1	3.06	−0.49	7.00
	qSI-C14-2	BC ₂ F ₁	2005AY	C14	161.6	PGML03864	155.2–163	3.39	−0.47	7.15
	qSI-C14-3	BC ₃ F ₀	2005AY	C14	195.0	CER0138	190.8–200	4.25	−0.58	9.25
	qSI-C14-4	BC ₃ F ₀	2005AY	C14	205.0	DC40046	203–209.4	3.56	−0.52	7.69
	qSI-C17-1	BC ₂ F ₁	2005AY	C17	77.5	NAU3309	71–82.4	3.88	−0.67	13.76
	qSI-C17-2	BC ₂ F ₁	2005AY	C17	88.4	NAU6542	83.7–92.3	6.28	−0.70	15.75
		BC ₂ F ₁	2005DN	C17	85.4	NAU3309	82.4–88.8	6.37	−0.81	18.92
	qSI-C17-3	BC ₂ F ₁	2005DN	C17	92.3	HAU0764	90.3–93.3	3.05	−0.51	7.63
	qSI-C17-4	BC ₂ F ₁	2005AY	C17	95.9	JESPR195	93.3–101.7	4.69	−0.59	11.29
	qSI-C18-1	BC ₂ F ₁	2005AY	C18	0.0	NAU6173	0–3.7	3.52	0.48	7.38
	qSI-C20-1	BC ₂ F ₁	2005AY	C20	56.1	SHIN-0087b	52.6–57.9	3.89	0.54	9.60
		BC ₃ F ₀	2005AY	C20	53.1	HAU1423b	48.2–57.1	4.66	0.59	9.48
	qSI-C20-2	BC ₂ F ₁	2005AY	C20	62.3	HAU0019	60.5–64.2	4.12	0.52	8.93
		BC ₃ F ₀	2005AY	C20	61.9	NAU4973	60.5–63.3	2.96	0.47	6.18
	qSI-C20-3	BC ₂ F ₁	2005AY	C20	67.2	HAU0175	64.2–68.1	4.84	0.57	10.39
	qSI-C20-4	BC ₂ F ₁	2005AY	C20	68.3	NAU5013	68.1–71.8	4.76	0.56	10.22
	qSI-C21-1	BC ₃ F ₀	2005AY	C21	100.6	NAU4014	97.4–108	3.48	0.50	6.93
	qSI-C22-1	BC ₁ S ₁	2005AY	C22	112.6	PGML00767	108.4–114	3.63	0.86	9.64

Table 3 (continued)

Trait	QTL	Gen	Env	C	Position (cM)	Nearest marker	Interval (cM)	LOD	Add	PVE (%)
LI	qSI-C22-2	BC ₁ S ₁	2005AY	C22	116.0	PGML04137	114–118.3	5.01	0.99	13.18
	qSI-C22-3	BC ₁ S ₁	2005AY	C22	120.5	CGR5566	119.4–125	3.39	0.80	8.48
	qSI-C25-1	BC ₁ S ₁	2005AY	C25	135.3	DPL0705b	132.1–140.7	5.08	−1.00	13.51
	qLI-C6-1	BC ₁ S ₁	2005AY	C6	36.6	HAU3350a	34.3–38.3	4.10	0.56	10.29
	qLI-C6-2	BC ₁ S ₁	2005AY	C6	42.3	TMB2959	40.8–42.5	3.31	0.50	8.44
	qLI-C6-3	BC ₁ S ₁	2005AY	C6	45.9	PGML00996	44.5–46.6	3.68	0.53	9.31
	qLI-C6-4	BC ₁ S ₁	2005AY	C6	48.6	CGR6019	46.6–51.6	2.97	0.52	8.57
	qLI-C8-1	BC ₂ F ₁	2005DN	C8	39.0	HAU1390	38.5–40.5	2.51	−0.31	6.14
	qLI-C8-2	BC ₂ F ₁	2005DN	C8	51.5	DPL0862	45.4–56.1	3.85	−0.40	10.15
	qLI-C8-3	BC ₂ F ₁	2005DN	C8	60.1	DPL0589	58.1–61.8	2.73	−0.34	7.33
	qLI-C11-1	BC ₂ F ₁	2005AY	C11	210.3	MUCS507	203.5–211	2.67	0.29	6.47
	qLI-C11-2	BC ₂ F ₁	2005AY	C11	219.1	HAU0512	213–231	3.01	0.33	8.42
	qLI-C12-1	BC ₃ F ₀	2005AY	C12	105.7	DPL0400	102.9–107.3	3.36	−1.97	7.39
	qLI-C14-1	BC ₂ F ₁	2005AY	C14	210.3	DPL0521	203–214.3	2.50	−0.33	8.34
		BC ₁ S ₁	2005AY	C14	214.3	HAU1219b	207.2–215.3	3.81	−0.65	12.29
	qLI-C16-1	BC ₂ F ₁	2005DN	C16	143.2	NAU6664	140.7–144.9	3.89	−0.40	9.54
	qLI-C16-2	BC ₂ F ₁	2005DN	C16	149.0	DPL0897	147.6–151.8	5.04	−0.44	12.12
	qLI-C16-3	BC ₂ F ₁	2005DN	C16	154.1	CGR5018	151.8–157.1	4.33	−0.41	10.53
	qLI-C16-4	BC ₂ F ₁	2005AY	C16	160.3	BNL1604	158.6–165.4	2.56	−0.32	7.82
	qLI-C16-5	BC ₂ F ₁	2005AY	C16	171.5	HAU1559	167.4–174.1	5.25	−0.42	13.23
		BC ₃ F ₀	2005AY	C16	169.4	HAU1559	165.7–174.1	4.22	−1.95	10.93
	qLI-C16-6	BC ₂ F ₁	2005AY	C16	175.7	NAU2556	174.1–176.7	4.85	−0.40	12.30
		BC ₃ F ₀	2005AY	C16	175.7	NAU2556	174.1–180	4.30	−1.83	9.60
	qLI-C16-7	BC ₃ F ₀	2005AY	C16	187.5	CGR6680	182.5–188.1	2.51	−1.49	6.26
	qLI-C17-1	BC ₃ F ₀	2005AY	C17	53.8	COT064	50–63.5	2.55	−1.83	6.01
	qLI-C17-2	BC ₁ S ₁	2005AY	C17	111.5	NAU4052	106.3–115.6	3.59	0.59	11.57
	qLI-C17-3	BC ₁ S ₁	2005AY	C17	119.4	CGR6185	118.3–125.1	4.06	0.56	10.17
	qLI-C21-1	BC ₂ F ₁	2005DN	C21	128.5	TMB2493	125.3–132.5	3.11	−0.34	7.22
	qLI-C21-2	BC ₁ S ₁	2005AY	C21	235.1	CICR0383	228.4–240	3.32	0.50	8.20
	qLI-C23-1	BC ₂ F ₁	2005DN	C23	50.2	CICR0425	42.2–56.3	4.08	0.49	14.85
	qLI-C25-1	BC ₃ F ₀	2005AY	C25	17.4	CGR5525a	13.1–19.1	3.01	1.55	6.54

C chromosome, Gen generation, Env environment, AY Anyang Experiment Farm, DN artificial disease nursery, PVE phenotypic variation explained

including 4 for FL (qFL-C10-1, qFL-C10-2, qFL-C10-3, and qFL-C10-4) with positive additive effects and 3 for FM (qFM-C10-3, qFM-C10-4, and qFM-C10-5) and 2 for BW (qBW-C10-1 and qBW-C10-2) with negative additive effects. C4-Cluster-1, on C4 (61–86 cM), harbored 5 QTLs, 3 (qFL-C4-1, qFL-C4-2, and qFL-C4-3) for FL, one (qFS-C4-1) for FS and one (qBW-C4-1) for BW, all with a positive additive effect. C21-Cluster-2, on C21 (83–101 cM), harbored 6 QTLs, namely, qFL-C21-2 for FL and qSI-C21-1 for SI with positive additive effects and qFM-C21-2, qFM-C21-3, qFM-C21-4, and qFM-C21-5 for FM with negative additive effects.

There were 3 QTL clusters related to fiber yield, namely, C6-Cluster-1, C17-Cluster-1 and C17-Cluster-2. Six QTLs were located in C17-Cluster-2 on C17 (111–120 cM): 2

(qBW-C17-1 and qBW-C17-2) for BW with negative additive effects and 2 (qLP-C17-4 and qLP-C17-5) for LP and 2 (qLI-C17-2 and qLI-C17-3) for LI with positive additive effects. C6-Cluster-1, in a region (36–59 cM) on C6, harbored 5 QTLs, namely, qSI-C6-1 for SI and qLI-C6-1, qLI-C6-2, qLI-C6-3, and qLI-C6-4 for LI, all with positive additive effects. C17-Cluster-1, on C17 (77–100 cM), harbored 7 QTLs, namely, qLP-C17-1, qLP-C17-2, and qLP-C17-3 for LP with positive additive effects and qSI-C17-1, qSI-C17-2, qSI-C17-3, and qSI-C17-4 for SI with negative additive effects.

C11-Cluster-1, on C11 (63–90 cM), was associated with fiber quality, harboring qFL-C11-2 and qFL-C11-3 for FL and qFS-C11-1 and qFS-C11-2 for FS, all with negative additive effects.

Discussion

The location of QTLs

The linkage map was constructed with 2292 SSR marker loci, covering 5115.16 cM of the AD genome with an average distance of 2.23 cM between markers (Shi et al. 2015). The length of the linkage map is similar to that of the AD genome in cotton, and the SSR marker loci are distributed throughout the genome. We used the high-density genetic linkage map and data from 5 backcross populations (BC₁F₁, BC₂F₁, BC₁S₁, BC₂F₁-DN, and BC₃F₀) in 4 different generations (BC₁F₁, BC₂F₁, BC₁S₁, and BC₃F₀) to identify the QTLs of fiber yield and fiber quality in 3 environments (the field in 2004, an artificial disease nursery in 2005, and the field in 2005). A total of 153 QTLs were identified, including 80 QTLs for 3 fiber quality traits and 73 QTLs for 3 yield traits in the present paper (Tables 2, 3; Fig. 2). Twenty-three QTLs were consistently detected in 2 or 3 populations, including 3 for FL, 5 for FS, 8 for FM, 4 for SI, and 3 for LI.

Among the 153 QTLs detected in the present study, 30 QTLs were reported in previous studies with a common marker in the confidence interval on the same chromosome. Ten QTLs for FL (qFL-C3-1, qFL-C4-2, qFL-C8-1, qFL-C8-3, qFL-C10-2, qFL-C10-4, qFL-C11-2, qFL-C16-2, qFL-C16-3, and qFL-C20-1) were reported previously (Chen et al. 2018; Kong et al. 2018; Lan et al. 2011; Said et al. 2015b; Sun et al. 2012; Wang et al. 2011, 2013, 2016, 2017a; Zhai et al. 2016; Zhang et al. 2016a). Of these QTLs, qFL-C3-1 was the same as that in three previous reports (Wang et al. 2013, 2016; Chen et al. 2018), and qFL-C16-3 was the same as that in three previous reports (Wang et al. 2011; Said et al. 2015b; Lan et al. 2011). Eight QTLs for FS (qFS-C5-1, qFS-C5-3, qFS-C10-3, qFS-C11-2, qFS-C16-1, qFS-C20-1, qFS-C21-3, and qFS-C21-5) were consistent with those reported previously (Said et al. 2015b; Shao et al. 2014; Tang et al. 2015; Wang et al. 2016; Zhai et al. 2016; Kong et al. 2018). Among these 8 common QTLs for FS, qFS-C10-3 may be the same as that in three previous reports (Shao et al. 2014; Tang et al. 2015; Kong et al. 2018). Of 7 common QTLs for FM, one QTL (qFM-C10-3) was reported by three researchers (Said et al. 2015b; Si et al. 2017; Yu et al. 2013). One QTL (qFM-C5-1) was reported by Yu et al. (2013) and Said et al. (2015b). The other 5 QTLs for FM (qFM-C15-2, qFM-C21-1, qFM-C21-2, qFM-C24-3 and qFM-C25-1) were reported in the previous studies (Said et al. 2015b; Liang et al. 2010; Song et al. 2017; Yang et al. 2015). Five QTLs for yield traits (qBW-C10-2, qBW-C21-3, qSI-C14-1, qSI-C18-1 and qLI-C17-1) were reported previously (Kong et al. 2018; Ning et al.

2014; Si et al. 2017; Wang et al. 2015; Wu et al. 2009). Nine QTLs detected in previous studies were confirmed in our advanced backcross populations, including 3 QTLs (qFL-C20-1, qFS-C11-2, and qFS-C20-1) reported by Zhai et al. (2016), 3 QTLs (qBW-C10-2, qFL-C10-4, and qFS-C10-3) reported by Kong et al. (2018), and 3 QTLs (qFL-C16-3, qFM-C21-1 and qFM-C24-3) reported by Lan et al. (2011), Liang et al. (2010), and Song et al. (2017), respectively. Therefore, 30 of the QTLs detected in this study were previously reported, and the other 123 QTLs are considered novel.

In summary, 23 QTLs (qFL-C16-4, qFL-C16-5, qFL-C20-1, qFS-C11-1, qFS-C11-2, qFS-C11-3, qFS-C11-4, qFS-C16-1, qFM-C1-1, qFM-C10-5, qFM-C15-3, qFM-C15-4, qFM-C21-1, qFM-C21-2, qFM-C21-3, qFM-C21-4, qSI-C14-1, qSI-C17-2, qSI-C20-1, qSI-C20-2, qLI-C14-1, qLI-C16-5, and qLI-C16-6) were stable and detected in 2 or more populations in this paper and 30 common QTLs (qFL-C3-1, qFL-C4-2, qFL-C8-1, qFL-C8-3, qFL-C10-2, qFL-C10-4, qFL-C11-2, qFL-C16-2, qFL-C16-3, qFL-C20-1, qFS-C5-1, qFS-C5-3, qFS-C10-3, qFS-C11-2, qFS-C16-1, qFS-C20-1, qFS-C21-3, qFS-C21-5, qFM-C5-1, qFM-C10-3, qFM-C15-2, qFM-C21-1, qFM-C21-2, qFM-C24-1, qFM-C25-1, qBW-C10-2, qBW-C21-3, qSI-C14-1, qSI-C18-1, and qLI-C17-1) were reported in the previous studies (Table S3).

There were 47 stable or common QTLs (qFL-C3-1, qFL-C4-2, qFL-C8-1, qFL-C8-3, qFL-C10-2, qFL-C10-4, qFL-C11-2, qFL-C16-2, qFL-C16-3, qFL-C16-4, qFL-C16-5, qFL-C20-1, qFS-C5-1, qFS-C5-3, qFS-C10-3, qFS-C11-1, qFS-C11-2, qFS-C11-3, qFS-C11-4, qFS-C16-1, qFS-C20-1, qFS-C21-3, qFS-C21-5, qFM-C1-1, qFM-C5-1, qFM-C10-3, qFM-C10-5, qFM-C15-2, qFM-C15-3, qFM-C15-4, qFM-C21-1, qFM-C21-2, qFM-C21-3, qFM-C21-4, qFM-C24-3, qFM-C25-1, qBW-C10-2, qBW-C21-3, qSI-C14-1, qSI-C17-2, qSI-C18-1, qSI-C20-1, qSI-C20-2, qLI-C14-1, qLI-C16-5, qLI-C16-6 and qLI-C17-1), of which 6 QTLs (qFL-C20-1, qFS-C11-2, qFS-C16-1, qFM-C21-1, qFM-C21-2, and qSI-C14-1) were both stable and common QTLs. Therefore, 17 QTLs (qFL-C16-4, qFL-C16-5, qFS-C11-1, qFS-C11-3, qFS-C11-4, qFM-C1-1, qFM-C10-5, qFM-C15-3, qFM-C15-4, qFM-C21-3, qFM-C21-4, qSI-C20-2, qSI-C17-2, qSI-C20-1, qLI-C14-1, qLI-C16-5, and qLI-C16-6) were considered novel stable QTLs.

The detection of QTLs in multiple populations or different genetic backgrounds indicated the stabilities of the genetic effects. These stable and common QTLs might increase the reliability and efficiency of selection and play important roles in the simultaneous improvement of fiber yield and quality by MAS (Shen et al. 2007; Sun et al. 2012; Tang et al. 2015; Wang et al. 2015; Zhai et al. 2016; Zhang et al. 2009).

Table 4 QTL clusters for fiber quality and yield traits in interspecific backcross populations

Cluster	Interval (cM)	C	No of QTL	QTL
C4-Cluster-1	61–86	C4	5	qFL-C4-1(+), qFL-C4-2(+) ^b , qFL-C4-3(+), qFS-C4-1(+), qBW-C4-1(+)
C6-Cluster-1	36–59	C6	5	qSI-C6-1(+), qLI-C6-1(+), qLI-C6-2(+), qLI-C6-3(+), qLI-C6-4(+)
C10-Cluster-1	167–192	C10	9	qFL-C10-1(+), qFL-C10-2(+) ^b , qFL-C10-3(+), qFL-C10-4(+) ^b , qFM-C10-3(-) ^b , qFM-C10-4(-), qFM-C10-5(-) ^a , qBW-C10-1(-) qBW-C10-2(-) ^b
C11-Cluster-1	63–90	C11	4	qFL-C11-2(-) ^b , qFL-C11-3(-), qFS-C11-1(-) ^a , qFS-C11-2(-) ^{ab}
C16-Cluster-1	137–161	C16	13	qFL-C16-1(+), qFL-C16-2(+) ^b , qFL-C16-3(+) ^b , qFS-C16-1(+) ^{ab} , qLP-C16-1(-) ^b , qLP-C16-2(-), qLP-C16-3(-), qLP-C16-4(-), qLP-C16-5(-), qLI-C16-1(-), qLI-C16-2(-), qLI-C16-3(-), qLI-C16-4(-)
C16-Cluster-2	169–193	C16	12	qFL-C16-4(+) ^a , qFL-C16-5(+) ^a , qFL-C16-6(+), qFS-C16-2(+), qFS-C16-3(+), qFS-C16-4(+), qLP-C16-6(-) ^{ab} , qLP-C16-7(-) ^a , qLP-C16-8(-), qLI-C16-5(-) ^a , qLI-C16-6(-) ^a , qLI-C16-7(-)
C17-Cluster-1	77–100	C17	7	qLP-C17-1(+) ^a , qLP-C17-2(+) ^{ab} , qLP-C17-3(+), qSI-C17-1(-), qSI-C17-2(-) ^a , qSI-C17-3(-), qSI-C17-4(-)
C17-Cluster-2	111–120	C17	6	qBW-C17-1(-), qLP-C17-4(+), qLP-C17-5(+) ^b , qBW-C17-2(-), qLI-C17-2(+), qLI-C17-3(+)
C21-Cluster-1	60–76	C21	4	qFL-C21-1(+), qFS-C21-4(+), qFM-C21-1(-) ^{ab} , qLP-C21-1(-)
C21-Cluster-2	83–101	C21	6	qFL-C21-2(+) ^b , qFM-C21-2(-) ^{ab} , qFM-C21-3(-) ^a , qFM-C21-4(-) ^a , qFM-C21-5(-), qSI-C21-1(+)

The data for LP QTLs are from our previous reports (Shi et al. 2015)

C chromosome

^aStable QTL

^bCommon QTL

Contributions of the A and D subgenomes to allotetraploid cottons

In the past 20 years, most of QTL mapping studies have clearly shown that more QTLs for fiber quality traits were situated on the D subgenome than on the A subgenome for fiber quality traits (Fang et al. 2014; Jiang et al. 1998; Patterson et al. 2003; Rong et al. 2007; Said et al. 2013; Shen et al. 2007; Yang et al. 2015). Some studies have shown that almost equal numbers of QTLs are on the two subgenomes (Ning et al. 2014; Wang et al. 2012b, 2015).

In the present study, more QTLs for FL and FS were located on the A subgenome than on the D subgenome (35 on the A subgenome and 22 on the D subgenome), while more QTLs or genes for FM were located on the D subgenome than on the A subgenome (8 on the A subgenome and 15 on the D subgenome). Overall, the number of QTLs for fiber quality traits on the A subgenome was larger than that on the D subgenome (43 vs. 37). However, for yield component traits, more QTLs were distributed on the D subgenome than on the A subgenome in our study. Using the same map and the same populations, 26 QTLs for LP were identified (Shi et al. 2015). A total of 99 QTLs for yield traits (BW, SI, LI, and LP) were found, 33 of which were located on the A subgenome, and 66 QTLs were located on the D subgenome (Table 5).

In summary, more QTLs for both fiber quality and fiber yield traits were detected on the D subgenome than that on the A subgenome (76 vs. 103) (Table 5).

QTL clusters for fiber yield and quality

Ten clusters were identified in this study. These clusters harbored many stable QTLs or common QTLs, of which 17 (qFL-C16-4, qFL-C16-5, qFM-C10-5, qFM-C21-1, qFM-C21-2, qFM-C21-3, qFM-C21-4, qFS-C11-1, qFS-C11-2, qFS-C16-1, qLI-C16-5, qLI-C16-6, qSI-C17-2, qLP-C16-6, qLP-C16-7, qLP-C17-1, and qLP-C17-2) were stable QTLs and 16 (qFL-C4-2, qFL-C10-2, qFL-C10-4, qFL-C11-2, qFL-C16-2, qFL-C16-3, qFM-C10-3, qFM-C21-1, qFM-C21-2, qFS-C11-2, qFS-C16-1, qBW-C10-2, qLP-C16-1, qLP-C16-6, qLP-C17-2, and qLP-C17-5) were common QTLs. Thus, 6 QTLs (qFS-C11-2, qFS-C16-1, qFM-C21-1, qFM-C21-2, qLP-C16-6, and qLP-C17-2) were both stable and common QTLs (Table 4; Table S1).

Among the ten clusters, one (C16-Cluster-1) resembled the C16-Cluster-Gh-2 cluster reported by Said et al. (2015a, b) and Wang et al. (2011). The other 9 clusters are considered novel.

All QTLs for both FL and FS showed the same additive effect direction in all 5 clusters (C4-Cluster-1, C11-Cluster-1, C16-Cluster-1, C16-Cluster-2, and C21-Cluster-1),

Table 5 Distributions of QTLs on the A and D subgenomes of allotetraploid cotton

C	FL	FS	FM	BW	SI	LI	LP	Fiber quality trait	Yield trait	Sum
C1			1				0	4	0	4
C2	4			1				6	1	7
C3	1			1	5		0	1	6	7
C4	3	1		1				5	1	6
C5		3	1				3	7	3	10
C6					1	4		0	5	5
C7								0	0	0
C8	3				1	3		7	4	11
C9	1	1			1		1	2	2	4
C10	4	3	5	2	1		2	13	5	18
C11	4	4	1	1		2		9	3	12
C12	1	1				1	2	3	3	6
C13		1						1	0	1
C14				2	4	1	2	2	9	11
C15	1		4	1			2	7	3	10
C16	6	4				7	8	12	15	27
C17				2	4	3	5	0	14	14
C18				4	1			0	5	5
C19				1				0	1	1
C20	1	1	7	1	4			15	5	20
C21	2	5		4	1	2	1	13	8	22
C22					3			0	3	3
C23	1					1		2	1	3
C24	1		3					4	0	4
C25			1		1	1		9	2	11
C26								0	0	0
A subgenome	21	14	8	6	9	10	8	43	33	76
D subgenome	12	10	15	15	18	15	18	37	66	103
Sum	33	24	23	21	27	25	26	80	99	179

The data for LP QTLs are from our previous report (Shi et al. 2015)

C chromosome

and QTLs for FL and FM showed opposite additive effect directions in each of 3 clusters (C10-Cluster-1, C21-Cluster-1, and C21-Cluster-2). These QTL clusters revealed a strong positive genetic correlation between FL and FS and a strong negative genetic correlation between FL and FM. Some previous reports revealed similar clusters (Sun et al. 2012; Zhang et al. 2013, 2016a; Fang et al. 2014; Zhai et al. 2016; Islam et al. 2016; Diouf et al. 2018), but these correlations were not explicitly mentioned in their reports. All QTLs for both LP and LI had the same additive effect direction in 3 clusters (C16-Cluster-1, C16-Cluster-2, and C17-Cluster-2), and QTLs for LP and SI had opposite additive effect directions in C17-Cluster-1. These QTL clusters revealed a strong positive genetic correlation between LP and LI and a strong negative genetic correlation between LP and SI. To the best of our knowledge, the same or similar results have not been reported. All QTLs for both FL and FS

had positive additive effects and all QTLs for both LP and LI had negative additive effects in 2 clusters (C16-Cluster-1 and C16-Cluster-2). All QTLs for both FL and FS had positive additive effects and all QTLs for both LP and FM had negative additive effects in one cluster (C21-Cluster-1). These QTL clusters revealed a strong negative genetic correlation between LP and FL and between LP and FS. Some previous reports detected similar clusters (Wang et al. 2011; Li et al. 2016b; Si et al. 2017), but these correlations were not explicitly mentioned in their reports.

These results provide an explanation for the significant phenotypic correlations between the related traits in different populations (Table S2) and indicate that these loci might function as pleiotropic genes or are closely linked to various other genes (Rong et al. 2007; Yu et al. 2013; Zhai et al. 2016).

In other words, 5 of the 10 clusters (C10-Cluster-1, C11-Cluster-1, C16-Cluster-1, C16-Cluster-2, and C17-Cluster-1), with stable or common QTLs related to 2 or more different traits, are important clusters and warrant further study for the simultaneous genetic improvement of fiber yield and quality in cotton (Table 4; Table S1). However, 3 clusters (C10-Cluster-1, C16-Cluster-1, and C16-Cluster-2) harbored negatively correlated stable QTLs or common QTLs between fiber quality and yield traits and could hinder the simultaneous improvement of these traits. Therefore, an in-depth study of this linkage mechanism and breaking the linkage drag between unfavorable QTLs/genes through gene fine mapping (Cao et al. 2015), gene-editing technology (Dahan-Meir et al. 2018; Durr et al. 2018) or other new technologies and methods would play an important role in cotton molecular breeding. In addition, with the same two parents (CCRI36 and Hai1), we have developed CSSLs that can be used for further study.

Conclusion

In conclusion, a total of 153 QTLs for fiber quality and yield traits were identified in 5 interspecific backcross populations using a high-density genetic linkage map. Of these QTLs, 30 were consistent with those identified previously. Importantly, 23 QTLs were stably detected in 2 or 3 populations or generations, 17 of which were novel stable QTLs. Ten QTL clusters for different traits were found, and 9 of them were novel.

The results provide valuable information for MAS in cotton breeding, QTL/gene cloning, understanding the genetic basis of fiber quality and yield traits in the two cultivated tetraploid species of cotton (*G. hirsutum* L. and *G. barbadense* L.) and genetically improving fiber quality and yield in cotton.

Acknowledgements This work was funded by the National Key R&D Program for Crop Breeding (2016YFD0100203) and the National Agricultural Science and Technology Innovation Project of the CAAS.

Author contributions YY conceived and designed the experiments. YS and BZ performed the experiments. AL and JL participated in field trials. JZ and MJ helped in data analyses. QL, JG, GQ, HS, WG SL, XX, XD and JP contributed reagents/materials/analysis tools. YS analyzed the data and drafted the manuscript. YY and JZ revised the manuscript. All the authors have read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

Ethical approval The authors declare that this study complies with the current laws of the country in which the experiments were performed. This article does not contain any studies with human participants or animals performed by any of the authors.

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