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Construction of a linkage map and QTL mapping for fiber quality traits in upland cotton (*Gossypium hirsutum* L.)

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With the development in spinning technology, the improvement of cotton fiber quality is becoming more and more important. The main objective of this research was to construct a high-density genetic linkage map to facilitate marker assisted selection for fiber quality traits in upland cotton (*Gossypium hirsutum* L.). A genetic linkage map comprising 421 loci and covering 3814.3 cM, accounting for approximately 73.35% of the cotton genome, was constructed using an F_2 population derived from cross GX1135 (P_1)×GX100-2 (P_2). Forty-four of 49 linkage groups were assigned to the 26 chromosomes. Fiber quality traits were investigated in F_2 population sampled from individuals, and in $F_{2:3}$, and $F_{2:4}$ generations sampled by lines from two sites and one respectively, and each followed a randomized complete block design with two replications. Thirty-nine quantitative trait loci were detected for five fiber quality traits with data from single environments (separate analysis each): 12 for fiber length, five for fiber uniformity, nine for fiber strength, seven for fiber elongation, and six for fiber micronaire, whereas 15 QTLs were found in combined analysis (data from means of different environments in $F_{2:3}$ generation). Among these QTLs, *qFL-chr5-2* and *qFL-chr14-2* for fiber length were detected simultaneously in three generations (four environments) and verified further by combined analysis, and these QTLs should be useful for marker assisted selection to improve fiber quality in upland cotton.

upland cotton (*Gossypium hirsutum* L.), fiber quality traits, genetic linkage map, marker assisted selection, QTLs

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Cotton (*Gossypium* spp.) is the most important natural fiber crop and is served as the second largest source of edible oil in the world. The genus *Gossypium* includes 45 diploid and 5 tetraploid species [1]. Cultivated types include two diploids, *Gossypium herbaceum* L. (A1) and *Gossypium arboreum* L. (A2), and two tetraploids, *Gossypium hirsutum* L. (AD1) and *Gossypium barbadense* L. (AD2). Of these, upland cotton (*G. hirsutum*) dominates the production of cotton fiber and accounts for 95% of the world's total production of cotton [2].

Cotton fiber is widely used as the raw materials for the textile industry. With the changes in spinning technology and diversificated uses, the improvement of cotton fiber quality is becoming extremely important [3]. However, fiber quality has a negative genetic correlation with lint yield [4,5], which has long been a major problem in cotton breeding. Recently, Chen et al. [6] integrated genome-wide expression profiling markers with linkage analysis to reveal the molecular mechanisms underlying fiber differential development between *G. barbadense* and *G. hirsutum*. The results suggested that differential gene regulation causes the difference in the quality of fiber between *G. barbadense* and *G. hirsutum*.

The development of molecular markers has made it possible for plant breeders to find a rapid and precise alternative approach for improving cotton lint yield and fiber quality traits [7]. Quantitative trait loci (QTL) mapping of fiber quality traits can be very helpful in revealing the genetic basis of various fiber quality characteristics and providing

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important information for improving cotton breeding strategies. QTLs conferring fiber quality traits have been identified and mapped using molecular markers in interspecific populations from crosses between *G. hirsutum* and *G. barbadense* [8–10]. A high-density interspecific genetic map was constructed, which includes 2316 loci on the 26 cotton chromosomes [11]. Unfortunately, these genetic maps developed from interspecific hybridization currently have limited use in conventional breeding [12]. Instead, saturated intraspecific upland cotton maps need to be constructed to offer more useful information. However, most intraspecific genetic maps were characterized by low marker coverage in the genome because the degree of molecular marker polymorphism is relatively low within *G. hirsutum*. Apparently, the current upland cotton genetic maps cannot meet the required coverage necessary for marker assisted selection (MAS). Therefore, it is necessary to construct a high-density genetic map of upland cotton using a large number of molecular markers [13].

To improve our understanding of the structure and genetic variability of the *G. hirsutum* genome, a comprehensive PCR-based marker linkage map for fiber quality that covered 70.6% of the upland cotton genome was constructed [14]. More recently, Zhang et al. [15] developed a composite crossing population in upland cotton and constructed a genetic map spanned 4184.4 cm, covering approximately 94.1% of the entire tetraploid cotton genome and containing 978 simple sequence repeat (SSR) loci. A draft physical map of a D-genome cotton species (*Gossypium raimondii* Ulbr., D5) has been completed [16–18] and the *G. hirsutum* genome is being sequenced (http://www.monsanto.com/newsviews/Pages/Monsanto-Illumina-Key-Milestone-Cotton-Genome-Sequencing.aspx), which will provide rich SSR markers and functional markers for construction of high-density genetic linkage map and QTL mapping for fiber quality traits to facilitate MAS. In the present study, a high-density genetic map was constructed using an F_2 population derived from an upland cotton hybrid and used for tagging cotton fiber quality in upland cotton.

1 Materials and methods

1.1 Plant materials

The hybrid of upland cotton ‘Xinza 1’ (*G. hirsutum*) from the cross of GX1135 (*G. hirsutum*) (P_1) and GX100-2 (*G. hirsutum*) (P_2) with significant competitive heterosis was bred by the Guoxin Seed Company (Hebei Province, China), and the hybrid was released as a cultivar in Anhui Province in 2006. In the present study, F_1 seeds were developed from a manual emasculated cross between P_1 and P_2 grown at the Guoxin South Propagation Station in Sanya, Hainan Province in winter 2006, and the F_1 seeds were then grown at the Xinzhou Cotton Breeding Station (Wuhan, 30°34′N, 114°16′E) in April 2007. The genotype of the F_1 individuals was distinguished by a codominant molecular marker, and an F_1 individual was self-pollinated to produce F_2 seeds. A total of 256 randomly selected F_2 seeds were cultured in nutrient solution [19] in green house at the China Agricultural University (Beijing) in October 2007. Each F_2 seedling was tagged, and root traits were scanned to survey the characters and development of relative traits (the results will be reported in another paper). All the F_2 seedlings were transported by air and transplanted at the Guoxin South Propagation Station and self-pollinated to produce F_3 seeds. The F_3 family lines were bulk self-pollinated to produce F_4 seeds. A population of 173 $F_{2:3}$ family lines were planted with the parents and F_1 as controls in 2008, and a population of 173 $F_{2:4}$ family lines were planted with the parents and F_2 as controls in 2009.

1.2 Field planting and examination

The field planting followed a randomized complete block design with two replications, at the Quzhou Experimental Station of the China Agricultural University (Handan, 36°78′N, 114°92′E) and the Guoxin Cotton Breeding Experimental Station (Cangzhou, 38°43′N, 116°09′E). The nutrition bowl cultivation method was implemented, and 25-day-old seedlings were transplanted in spaced 30 cm between plants in two-row plot. Plots were 4 m in length with 80 cm row spacing for the experiment at Handan, and 4 m in length and 80 cm, 60 cm row spacing alternately for the experiment at Cangzhou in 2008. The direct seeding method was carried out and planted in two-row plot, 80 cm, 60 cm wide alternately and 4 m long in Handan in 2009. Field management followed conventional standard field practices.

Fiber samples were collected from plants growing in the middle of the interior of each plot. Fiber quality traits were investigated in F_2 population sampled from individuals, and in $F_{2:3}$, and $F_{2:4}$ generations sampled by lines from two sites and one, respectively, and each followed a randomized complete block design with two replications. Fiber quality traits were measured with an HVI 900 instrument (USTER® HVISPECTRUM, SPINLAB, United States) at the Cotton Fiber Quality Inspection and Test Center of Ministry of Agriculture (Anyang, China). The fiber quality traits included 2.5% fiber span length (mm), fiber length uniformity ratio, fiber strength (cN/tex), fiber elongation, and fiber fineness (micronaire reading).

1.3 DNA extraction and genotype analysis

Young leaves were collected from labeled F_2, P_1, P_2, and F_1 individuals, frozen in liquid nitrogen, and stored at −80°C until analysis. Genomic DNA was individually extracted according to the CTAB method [20]. A total of 16405 SSR primer pairs were used to screen for polymorphic markers between P_1 and P_2. Among these primers, 13468 pairs of primers included types of BNL, NAU, TM, JESPER, CIR,

HAU, CM, MUSS, MUSB, and MUCS, which were previously described in detail [8–10,14,21,22]; information on these primers can be obtained from the Cotton Microsatellite Database (http://www.cottonmarker.org). The remaining 2937 primer pairs were designed and developed from the DNA sequence library [23]. The 450 SSR primer pairs that showed polymorphisms between the two mapping parents were used to genotype 173 individuals from the F_2 population. The procedure for SSR analysis was that described by Mei et al. [24].

1.4 Map construction and QTL analysis

MAPMAKER 3.0b [25] was implemented to construct a genetic linkage map. The assignment of linkage groups to chromosomes was based on backbone linkage maps [4,8,9, 13,14,26]. When no chromosome inference was available, the linkage group was described as un××, where ×× refers to its serial number. QTLs were analyzed by composite interval mapping [27] using the computer program QTL Cartographer 2.5 [28].

A stringent LOD threshold of 3.0 was used to declare a suggestive QTL, as described by Lander et al. [29], whereas the same QTL in another environment with LOD of at least 2.0 was considered to be a common QTL, as described by Shen et al. [30]. QTL mapping was carried out for data sets from single environment (separate analysis for each environment in three generations) following Zhang and Xu [31], and a set of data from the means of different environments in $F_{2:3}$ generation (combined analysis). The graphic representation of the linkage group and QTLs marked were created by Map Chart 2.2, following Voorrips et al. [32].

2 Results

2.1 Evaluation of fiber quality traits in the F_2, $F_{2:3}$, $F_{2:4}$ populations and two parents

Midparent heterosis of fiber quality traits was assessed. 'Xinza 1' was an elite hybrid upland cotton and showed significant heterosis in seed-cotton yield and lint yield, the mid-parent heterosis values were 56.23% and 62.01%, respectively. In contrast, fiber quality traits showed almost no heterosis. The phenotypic data for fiber quality traits of the F_2, $F_{2:3}$, $F_{2:4}$ populations and F_1, the two parents are summarized in Table 1. The values of most fiber quality traits in the F_2, $F_{2:3}$ and $F_{2:4}$ populations fell between those of the two parents. Skewness and kurtosis values (data not shown) were calculated; the results indicated that all fiber quality traits fit a normal distribution and all the traits expressed transgressive segregation in both directions in the F_2, $F_{2:3}$ and $F_{2:4}$ populations (Figure S1).

Table 1 Phenotypic values for fiber quality traits of the F_2, $F_{2:3}$, and $F_{2:4}$ populations and midparent heterosis of F_1 and F_2

Traits	Mean	SD	Min	Max	GX1135	GX100-2	Xinza 1	Midparent heterosis (%)
07Hn[a)]								
Fiber length (mm)	28.31	0.94	25.65	31.65	–	–	–	–
Fiber uniformity ratio	83.34	1.18	79.90	85.80	–	–	–	–
Fiber strength (cN/tex)	25.95	1.33	22.00	29.70	–	–	–	–
Fiber elongation	6.36	0.14	5.80	6.70	–	–	–	–
Micronaire	3.65	0.51	2.16	4.92	–	–	–	–
08Qz[b)]							F_1	
Fiber length (mm)	29.72	0.88	27.01	31.88	29.88	29.51	30.17	1.60
Fiber uniformity ratio	84.73	0.77	82.50	86.90	84.15	84.80	83.40	–1.27
Fiber strength (cN/tex)	29.36	1.10	26.55	31.90	29.50	28.90	28.95	–0.86
Fiber elongation	6.51	0.09	6.15	6.70	6.55	6.50	6.45	–1.15
Micronaire	4.64	0.38	3.55	5.72	5.31	4.59	4.26	–14.00
08Hj[c)]							F_1	
Fiber length (mm)	29.66	0.94	27.18	32.47	29.85	29.19	30.35	2.81
Fiber uniformity ratio	84.13	0.91	81.90	86.55	85.00	83.50	83.70	–0.65
Fiber strength (cN/tex)	28.32	1.14	25.80	31.85	29.05	27.50	28.10	–0.62
Fiber elongation	6.42	0.11	6.10	6.70	6.40	6.35	6.25	–1.96
Micronaire	4.84	0.41	3.63	6.15	4.95	4.65	4.15	–13.60
09Qz[d)]							F_2	
Fiber length (mm)	30.21	0.87	28.14	32.59	29.09	30.11	30.62	3.45
Fiber uniformity ratio	84.65	0.89	82.45	86.40	84.30	85.40	85.85	1.18
Fiber strength (cN/tex)	32.82	1.23	29.75	36.20	32.50	31.50	32.15	0.47
Fiber elongation	6.70	0.09	6.45	6.95	6.60	6.65	6.80	2.64
Micronaire	3.91	0.30	3.12	4.66	4.09	3.85	4.61	16.14

a) Fiber quality data of F_2 harvested from Hainan in 2007; b) Fiber quality data of $F_{2:3}$ harvested from Handan in 2008; c) Fiber quality data of $F_{2:3}$ harvested from Cangzhou in 2008; d) Fiber quality data of $F_{2:4}$ harvested from Handan in 2009. –, missing data.

2.2 Correlation analyses of common fiber quality traits among the F_2, $F_{2:3}$ and $F_{2:4}$ generations

Correlation analysis was carried out using the mean values of F_2, $F_{2:3}$ and $F_{2:4}$ (Table 2). The majority of fiber quality traits were significantly associated with each other. Correlation analysis between traits of different generations was conducted using the mean value of the four environments too (Table 3). All correlation of fiber length was significantly positively correlated among generations, and the correlation coefficients among generations varied greatly from 0.31 to 0.52. The majority of correlation coefficient of fiber uniformity ratio was significantly positively correlated among generations. Correlation analysis of fiber strength, fiber elongation and micronaire showed the similar tendency among generations.

2.3 Linkage map construction

To construct a high-density genetic linkage map in upland

Table 2 Correlation analyses among fiber quality traits of the F_2, $F_{2:3}$, and $F_{2:4}$ populations

Trait	Population	Fiber length	Fiber uniformity ratio	Fiber strength	Fiber elongation
Fiber uniformity ratio	07Hn F_2[a)]	0.51**			
	08Qz $F_{2:3}$[b)]	0.46**			
	08Hj $F_{2:3}$[c)]	0.48**			
	09Qz $F_{2:4}$[d)]	0.46**			
Fiber strength	07Hn F_2	0.52**	0.48**		
	08Qz $F_{2:3}$	0.71**	0.35**		
	08Hj $F_{2:3}$	0.70**	0.49**		
	09Qz $F_{2:4}$	0.58**	0.37**		
Fiber elongation	07Hn F_2	0.45**	0.41**	0.79**	
	08Qz $F_{2:3}$	0.56**	0.45**	0.47**	
	08Hj $F_{2:3}$	0.60**	0.56**	0.62**	
	09Qz $F_{2:4}$	0.53**	0.33**	0.60**	
Micronaire	07Hn F_2	–0.28**	0.11	0.09	0.35**
	08Qz $F_{2:3}$	–0.12	0.27**	–0.38**	0.24**
	08Hj $F_{2:3}$	0.02	0.32**	–0.18*	0.34**
	09Qz $F_{2:4}$	–0.12	0.07	–0.17*	0.19*

a) Fiber quality data of F_2 harvested from Hainan in 2007; b) Fiber quality data of $F_{2:3}$ harvested from Handan in 2008; c) Fiber quality data of $F_{2:3}$ harvested from Cangzhou in 2008; d) Fiber quality data of $F_{2:4}$ harvested from Handan in 2009. "*" and "**" indicate that the correlation is significant at 0.05 and 0.01 probability levels, respectively.

Table 3 Correlation analyses of the same fiber quality traits among different generations

Trait	07Hn F_2[a)]	08Qz $F_{2:3}$[b)]	08Hj $F_{2:3}$[c)]
08Qz $F_{2:3}$ Fiber length	0.45**		
08Hj $F_{2:3}$ Fiber length	0.40**	0.52**	
09Qz $F_{2:4}$[d)] Fiber length	0.31**	0.51**	0.41**
08Qz $F_{2:3}$ Fiber uniformity ratio	0.16*		
08Hj $F_{2:3}$ Fiber uniformity ratio	0.05	0.26**	
09Qz $F_{2:4}$ Fiber uniformity ratio	0.20**	0.24**	0.17*
08Qz $F_{2:3}$ Fiber strength	0.34**		
08Hj $F_{2:3}$ Fiber strength	0.13	0.32**	
09Qz $F_{2:4}$ Fiber strength	0.11	0.48**	0.35**
08Qz $F_{2:3}$ Fiber elongation	0.24**		
08Hj $F_{2:3}$ Fiber elongation	–0.12	0.19*	
09Qz $F_{2:4}$ Fiber elongation	0.08	0.32**	0.32**
08Qz $F_{2:3}$ Micronaire	0.06		
08Hj $F_{2:3}$ Micronaire	0.07	0.24**	
09Qz $F_{2:4}$ Micronaire	0.05	0.32**	0.25**

a) Fiber quality data of F_2 harvested from Hainan in 2007; b) Fiber quality data of $F_{2:3}$ harvested from Handan in 2008; c) Fiber quality data of $F_{2:3}$ harvested from Cangzhou in 2008; d) Fiber quality data of $F_{2:4}$ harvested from Handan in 2009. "*" and "**" indicate that the correlation is significant at 0.05 and 0.01 probability levels, respectively.

cotton, 16405 primer pairs were screened between P_1 and P_2. The 450 SSR primer pairs that showed polymorphism between the two mapping parents were used to construct a linkage map using the F_2 population. *Chi*-square goodness-of-fit test was conducted to determine whether the genotypic frequencies differ significantly from the expected segregation ratio. Most of the loci (439 of 450) fitted to the segregation ratio of 1∶2∶1 or 1∶1 and were used to construct the linkage map. The genetic linkage map, consisting of 421 loci linked into 49 groups and left 29 loci unlinked and covering 3814.3 cm of the total recombination length of the cotton genome, was constructed with an average interval of 8.89 cM between adjacent loci and accounted for approximately 73.35% of the recombination length of the upland cotton genome. Forty-four of 49 linkage groups were assigned to the 26 chromosomes based on previously chromosome-anchored backbone linkage maps [8–10,14,21,22]. The remaining five linkage groups named 'Un 01' to 'Un 05' tentatively could not be associated with any chromosome.

2.4 QTL mapping for fiber quality traits

Thirty-nine QTLs for fiber quality traits were identified in the four environments in separate analysis, and fifteen of them were detected in the combined analysis in $F_{2:3}$ generation (Table 4).

Table 4 QTLs for fiber quality traits in the F_2, $F_{2:3}$, and $F_{2:4}$ populations identified using composite interval mapping

Trait	Environment	QTL	Chr.	Maker interval		Position (cM)	LOD	A[a)]	D[b)]	Var (%)[c)]
Fiber length	08Qz	*qFL-chr5-1**	5	MUSS193	NAU2865	35.68	7.46	–0.52	–0.01	14.77
	08Hj		5	MUSS193	NAU2865	33.68	9.45	–0.62	–0.08	20.12
	07Hn	*qFL-chr5-2*#*	5	NAU4034	HAU1316	44.29	2.47	–0.08	–0.29	5.40
	08Qz		5	HAU1603	TMB1296	38.92	7.42	–0.50	0.02	14.06
	08Hj		5	NAU4034	HAU1316	54.29	5.32	–0.48	0.19	15.73
	09Qz		5	HAU1315	NAU4034	42.67	7.62	–0.58	0.15	17.43
	08Qz	*qFL-chr10-1*#*	10	BNL2960	CGR5873	79.66	4.58	0.34	0.10	10.50
	09Qz		10	CGR5873	GH144	83.43	2.13	0.17	0.12	3.98
	08Qz	*qFL-chr13-1*#*	13	DPL687	DPL286	140.49	8.76	–0.47	–0.31	20.18
	08Hj		13	DPL687	DPL286	140.49	3.07	–0.26	–0.20	6.56
	07Hn	*qFL-chr14-1*#*	14	HAU1455	GH120	72.60	2.77	0.37	–0.14	6.51
	08Qz		14	CGR6683	HAU1057	83.06	3.15	0.30	–0.06	5.54
	08Hj		14	DPL565	CGR6683	78.05	2.58	0.34	–0.15	5.37
	07Hn	*qFL-chr14-2*#*	14	HAU1057	NAU3839	83.85	2.47	0.35	–0.09	5.96
	08Qz		14	NAU3308	CGR6802	88.52	3.42	0.33	–0.05	6.27
	08Hj		14	CGR6802	CGR6784	91.93	3.71	0.41	–0.18	7.34
	09Qz		14	BNL3033	BNL2469	84.44	3.25	0.35	–0.13	5.98
	07Hn	*qFL-chr3-1*	3	CER028	GH663	12.54	3.02	0.07	0.37	6.91
	08Hj	*qFL-chr3-2*	3	CGR6528	CGR6017	39.95	3.56	0.39	–0.14	6.33
	09Qz	*qFL-chr8-1*	8	GH398	DPL090	54.13	3.17	–0.15	0.47	7.41
	09Qz	*qFL-chr11-1*	11	CGR5602	DPL050a	69.77	4.22	0.24	0.20	10.64
	07Hn	*qFL-chr12-1*	12	DPL303	NAU943	13.49	3.77	–0.41	0.01	9.24
	08Hj	*qFL-chr13-2*	13	BNL1495	DPL687	128.09	3.49	–0.18	–0.31	6.20
Fiber uniformity ratio	07Hn	*qFU-chr2-1*#*	2	TMB1268	JESP304	33.61	2.91	–0.54	0.53	7.35
	08Hj		2	JESP304	CIR112	34.6	3.01	0.22	–0.45	6.09
	08Hj	*qFU-chr5-1*#*	5	MUSS193	NAU2865	35.68	6.54	–0.39	–0.28	15.93
	08Qz		5	NAU2865	GH388	37.34	4.46	–0.41	0.02	11.42
	09Qz	*qFU-chr14-1*	14	CGR5675	CGR5871a	37.57	3.17	0.00	0.40	7.12
	07Hn	*qFU-chr18-1*	18	GH60	DC40150a	35.85	3.38	0.32	0.35	9.11
	08Hj	*qFU-chr26-1*	26	BNL2495	DPL070	89.09	3.52	0.44	0.09	7.75
Fiber	07Hn	*qFS-chr1-1**	1	DPL182	DC40175	77.62	3.26	–0.41	0.78	7.92

(*To be continued on the next page*)

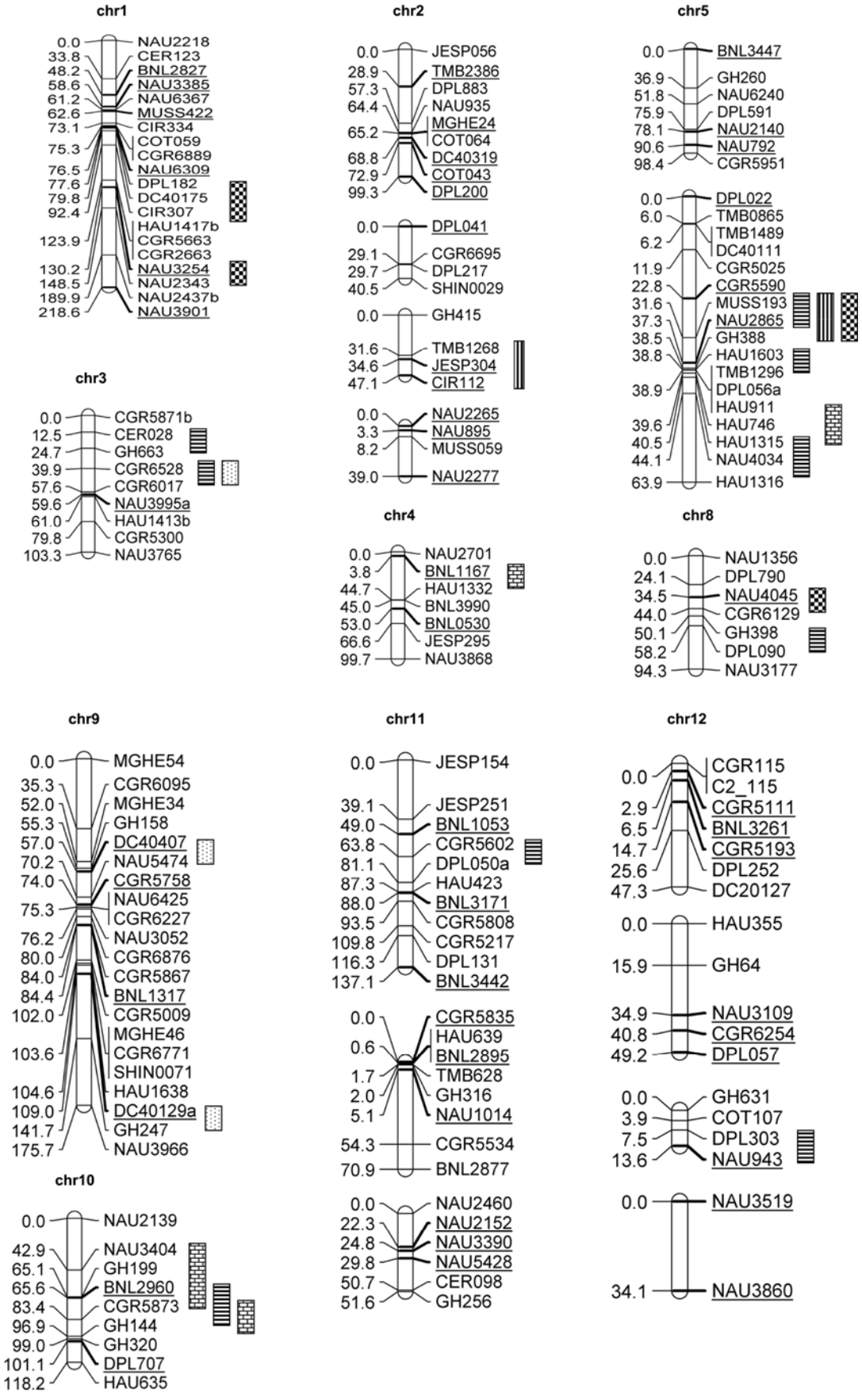
(*Continued*)

Trait	Environment	QTL	Chr.	Maker interval		Position (cM)	LOD	A[a)]	D[b)]	Var (%)[c)]
strength	08Hj		1	DC40175	CIR307	87.83	2.18	–0.19	0.58	7.06
	09Qz		1	CIR307	HAU1417b	100.44	3.47	–0.48	0.85	12.46
	08Qz	*qFS-chr5-1*#*	5	NAU2865	GH388	37.34	3.39	–0.43	–0.04	7.35
	08Hj		5	MUSS193	NAU2865	35.68	4.69	–0.37	–0.32	11.65
	09Qz		5	NAU2865	GH388	37.34	3.24	–0.59	0.18	7.78
	08Qz	*qFS-chr13-1*#*	13	DPL687	DPL286	140.49	8.22	–0.54	–0.51	22.08
	09Qz		13	DPL687	DPL286	142.49	2.58	–0.10	–0.54	7.14
	08Qz	*qFS-chr18-1*#*	18	CIR099	CIR216	67.40	2.19	–0.46	0.52	7.70
	09Qz		18	DPL077	CIR099	52.20	2.36	–0.51	0.20	6.33
	08Qz	*qFS-chr1-2*	1	NAU3254	NAU2343	130.31	3.64	–0.49	0.06	7.60
	07Hn	*qFS-chr8-1*	8	NAU4045	CGR6129	34.52	3.28	0.70	–0.13	8.91
	08Hj	*qFS-chr17-1*	17	HAU1413a	HAU1417a	0.01	3.61	0.33	–0.04	8.45
	08Qz	*qFS-chr18-2*	18	BNL243	CER168	19.66	3.29	0.28	–0.69	9.78
	09Qz	*qFS-chr24-1*	24	NAU4064	CGR6508	99.98	3.03	–0.20	–0.67	9.51
Fiber elongation	08Hj	*qFE-chr5-1*#*	5	HAU746	HAU1315	39.76	4.95	–0.05	–0.01	10.62
	09Qz		5	HAU911	HAU746	39.08	4.66	–0.05	0.01	10.55
	08Hj	*qFE-chr10-1**	10	BNL2960	CGR5873	65.66	2.87	–0.05	0.02	5.89
	09Qz		10	NAU3404	GH199	64.97	3.54	0.01	0.04	7.67
	07Hn	*qFE-chr24-1*#*	24	DPL588	GH197	132.22	3.70	–0.02	0.09	10.76
	08Hj		24	DPL588	GH197	132.22	3.73	–0.04	–0.01	8.06
	09Qz		24	CGR6508	DPL588	119.15	2.85	–0.02	–0.02	9.44
	07Hn	*qFE-chr4-1*	4	BNL1167	HAU1332	32.79	3.31	–0.07	0.07	9.28
	08Hj	*qFE-chr10-2*#*	10	CGR5873	GH144	89.43	5.01	0.05	0.02	13.70
	08Qz	*qFE-chr24-2*	24	NAU3934	CGR5423	56.54	4.79	0.00	0.05	10.84
	08Qz	*qFE-chr25-1*	25	CER042	GH220	35.92	3.82	–0.01	–0.03	9.02
Fiber micronaire	08Hj	*qFM-chr19-1**	19	CGR5539	NAU2894	67.87	3.29	0.17	0.00	9.66
	09Qz		19	CGR5539	NAU2894	65.87	2.34	0.01	0.19	9.59
	08Qz	*qFM-chr3-1*	3	CGR6528	CGR6017	39.95	3.05	–0.17	0.14	6.48
	08Qz	*qFM-chr9-1*#*	9	DC40407	NAU5474	65.01	4.59	–0.27	0.04	13.16
	08Hj	*qFM-chr9-2*#*	9	DC40129a	GH247	131.23	3.06	–0.02	–0.23	13.27
	09Qz	*qFM-chr19-2*	19	DPL210	GH72	37.45	4.72	–0.17	0.07	11.13
	08Hj	*qFM-chr26-1*	26	NAU2175	DPL491	44.01	3.27	0.15	0.00	16.02

a) Additive effect: positive values indicate that GX1135 alleles increase the traits scores, and negative values indicate that GX100-2 alleles increase the trait scores; b) dominance effect: positive values of the dominance effect indicate that heterozygotes have higher phenotypic values than the respective means of two homozygotes, and negative values indicate that heterozygotes have lower values than the means of the two homozygotes; c) phenotypic variation explained by a single QTL. #, The QTL was detected in combined analysis. *, QTL were identified in two or more environments.

(i) Fiber length. Twelve QTLs for fiber length were identified, in which QTLs *qFL-chr5-2* and *qFL-chr14-2* were detected in the four environments and in the combined analysis simultaneously (Table 4, Figure 1). QTL *qFL-chr5-2* was mapped in the same interval in the four environments but gene effects differed in magnitude, which had a range of phenotypic variance (PV) from 5.40% to 17.43%. At this QTL, the GX100-2 allele increased fiber length. QTL *qFL-chr14-2* was another major QTL detected in the four environments. All additive effects were positive, indicating that the GX1135 allele increased phenotypic effect. The two QTLs should be suitable for MAS in cotton breeding because they were stably expressed in all experimental environments.

(ii) Fiber uniformity ratio. Five QTLs for fiber uniformity ratio were identified on chromosomes 2, 5, 14, 18, and 26 (Table 4). Two QTLs were identified on chromosomes 2 and 5 in more than one environment. The additive effect of QTL *qFU-chr2-1* was negative in the 07Hn environment, indicating that the GX100-2 allele increases phenotypic effect, whereas the additive effect was positive in the 08Hj environment, indicating that the GX1135 allele increases phenotypic effect; this QTL contributed 7.35% and 6.09% of phenotypic effect in 07Hn and 08Hjv environments, respectively. QTL *qFU-chr5-1* contributed 11.42% and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chr5
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chr9
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39.1 JESP251
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81.1 DPL050a
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93.5 CGR5808
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24.8 NAU3390
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51.6 GH256
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C2_115
2.9 CGR5111
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40.8 CGR6254
49.2 DPL057
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3.9 COT107
7.5 DPL303
13.6 NAU943
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34.1 NAU3860
chr10
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42.9 NAU3404
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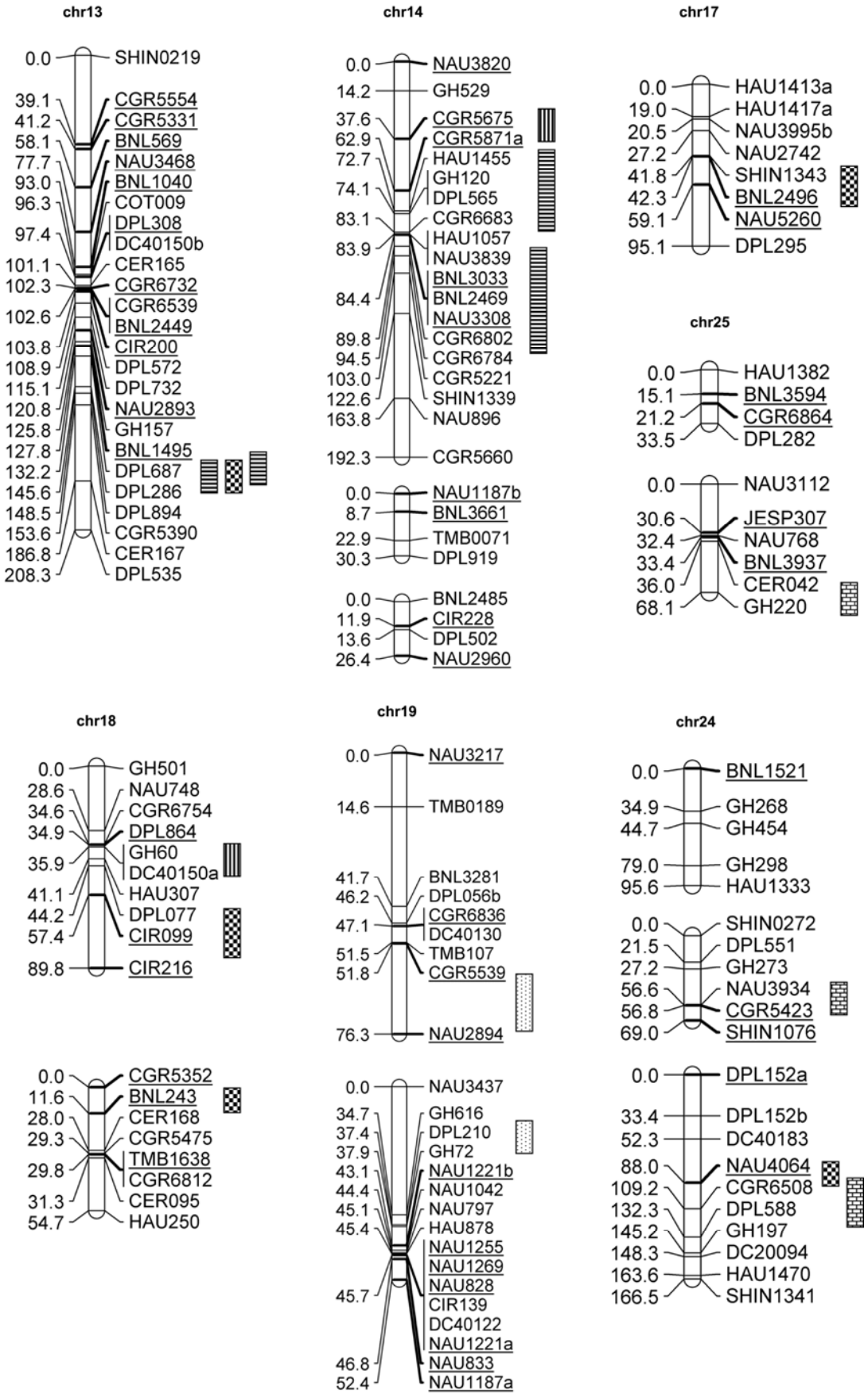
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22.9 TMB0071
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13.6 DPL502
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chr17
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20.5 NAU3995b
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59.1 NAU5260
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chr25
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15.1 BNL3594
21.2 CGR6864
33.5 DPL282
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33.4 BNL3937
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chr18
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28.6 NAU748
34.6 CGR6754
34.9 DPL864
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DC40150a
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44.2 DPL077
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89.8 CIR216
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28.0 CER168
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CGR6812
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chr19
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37.9 GH72
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44.4 NAU1042
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NAU1255
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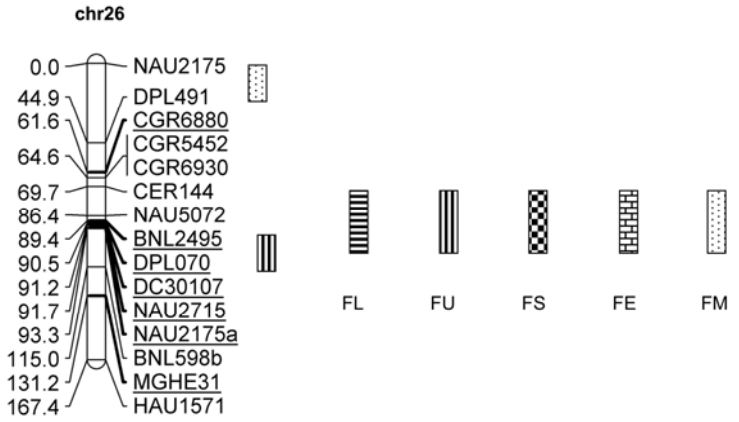

Figure 1 Mapping of QTLs for fiber quality traits in four environments. FL, fiber length; FU, fiber uniformity; FM, fiber micronaire; FE, fiber elongation; FS, fiber strength (Only those chromosomes which QTL were mapped to are shown). Markers underlined were published previously.

15.93% of PV in the 08Qz and 08Hj environments, respectively. This QTL were also detected in the combined analysis.

(iii) Fiber strength. Nine QTLs for fiber strength were detected in which two QTLs, *qFS-chr5-1* and *qFS-chr18-1*, were detected in the combined analysis simultaneously (Table 4). QTL *qFS-chr1-1* was detected in three environments, explaining from 7.06% to 12.46% of PV, and its additive effect was negative, indicating that the GX100-2 allele increases PV. QTL *qFS-chr5-1* was also detected in three environments. The QTLs *qFL-chr5-1* and *qFU-chr5-1* were also identified and mapped in the same interval, suggesting that these traits are controlled by the same genes and represent QTLs with pleiotropic effects.

(iv) Fiber elongation. Seven significant QTLs for fiber elongation were detected on chromosomes 4, 5, 10, 24, and 25 (Table 4). QTL *qFE-chr24-1* was identified and mapped in neighboring intervals in the three environments, and which was detected in the combined analysis too, with a range of LOD scores from 2.85 to 3.73. At this QTL, the GX1135 allele conferred finer fiber. In addition, a significant QTL *qFE-chr10-2* was meanwhile detected on chromosome 10 in the combined analysis, which showed the largest effects and explained 13.70% of PV.

(v) Fiber micronaire. Six QTLs for fiber micronaire were identified. QTL *qFM-chr19-1* was identified in two environments. Its additive effect was positive, indicating that the GX1135 allele increases PV, contributing 9.66% and 9.59% of PV in 08Hj and 09Qz environments, respectively. In addition, QTL *qFM-chr9-1* and *qFM-chr9-2* were detected in the combined analysis, which explained 13.16% and 13.27% of PV, respectively (Table 4).

3 Discussion

3.1 QTLs for cotton fiber quality traits

Here we found many common characteristics of QTLs related to fiber quality traits as described in the previous reports involving interspecific maps [3,10,23,33–38] and intraspecific maps [12,15,26,30,39–46], although few common markers were used in the present research and the previous studies, and the maps covered different region parts of cotton genome, making it difficult to compare the common QTLs, some QTLs were detected and mapped on the same chromosomes and affect common traits. These include seven QTLs for fiber length located in the same chromosomal regions as reported earlier [10,26,34,41,42], two QTLs for fiber uniformity ratio located in the same chromosomal regions [43,46], two QTLs for fiber micronaire [10,43,44], three QTLs for fiber elongation [30,36,42,43,46,47], and 4 QTLs for fiber strength [26,34,36,43,44,46,47]. For example, the chromosome regions where QTLs were detected for fiber length in our research matched those in an interspecific map developed from an F_2 population [10]; the QTLs may be common QTLs for fiber quality traits. These stable and consensus QTLs for fiber quality traits will enable the use of MAS to improve fiber quality of future cotton cultivars. To use MAS and dissect the genetic basis of fiber quality traits, however, it is necessary to develop more common SSR markers for use by different research groups.

3.2 Marker assisted selection for fiber quality traits

The demand for improved cotton fiber quality has risen with the advent of open-end, air-jet, and vortex spinning. Breeders have long recognized a significant negative association between lint yield and fiber quality. Although conventional breeding has played a vital role in the genetic improvement of lint yield and fiber quality in upland cotton, the achievement and progress has been slow [14].

The utilization of molecular markers makes it possible for plant breeders to identify rapid and precise approaches to conventional selection schemes [7]. For example, the major QTL *QTLFS1* was detected in three environments (Nanjing and Hainan, China, and College Station, Texas, USA) using F_2 and F_3 populations derived from a cross be-

tween 7235 and TM-1; this QTL was found to be associated with eight markers and explained more than 30% of the PV [45]. MAS revealed that DNA markers linked to *QTLFS1* could be used to increase the fiber strength of upland cotton. Guo et al. [48] provided a successful example of MAS pyramiding for QTLs for favorable traits in breeding programs; two QTLs were detected for fiber strength, which greatly improved the selection efficiency for fiber strength by MAS. Shi et al. [49] used two SSR markers linked tightly with a major QTL for fiber strength to increase fiber strength through MAS. Dong et al. [50] pyramided high fiber strength genes and an insect resistance gene by MAS. The results indicated that the genetic effect of the QTL was stable and significant in different environmental conditions. Thus, major QTLs were both possible and efficient to improve fiber quality of cotton by MAS. In the *t1* locus region on chromosome 6, Wan et al. [51] detected QTLs affecting fiber length, fiber strength, fiber length uniformity, and spiny bollworm resistance that increased the trait phenotypic values. Because all the QTLs were mapped within about 5 cM of the *t1* locus, this locus could be considered as the candidate gene for the QTLs, which should be particularly useful in MAS manipulation of fiber yield and quality.

In the present research, QTLs *qFL-chr5-2* and *qFL-chr14-2* for fiber length were detected in three generations (four environments) and the combined analysis (data from means of different environments in $F_{2:3}$ generation) simultaneously. That is, the two QTLs were expressed stably in different generations and environments, which should be useful for MAS for fiber quality traits in upland cotton. Dong et al. [51] screened three SSR markers linked with QTLs for fiber length and studied the effect of MAS and pyramiding breeding in the three combinations. These results suggest that the construction of a saturated linkage map for *G. hirsutum*, the DNA markers associated with the QTL is an effective means to improve fiber quality by MAS and by pyramiding QTL in upland cotton breeding programs.

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Supporting Information

Figure S1 Variation of fiber quality traits in F_2, $F_{2:3}$ and $F_{2:4}$ populations.

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