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ORIGINAL PAPER

Mapping quantitative trait loci for lint yield and fiber quality across environments in a *Gossypium hirsutum* × *Gossypium barbadense* backcross inbred line population

Jiwen Yu · Ke Zhang · Shuaiyang Li · Shuxun Yu · Honghong Zhai · Man Wu · Xingli Li · Shuli Fan · Meizhen Song · Daigang Yang · Yunhai Li · Jinfa Zhang

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Abstract Identification of stable quantitative trait loci (QTLs) across different environments and mapping populations is a prerequisite for marker-assisted selection (MAS) for cotton yield and fiber quality. To construct a genetic linkage map and to identify QTLs for fiber quality and yield traits, a backcross inbred line (BIL) population of 146 lines was developed from a cross between Upland cotton (*Gossypium hirsutum*) and Egyptian cotton (*Gossypium barbadense*) through two generations of backcrossing using Upland cotton as the recurrent parent followed by four generations of self pollination. The BIL population together with its two parents was tested in five environments representing three major cotton production regions in China. The genetic map spanned a total genetic distance of 2,895 cM and contained 392 polymorphic SSR loci with an average genetic distance of 7.4 cM per marker. A total of 67 QTLs including 28 for fiber quality and 39 for yield and its components were detected on 23 chromosomes, each of which explained 6.65–25.27 % of the phenotypic variation. Twenty-nine QTLs were located on the At subgenome originated from a cultivated diploid cotton, while 38 were on the Dt subgenome from an ancestor that does not produce spinnable fibers. Of the eight common QTLs (12 %) detected in more than two environments, two were for fiber quality traits including one for fiber strength and one for uniformity, and six for yield and its components including three for lint yield, one for seedcotton yield, one for lint percentage and one for boll weight. QTL clusters for the same traits or different traits were also identified. This research represents one of the first reports using a permanent advanced backcross inbred population of an interspecific hybrid population to identify QTLs for fiber quality and yield traits in cotton across diverse environments. It provides useful information for transferring desirable genes from *G. barbadense* to *G. hirsutum* using MAS.

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J. Yu · K. Zhang · S. Li · S. Yu (✉) · H. Zhai · M. Wu · X. Li · S. Fan · M. Song · D. Yang · Y. Li
State Key Laboratory of Cotton Biology, Cotton Research Institute, Chinese Academy of Agricultural Science, Anyang 455000, Henan, China
e-mail: yujw666@hotmail.com

J. Zhang (✉)
Department of Plant and Environmental Sciences, New Mexico State University, Las Cruces, NM 88003, USA
e-mail: jinzhang@nmsu.edu

Introduction

Cotton is an important economic crop worldwide, which provides the most important natural fiber for the textile industry. There are four cultivated cotton species including two diploids *Gossypium herbaceum* L. and *G. arboreum* L., and two tetraploids *Gossypium hirsutum* L. and *Gossypium barbadense* L. However, approximately 95 % of the world cotton production is from Upland cotton (*G. hirsutum* L.) (Chen et al. 2007). Another cultivated tetraploid species, *G. barbadense* L., has superior extra-long, strong and fine fiber properties, but is grown in only limited areas due to its relatively low yield and narrow adaptation. The demand for higher cotton fiber quality has increased with the advent of more open-end, air-jet and vortex spinning technologies. However, it is a challenging task for breeders to develop cultivars with both high yield and good fiber quality. Attempts in utilizing interspecific crosses between Upland cotton and *G. barbadense* by conventional breeding have been made for more than a century, but with a very limited

impact on cultivar development, because of the negative genetic correlation between fiber quality and lint yield, linkage drag and hybrid breakdown (Zhang and Percy 2007). However, molecular quantitative genetics using molecular markers has facilitated the application of mapping quantitative trait loci (QTLs) for fiber quality and yield and marker-assisted selection (MAS) to simultaneously improve cotton yield and fiber quality.

Since the first molecular linkage map in cotton was reported by Reinisch et al. (1994), many interspecific genetic maps have been developed from crosses between Upland cotton and *G. barbadense* (Jiang et al. 1998, 2000; Kohel et al. 2001; Paterson et al. 2003; Zhang et al. 2002, 2008; Lacape et al. 2003, 2005, 2009; Nguyen et al. 2004; Rong et al. 2004; Park et al. 2005; Song et al. 2005; Han et al. 2004, 2006; Guo et al. 2007; He et al. 2005, 2007; Lin, et al. 2005, 2009; Yu et al. 2007, 2010, 2011). Many of these linkage maps were used to identify QTLs for fiber quality and yield traits. Though numerous QTLs have been reported (Zhang and Percy 2007; Lacape et al. 2010), few reliable and stable major QTLs were validated due mainly to the lack of permanent mapping populations that can be repeatedly tested in multiple environments. Ways of improving the power and accuracy in QTL detection are increasing population size, number of DNA makers, and testing environments (Asins 2002). One major QTL for fiber strength was identified in an $F_2/F_{2:3}$ population and its derived recombinant inbred lines (RILs) (Shen et al. 2005, 2007). Therefore, stable major QTLs could be identified through replicated trials in multiple environments and using proper mapping populations.

Although the importance of developing permanent RIL populations from interspecific *G. hirsutum* × *G. barbadense* was long recognized, hybrid breakdown and weakness due to the interspecific incompatibilities have impeded the successful use of the RIL populations in marker and QTL mapping until recently. However, only fiber quality traits were evaluated and no yield and yield traits have been mapped using an interspecific RIL population due to the poor field performance and low productivity (Lacape et al. 2010). To circumvent this problem, we resorted to develop a backcross inbred line (BIL) population from a cross between Upland cotton and *G. barbadense* to identify QTLs including stable ones for fiber quality and yield traits in different environments (years and locations). The use of the BIL strategy, proposed by Wehrhahn and Allard (1965), is especially suitable for identification and introgression of desirable genes from a wild or unadapted germplasm into an elite background and has been used in many crops (e.g. Matsubara et al. 2008). Using BILs, only limited regions from a donor parent are transferred to a recurrent parent through backcrossing, which can be repeatedly tested and mapped. In interspecific Upland cotton × *G. barbadense* crosses, "crazy" segregants, which are infertile or poorly productive and often encountered in early segregating or RIL populations, are minimized through backcrossing, and chromosome segments transferred from *G. barbadense* to Upland cotton are stabilized through several generations of backcrossing followed by selfing. This study represents one of the first reports using BILs in cotton to identify congruent QTLs from different environments.

Materials and methods

Materials and field tests

An interspecific backcross inbred line (BIL) population of 146 lines was used in this study. The BIL population was developed from a cross between Upland cotton SureGrow (SG 747) and *G. barbadense* Giza 75 through two generations of backcrossing using SG 747 as the recurrent parent followed by four generations of selfing. The 146 BILs and their two parents were planted in five environments in three locations: Anyang, Henan province in 2006, 2007 and 2008; Wangjing, Anhui province in 2007; and Aksu, Xinjiang Uyghur Autonomous Region in 2007. The three locations represent the major cotton production regions with three different cultivation systems in China-Yellow River valley (Henan), Yangtze River valley (Anhui) and Northwest (Xinjiang). The 148 entries were arranged in a randomized complete block design with two replications and single row plots in each environment. Seeds were sown in April in each location and crop management followed local recommendations for that location. At Anyang, Henan, cotton seeds were sown directly to the field under plastic mulch. The plot length was 8 m with a row spacing of 0.75 m and plant spacing of 0.23 m and seedlings were thinned to 32 plants $plot^{-1}$. At Wangjiang, Anhui, seeds were firstly sown in pots made of the field soil in a seedbed nursery and seedlings at 3–4 true leaf stage were then transplanted to the field. The plot length was 3.8 m with a row spacing of 0.8 m and plant spacing of 0.42 m and contained 9 plants $plot^{-1}$. At Aksu, Xinjiang, a high seeding rate was used with a plant spacing of 0.11 m and row spacing of 0.38 m and the plot length was 4 m with 40 plants.

Trait evaluation

At plant maturity, 25 open boll samples per plot (1 boll from the middle of the plants per plant) were hand harvested in each test for evaluation of fiber quality traits using the High Volumn Instrument (HVI) 900 (Test Center of Cotton Fiber Quality affiliated with the Agriculture

Ministry of China, China Cotton Research Institute, Chinese Academy of Agricultural Science, Anyang, Henan, China). The fiber quality traits measured were fiber length (FL), fiber strength (FS), micronaire (MC), fiber elongation (FE), and fiber uniformity (FU). Individual plots were then hand harvested for determination of yield and yield component traits including seedcotton yield (SCY)-accumulated weight in kg ha^{-1}, lint yield (LY)-accumulated SCY weight in kg ha^{-1} multiplied by lint percentage, boll weight (BW) in g per boll, lint percentage (LP) − lint weight divided by seedcotton weight in the 25 boll samples. However, yield data were not collected in Wangjiang, Anhui due to excessive rains in the fall, while fiber quality for each genotype was tested using bulked samples from the two replicates in Anyang, Henan, China 2006; Wangjiang, Anhui, China 2008; and Aksu, Xinjiang, China 2008, in order to reduce testing costs. Due to genotype × environment interactions, analysis of variance was performed for each trait with replicates.

DNA extraction and marker analysis

The genomic DNA was extracted from young leaves of the 146 individual BIL lines and the two parents using a miniprep method as described by Zhang and Stewart (2000). A total of 2,041 simple sequence repeat (SSR) primer pairs were chosen according to other genetic maps (Lacape et al. 2003; Rong et al. 2004; Guo et al. 2007; Yu et al. 2007) and used to screen the parents for polymorphism. These SSR primer sequences are available in http://www.cottonmarker.org. SSR–PCR amplifications were performed using a Programmable Thermal Controller (MJ Research), and PCR product electrophoresis and silver staining were conducted as described by Zhang et al. (2000, 2002).

Map construction and QTL mapping

A Chi-square test was performed to determine if the genotypic frequency at each locus deviated from the expected 55 (aa for the recurrent parent genotype): 9 (A_ for the donor genotype) for a dominant marker or 55 (aa): 2 (Aa): 7 (AA) segregation ratio for a co-dominant marker in the BC_2F_4-derived BIL population. The expected heterozygosity is 3.2 % for the BIL population. However, the heterozygosity of the BIL population was not evaluated in this study, because heterozygous marker loci were scored as missing. Therefore, linkage mapping was based on the final ratio of homozygotes. JoinMap 3.0 (Stam 1993) was used to construct a linkage map, and a logarithm of odds (LOD) threshold of 5.0 and a maximal distance of 50 cM were used. When markers from the same chromosome were broken down to several linkage groups, reference maps (Lacape et al. 2003; Guo et al. 2007; Yu et al. 2007; Lin et al. 2009) were used to join them. For QTL mapping, the IciMapping software (v3.2; http://www.isbreeding.net/), an integrated software for building linkage maps and mapping QTLs which can handle various mapping populations including BILs in this study, was used (Li et al. 2007). Inclusive composite interval mappinng method (ICIM) was used to map QTLs at a walk speed of 1 cM and LOD threshold values were estimated by 1,000 permutations to declare significant QTL (Churchill and Doerge 1994). A location QTL confidence interval (95 %) was set as a mapping distance interval corresponding to one LOD decline on either side of the peak. QTLs for the same trait across different years and environments were declared as a "common" QTL when their confidence intervals overlapped. The QTL nomenclature system proposed by McCouch et al. (1997) was adopted in the current study. The designation begins with "q", followed by an abbreviation of the trait name (e.g. FL for fiber length, FS for fiber strength), year, abbreviation of the location, the chromosome name, and finally the serial number.

Results

Performance of parents and BIL population

The BIL population of 146 lines together with the two parents was tested in five environments. Date for yield traits were collected in Anyang in 3 years (2006–2008) and Xinjiang in 2007, while fiber quality data were collected in Anyang (2007 and 2008), Xinjiang in 2007 and Wangjiang in 2007. A combined analysis of variance indicated that significant variations due to genotype and genotype × environment existed for all the traits. Therefore, the phenotypic data for fiber quality and yield traits of the BIL population and the parents for the individual tests are summarized in Table 1. Except for fiber uniformity, the differences in fiber length, strength, and micronaire, seedcotton yield, lint yield, boll weight and lint percentage between the two parents were significant. All the nine traits tested fit to the normal distribution according to skewness when each trait in each environment was subjected to the analysis (Table 1). As compared with the two parents, the phenotypic distributions and the wide range of variation of the traits indicated overall transgressive segregations in the BIL population. For yield and yield components, except for boll weight which did not display transgressive segregations all of the traits exhibited both positive and negative transgressive segregations. Lint percentage displayed mostly negative transgressive segregation, while the reverse was true for seedcotton yield, which resulted

Table 1 Performance of backcross inbred lines (BILs) of SG 747 × Giza 75 hybrid and their parents

Trait	Environment	Parent		Diff.	BILs			Skewness	LSD (0.05)
		SG 747	Giza 75		Min.	Max.	Mean		
Fiber length (mm)	Anyang 2008	27.54	42.58	*	25.97	33.07	29.43	0.1	1.52
	Anyang 2007	29.13	33.86	*	25.9	32.77	29.4	0.12	1.47
Fiber strength (cN/tex)	Anyang 2008	27.3	42.1	*	25.9	33.45	29.26	0.26	2.5
	Anyang 2007	25.75	36.6	*	26.42	32.78	29.02	0.3	2.15
Micronaire (unit)	Anyang 2008	6.3	5.6	*	3.57	5.79	4.62	−0.04	0.54
	Anyang 2007	6.15	4.49	*	3.97	6.16	4.84	0.6	0.49
Elongation (%)	Anyang 2008	6.35	7	*	6.1	6.8	6.42	0.47	0.22
	Anyang 2007	6.05	5	*	5.97	6.8	6.39	−0.09	0.63
Uniformity (%)	Anyang 2008	85.5	85.9	ns	81.1	85.85	84.18	−0.55	1.93
	Anyang 2007	85.35	85.3	ns	81.77	85.78	84.15	−0.7	1.98
Boll weight (g/boll)	Anyang 2008	5.21	3.33	*	3.74	6.17	4.93	−0.25	0.64
	Anyang 2007	6.27	3.53	*	3.96	6.58	5.13	0.18	0.92
	Anyang 2006	6.18	3.87	*	3.69	5.8	4.77	−0.44	0.36
	Xinjiang 2007	5.4	3.2	*	2.95	5.75	4.57	−0.77	0.85
Lint percent (%)	Anyang 2008	40.48	34.84	*	31.96	42.94	36.44	0.13	2.57
	Anyang 2007	43.36	36.57	*	33.48	44.38	38.98	0.14	3.03
	Anyang 2006	40.19	35.26	*	30.58	40.78	35.93	−0.21	1.62
	Xinjiang 2007	43.1	40.62	*	29.72	42.85	38.23	−0.47	2.08
Lint yield (kg/ha)	Anyang 2008	528	112	*	86	1,103	417	0.72	213
	Anyang 2007	647	304	*	314	1,290	719	0.28	333
	Anyang 2006	954	309	*	272	1,229	740	0.1	195
	Xinjiang 2007	1,509	800	*	522	1,651	1,056	−0.01	550
Seedcotton yield (kg/ha)	Anyang 2008	1,422	836	*	250	2,640	1,139	0.58	563
	Anyang 2007	1,496	833	ns	831	2,952	1,836	0.14	783
	Anyang 2006	2,378.85	878	*	770	3,406	2,054	0.03	509
	Xinjiang 2007	3,501	1970	*	1348	4,306	2,758	0.06	1,429

Yield data were not collected in Wangjiang, Anhui due to excessive rains in the fall, while fiber quality for each genotype was tested using bulked samples from the two replicates in Anyang 2006; Wangjinag, Anhui 2007; and Aksu, Xinjiang 2007. Due to genotype × environment interactions, analysis of variance was performed for each trait with replicates

ns no significant difference

* Significant difference between the parents at $P = 0.05$

in both negative and positive transgressive segregations for lint yield. For fiber quality traits, negative transgressive segregations were noted for length, strength, micronaire and uniformity, while only positive transgressive segregation occurred for fiber elongation. The results indicated that further yield improvement in Upland cotton is possible through interspecific backcross breeding, but not through boll weight or lint percentage. Micronaire can also be reduced, thereby increasing fiber finesses in backcross progenies.

Construction and characterization of a linkage map

The genetic map spanned a total of 2,895 cM in genetic distance including 392 SSR polymorphic loci with an average genetic distance of 7.4 cM per marker. In the map, 29 linkage groups were assigned to 26 chromosomes, with 2–25 loci and 34.7–190.2 cM per chromosome. The density of markers also varied between chromosomes, ranging from 4.4 cM (c06) to 18.3 cM (c04). The largest gap between two adjacent loci was 42.5 cM (on c5). Chromosomes with more than 20 loci were c5, c12, c16, c18, c19, c21 and c26, and chromosomes with less than 10 loci were c4 and c17. The total genetic length of the At and Dt subgenomes was 1,354 and 1,541 cM, with 179 and 213 loci, respectively. The average distance between two markers for At and Dt subgenomes was 7.6 and 7.2 cM, respectively. The Dt subgenome was longer than the At subgenome and had more polymorphic markers assigned in the current study (Table 2).

Segregation distortions

A total of 100 segregation distorted (SD) loci were identified, accounting for 25.5 % of the 392 mapped loci with 71 loci segregating toward the Upland cotton alleles and 29 toward the *G. barbadense* alleles. These SD loci were unevenly distributed on the 26 cotton chromosomes with 1–8 loci on each chromosome (Table 2). A slightly more SD segregating loci were located on the At subgenome than on the Dt subgenome (52 vs. 48). The most SD loci were on c2, c3, c5, c12, c19 and c26 (~ 1/3 of the loci were distorted), and only one SD locus on c17 and c21 each. There were several SD regions on c3, c5, c6, and c26 (6 SD loci each). The SD loci exhibited a phenomenon in which loci skewing toward the same species alleles appeared to be on the same chromosome, such as all of the six loci skewing toward the Upland cotton alleles on c26. In *G. hirsutum* × *G. barbadense* interspecific crosses, 10–20 % SSR loci have been reported to have SD in F_2 or BC_1 (Guo et al. 2007; Yu et al. 2007, 2011). Repeated inbreeding (backcross and self pollination) may increase SD, as demonstrated in the current study. SD has been also frequently observed in other plants (e.g. Xu et al. 1997).

Table 2 Genetic distances, marker loci, and QTL distributions among chromosomes in the backcross inbred line population of SG 747 × Giza 75 hybrid

Chromosome	No. of loci	Length (cM)	Average interval (cM)	No. distorted	No. of QTLs
c1-1	8	54.6	6.8	2	4
c1-2	2	34.7	17.4	0	0
c2	10	73.7	7.4	6	0
c3	17	139	8.2	7	2
c4	6	110	18.3	2	0
c5	22	190.2	8.6	7	4
c6	16	70.6	4.4	4	0
c7	10	78.4	7.8	2	5
c8	13	93.4	7.2	3	0
c9	11	82.2	7.5	4	5
c10	11	58.3	5.3	4	1
c11	18	97.3	5.4	3	4
c12	22	153.7	7	6	2
c13	13	117.9	9.1	2	2
A subgroup	179	1354	7.6	52	29
c14-1	7	69.6	9.9	2	4
c14-2	3	42.5	14.2	0	0
c15	17	172	10.1	4	1
c16	22	118.3	5.4	5	4
c17	4	54.7	13.7	1	0
c18	23	145.9	6.3	5	7
c19	25	169.1	6.8	7	2
c20	13	73.8	5.7	4	2
c21	22	114.7	5.2	2	3
c22	17	99.1	5.8	1	3
c23	10	124	12.4	3	0
c24	15	83.4	5.6	4	5
c25-1	8	76.6	9.6	1	1
c25-2	4	58.1	14.5	1	1
c26	23	139.4	6.1	8	5
D subgroup	213	1,541.2	7.2	48	38
Total	392	2,895.2	7.4	100	67

QTLs for fiber quality traits, yield and yield components

A total of 67 QTLs were detected on 23 chromosomes by inclusive composite interval mapping (ICIM), each explaining 6.65–25.27 % of the phenotypic variation. Of the 67 QTLs, 29 were located on the At subgenome, and 38 on the Dt subgenome derived from an ancestor that does not produce spinnable fibers. There were 28 QTLs affecting five fiber quality traits and 39 QTLs affecting four yield and its components detected from the BIL population. Eight common QTLs (12 %) were detected in more than two environments, Among the eight common QTLs, two were for fiber quality traits including one for fiber strength and one for uniformity, and six for yield and its components including three for lint yield, one for seedcotton yield, one for lint percentage and one for boll weight (Fig. 1; Tables 3, 4).

Fiber length

There were a total of four QTLs affecting FL which were located on four chromosomes (c5, c11, c12 and c21). From 8.23 to 16.72 % of the phenotypic variance (PV) could be explained by a single QTL. Two QTLs (qFL-07W-c11-1 and qFL-08A-c12-1) had alleles with positive effective from Giza 75 (called Gb alleles hereafter). The direction of the additive effect in the other two QTLs (qFL-07X-c5-1 and qFL-08A-c21-1) was contributed by the SG 747 (called Gh hereafter) allele.

Fiber strength

A total of four QTLs for FS were detected on c11, c20 and c21 in four environments and one common QTL was found on c11. The common QTL was supported by two QTLs (qFS-07X-c11-1 and qFS-07W-c11-1) detected in two environments (Xinjiang 2007 and Wangjiang 2007) which were on c11 in the same marker interval between NAU5480 and NAU3117. The Gb alleles for both QTLs increased fiber strength by 0.84–1.07 cN/tex, explaining 14.95 and 14.42 % of the PV, respectively. These two

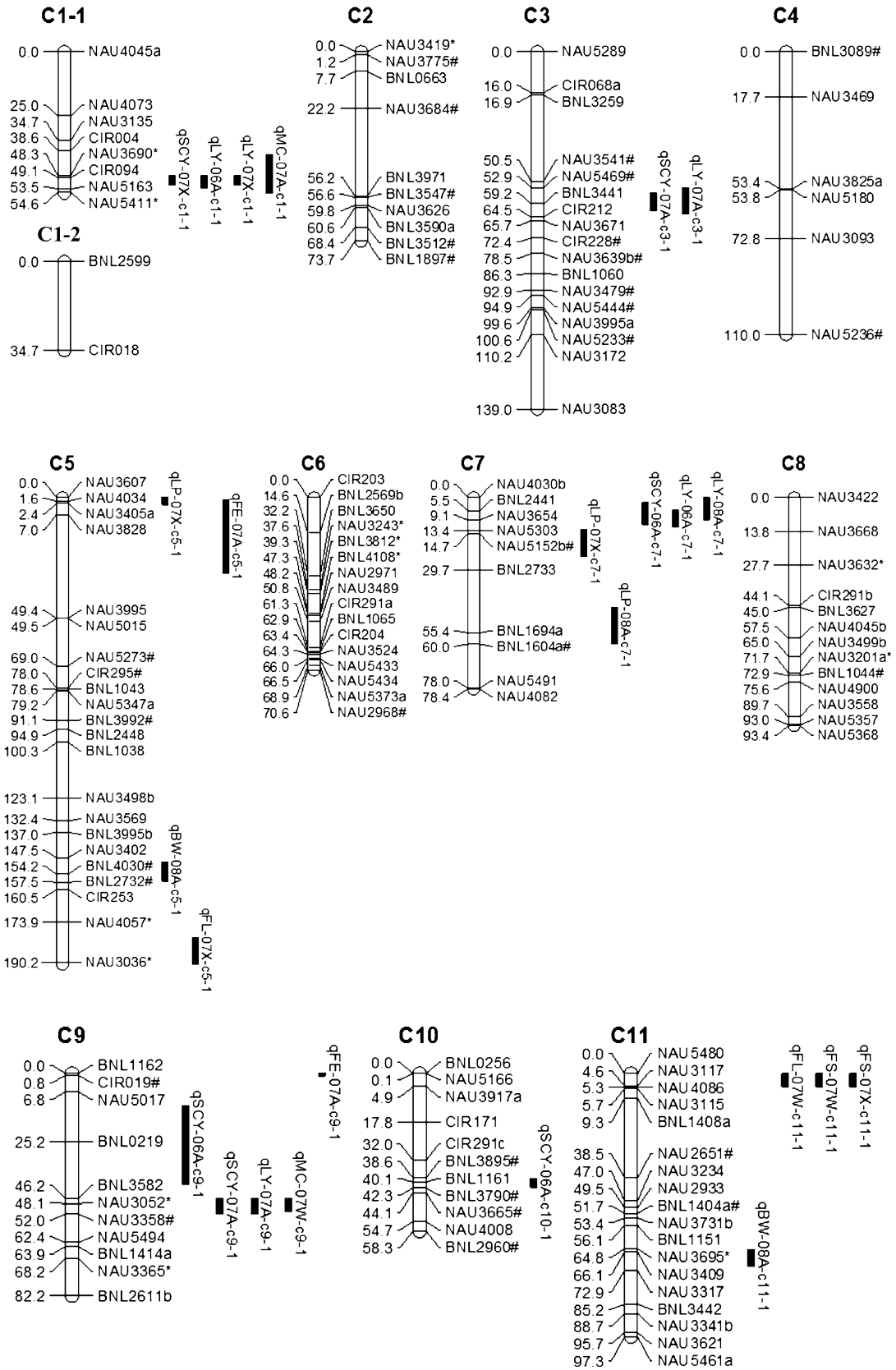

Fig. 1 QTLs identified in the backcross inbred line population derived from an interspecific *G. hirsutum* × *G. barbadense* hybrid (SG 747 × Giza 75). *Markers skewed toward the Giza 75 allele and #markers skewed toward the SG 747 allele

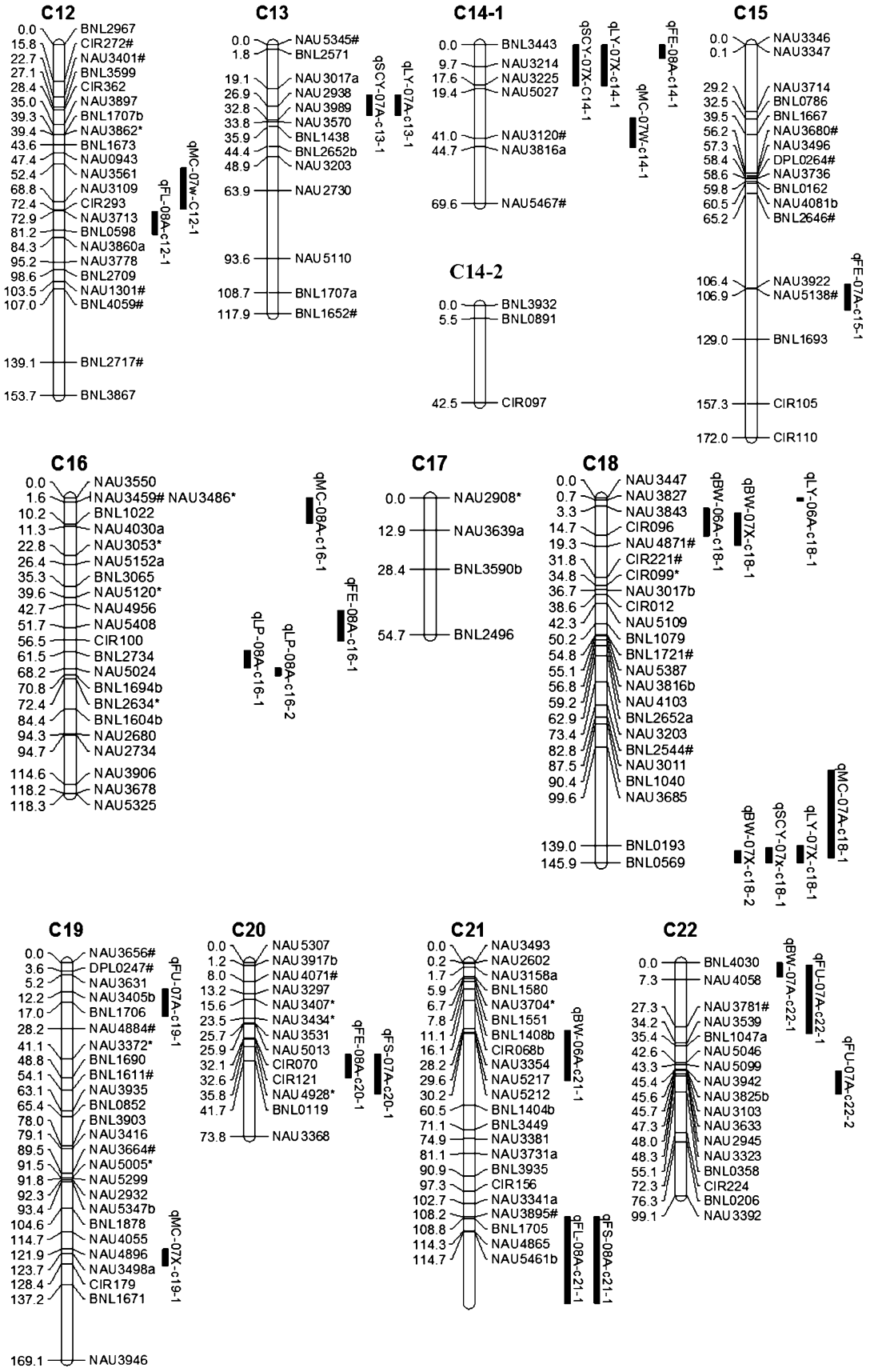

Fig. 1 continued

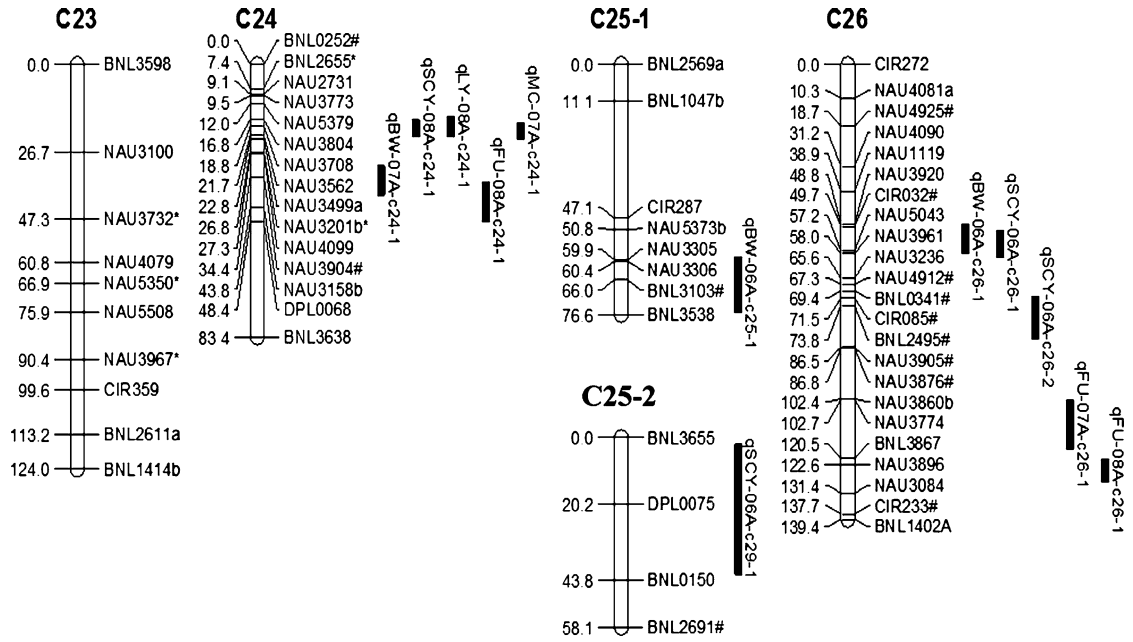

Fig. 1 continued

QTLs could be a stable and common QTL and were, therefore, named qFS-c11-1. The positive additive effects for the other two QTLs were both from the Gh alleles.

Micronaire

For MC, eight QTLs were identified on c1, c9, c12, c14, c16, c18, c19 and c24 in four environments, explaining 7.16–17.57 % of the PV. The Gb allele decreased micronaire value by 0.13–0.28 in five of the eight QTLs, as expected from the Gb parent with significantly lower micronaire, explaining 9.06–12.55 % of the PV. The Gh alleles for the other three QTLs increased micronaire value by 0.15–0.22, explaining 7.39–17.57 % of the PV, respectively.

Fiber elongation

A total of six QTLs for FE were identified and mapped on six chromosomes (c5, c9, c14, c15, c16, and c20), explaining 6.65–17.14 % of the PV. Except for the Gb allele for the qFE-08A-c14-1 which reduced FE, the Gh alleles for the other five QTLs increased fiber elongation by 0.05–0.21 %, explaining 8.14–17.14 % of the PV.

Fiber uniformity

For FU, six QTLs were identified on c19, c22, c24 and c26, explaining 14.59–22.68 % of the PV. The Gh alleles increased fiber uniformity value by 0.52–0.72 in all of the six QTLs. The QTL qFU-07A-c26-1 overlapped with qFU-08A-c26-1 through the bridge marker BNL3867, and the two QTLs were identified in two environments of the same location (Anyang 2007 and Anyang 2008). Therefore, we suggested these two QTLs being a common QTL which is named qFU-c26-1. Another two QTLs (qFU-07A-c22-1 and qFU-07A-c22-2) were mapped on c22 in the same test (Anyang 2007), explaining 17.89 and 14.59 % of the PV, respectively.

Boll weight

A total of 10 QTLs for BW were detected and mapped on eight chromosomes (c5, c11, c18, c21, c22, c24, c25, and c26), explaining 8.48–25.27 % of the PV. Except for the Gb allele for the qBW-07A-c24-1, the Gh alleles for the other nine QTLs increased BW. There were three QTLs detected on c18 in two environments (Anyang 2006 and Xinjiang 2007). The two QTLs qBW-06A-c18-1 and qBW-07X-c18-1 overlapped by one bridge marker CIR096, explaining 16.40 and 10.52 % of the PV, respectively. Therefore, they are named as a common QTL qBW-c18-1. The third QTL qBW-07X-c18-2 was located at the other end of c18, explaining 19.58 % of the PV.

Lint percentage

There were a total of five QTLs affecting LP which were located on three chromosomes (c5, c7, and c16), explained 15.19–18.06 % of the PV. The two QTLs on c7 including qLP-07X-c7-1 and qLP-08A-c7-1 were close to each other, but not overlapped; however, we still suggest that they belong to a common QTL, named qLP-c7-1. The two

Table 3 QTLs detected for fiber quality traits in the backcross inbred line (BIL) population of an interspecific hybrid (SG 747 × Giza 75)

Trait	Env	QTL name	Marker interval	LOD	Add	PV %	Direction
Fiber length (mm)	2008 Anyang	qFL-08A-c12-1	NAU3713-BNL0598	4.33	−0.77	16.72	Giza 75
		qFL-08A-c21-1	BNL1705-NAU4865	4.29	0.7	12.18	SG 747
	2007 Wangjiang	qFL-07W-c11-1	NAU5480-NAU3117	2.65	−0.52	8.23	Giza 75
	2007 Xinjiang	qFL-07X-c5-1	NAU4057-NAU3036	4.34	0.42	13.1	SG 747
Fiber strength (cN/tex)	2008 Anyang	qFS-08A-c21-1	BNL1705-NAU4865	2.72	0.74	8.38	SG 747
	2007 Anyang	qFS-07A-c20-1	BNL119-NAU3368	3.25	0.43	12.21	SG 747
	2007 Wangjiang	qFS-07W-c11-1	NAU5480-NAU3117	3.22	−1.07	14.95	Giza 75
	2007 Xinjiang	qFS-07X-c11-1	NAU5480-NAU3117	2.7	−0.84	14.42	Giza 75
Micronaire (unit)	2008 Anyang	qMC-08A-c16-1	NAU3486-BNL1022	2.62	0.16	12.55	SG 747
	2007 Anyang	qMC-07A-c1-1	CIR094-NAU5163	2.61	0.19	12.22	SG 747
		qMC-07A-c18-1	BNL0193-BNL0569	2.93	−0.15	7.39	Giza 75
		qMC-07A-c24-1	NAU3708-NAU3562	6.14	−0.22	17.57	Giza 75
	2007 Wangjiang	qMC-07W-c9-1	BNL3582-NAU3052	2.56	0.13	7.16	SG 747
		qMC-07W-c12-1	NAU3109-CIR293	3.16	0.26	9.06	SG 747
		qMC-07W-c14-1	NAU3120-NAU3816a	3.46	0.28	9.13	SG 747
	2007 Xinjiang	qMC-07X-c19-1	NAU3498a-CIR179	2.96	−0.21	14.45	Giza 75
Fiber elongation (%)	2008 Anyang	qFE-08A-c14-1	BNL3443-NAU3214	2.71	−0.06	6.65	Giza 75
		qFE-08A-c16-1	NAU5408-CIR100	4.36	0.06	11.26	SG 747
		qFE-08A-c20-1	BNL119-NAU3368	6.37	0.05	17.14	SG 747
	2007 Anyang	qFE-07A-c5-1	NAU3405a-NAU3828	2.58	0.17	10.1	SG 747
		qFE-07A-c9-1	BNL1162-CIR019	3.77	0.21	10.35	SG 747
		qFE-07A-c15-1	NAU5138-BNL1693	2.96	0.21	8.14	SG 747
Uniformity (%)	2008 Anyang	qFU-08A-c24-1	NAU3904-NAU3158b	4.13	0.62	20.35	SG 747
		qFU-08A-c26-1	BNL3867-NAU3896	4.4	0.61	19.64	SG 747
	2007 Anyang	qFU-07A-c19-1	NAU3405b-BNL1706	3.67	0.57	18.48	SG 747
		qFU-07A-c22-1	NAU4058-NAU3781	2.63	0.65	17.89	SG 747
		qFU-07A-c22-2	NAU3323-BNL0358	2.77	0.52	14.59	SG 747
		qFU-07A-c26-1	NAU3774-BNL3867	3.34	0.72	22.68	SG 747

Env environment, *Add* additive effect, *LOD* logarithm of odds score, *PV %* phenotypic variation explained by an individual QTL

QTLs explained 16.67 and 15.19 % of the PV, respectively; however, the additive effects were opposite. The other two QTLs qLP-08A-c16-1 and qLP-08A-c16-2) were mapped in a close proximity on c16 in the same test (Anyang 2008), explaining 7.06 and 8.17 % of the PV, respectively.

Seedcotton yield

A total of 13 QTLs for SCY were identified and mapped onto 11 chromosomes (c1, c3, c7, c9, c10, c13, c14, c18, c24, c25, and c26), explaining 6.96–19.13 % of the PV. The Gh alleles increased seedcotton yield by 146–353 kg ha^{-1} in all of the 13 QTLs. One common QTL named qSCY-c9-1 was found on c9 in that the confidence interval of the qSCY-06A-c9-1 was overlapped with that of qSCY-07A-c9-1, and covered by one common marker BNL3582. The two QTLs explained 12.96 and 9.97 % of the PV, respectively. The Gh alleles increased SCY by 293–146 kg ha^{-1}. Two other QTLs (qSCY-06A-c26-1 and qSCY-06A-c26-2) were mapped within a 10-cM region on c26 in the same test (Anyang 2006), explaining 7.06 and 8.17 % of the PV, respectively.

Lint yield

For LY, 11 QTLs were identified and mapped onto c1, c3, c7, c9, c13, c14, 18, and c24, explaining 6.82–16.77 % of the PV. All the 11 Gh alleles contributed to the increase in LY by 60–141 kg ha^{-1}. Three common QTLs were found on c1, c7 and c18. One common QTL qLY-c1-1 was found in an overlapped region on c1 in two environments (Anyang 2006 and Xinjiang 2007), as supported by the marker interval between CIR094 and NAU5163. The percentage of PV explained by the two QTLs was 15.44 and 10.33 %, respectively, and the Gh allele increased LY by 124–141 kg ha^{-1}. Another common QTL qLP-c7-1 was identified on c7 in two tests in the same location (Anyang 2006 and 2008). The confidence interval of qLY-06A-c7-1

Table 4 QTLs detected for yield and yield component traits in the backcross inbred line (BIL) population of an interspecific hybrid (SG 747 × Giza 75)

Trait	Env	QTL name	Marker interval	LOD	Add	PV %	Direction
Boll weight (g/boll)	2008 Anyang	qBW-08A-c5-1	NAU3402-BNL4030	3.08	0.26	12.45	SG 747
		qBW-08A-c11-1	NAU3409-NAU3317	6.59	0.25	21.12	SG 747
	2007 Anyang	qBW-07A-c22-1	BNL4030-NAU4058	2.99	0.28	12.04	SG 747
		qBW-07A-c24-1	NAU3904-NAU3158b	2.77	−0.29	13.54	Giza 75
	2006 Anyang	qBW-06A-c18-1	NAU3843-CIR096	3.21	0.21	16.4	SG 747
		qBW-06A-c21-1	NAU5212-BNL1404b	4.15	0.31	25.27	SG 747
		qBW-06A-c25-1	NAU3306-BNL3103	2.54	0.21	8.48	SG 747
		qBW-06A-c26-1	CIR032-NAU5043	2.8	0.23	14.44	SG 747
	2007 Xinjiang	qBW-07X-c18-1	CIR096-NAU4871	2.67	0.2	10.52	SG 747
		qBW-07X-c18-2	BNL0193-BNL0569	4.59	0.32	19.58	SG 747
Lint percent (%)	2008 Anyang	qLP-08A-c5-1	NAU4034-NAU3405a	2.87	−1.26	18.06	Giza 75
		qLP-08A-c7-1	BNL1694a-BNL1604a	3.33	−1.41	15.19	Giza 75
		qLP-08A-c16-1	BNL2734-NAU5024	3.84	−1.39	17.5	Giza 75
		qLP-08A-c16-2	NAU5024-BNL1694b	4.2	−1.43	17.64	Giza 75
	2007 Xinjiang	qLP-07X-c7-1	NAU5152b-BNL2733	2.73	1.65	16.67	SG 747
Seedcotton yield (kg/ha)	2008 Anyang	qSCY-08A-c24-1	NAU3708-NAU3562	3.07	174.9	8.75	SG 747
	2007 Anyang	qSCY-07A-c3-1	NAU5469-BNL3441	3.18	182.04	7.99	SG 747
		qSCY-07A-c9-1	NAU3052-NAU3358	2.94	144.54	9.97	SG 747
		qSCY-07A-c13-1	NAU2938-NAU3989	5.09	291.06	19.13	SG 747
	2006 Anyang	qSCY-06A-c7-1	BNL2441-NAU3654	3.3	230.84	9.26	SG 747
		qSCY-06A-c9-1	NAU5017-BNL0219	4.23	293.42	12.96	SG 747
		qSCY-06A-c10-1	BNL3895-BNL1161	6.48	352.51	14.34	SG 747
		qSCY-06A-c26-1	CIR032-NAU5043	2.58	205.9	7.06	SG 747
		qSCY-06A-c26-2	BNL2495-NAU3905	3.91	308.22	8.17	SG 747
		qSCY-06A-c25-1	DPL0075-BNL0150	5.09	315.19	15.27	SG 747
	2007 Xinjiang	qSCY-07X-c1-1	NAU3690-CIR094	3.2	343.24	9.87	SG 747
		qSCY-07X-c14-1	BNL3443-NAU3214	2.51	266.92	6.96	SG 747
		qSCY-07X-c18-1	BNL0193-BNL0569	2.56	308.93	8.03	SG 747
Lint yield (kg/ha)	2008 Anyang	qLY-08A-c7-1	NAU4030b-BNL2441	2.68	81.93	11.03	SG 747
		qLY-08A-c24-1	NAU3708-NAU3562	2.77	63.38	7.88	SG 747
	2007 Anyang	qLY-07A-c9-1	NAU3052-NAU3358	2.76	59.54	9.64	SG 747
		qLY-07A-c13-1	NAU2938-NAU3989	4.35	114.02	16.77	SG 747
		qLY-07A-c3-1	NAU5469-BNL3441	2.64	70.46	6.82	SG 747
	2006 Anyang	qLY-06A-c18-1	NAU3447-NAU3827	3.08	77.98	7.71	SG 747
		qLY-06A-c1-1	CIR094-NAU5163	4.22	124	15.44	SG 747
		qLY-06A-c7-1	BNL2441-NAU3654	4.1	107.67	14.95	SG 747
	2007 Xinjiang	qLY-07X-c1-1	NAU3690b-CIR094	3.37	140.86	10.33	SG 747
		qLY-07X-c14-1	BNL3443-NAU3214	2.5	106.65	6.88	SG 747
		qLY-07X-c18-1	BNL0193-BNL0569	2.61	125.03	8.26	SG 747

Env environment, *Add* additive effect, *LOD* logarithm of odds score, [d]*PV %* phenotypic variation explained by an individual QTL

was overlapped with that of qLY-08A-c7-1 and contained two common markers BNL2441 and NAU3654. The two QTLs explained 14.95 and 11.03 % of the PV, respectively, and the Gh allele increased LY by 82–108 kg ha^{-1}. The third one was found on c18 in two environments (Anyang 2006 and Xinjiang 2007), but the confidence interval of the two individual QTLs were not overlapped. However, we still suggest it being a common QTL, which explained more than 15 % of the PV and the Gh allele increased LY by 78–125 kg ha^{-1}.

QTL clustering

Several QTL clusters or co-localization QTLs were observed on almost half of the tetraploid cotton chromosomes, including c1, c7, c9, c11, c14, c16, c18, c24, and c26. Some co-localized QTLs were mapped to the same regions affecting the same traits, and some were about fiber quality traits (c11 for FS and c26 for FU) or yield traits (c18 for BW; c16 for LP; c9 and c26 for SCY; and c1 and c7 for LY). Importantly, some QTLs affected not only different fiber quality traits but also different yield traits including QTLs affecting more than three traits and more than three QTLs on c1, c7, c9, c14, c18 and c24. For example, one FU-QTL, one MC-QTL, one SCY-QTL, one LY-QTL and one BW-QTL were all found within a 15 cM region of c24 between NAU3708 and NAU3158b affecting both fiber quality and yield traits. A c18 region between BNL193 (139 cM) and BNL569 (145.9 cM) carried QTLs for micronaire, boll weight, lint yield, and seedcotton yield.

Discussion

QTL clustering

Clusters of QTLs for different fiber quality and yield component traits in the same genomic region were reported previously (Lacape et al. 2005, 2010; He et al. 2005, 2007; Rong et al. 2007; Ulloa and Meredith 2000; Shappley et al. 1998; Shen et al. 2005, 2007; Zhang et al. 2009). Our data based on five environments also confirmed this phenomenon. Clustering QTLs in the tetraploid cotton could be explained by gene/QTL linkage or pleiotropic effects from a single QTL. Rong et al. (2007) proposed that cotton fiber quality QTLs may represent groups of coordinately regulated genes and/or groups of small gene families that have undergone proximal duplication followed by sub- or neofunctionalization. However, this hypothesis remains to be tested.

Contributions of the At and Dt subgenomes to allotetraploid cottons

In the last decade, numerous molecular mapping studies have clearly shown that many QTLs for fiber quality traits were located on the Dt subgenome of the tetraploid cotton (Jiang et al. 2000; Paterson et al. 2003; Chee et al. 2005a, b; Draye et al. 2005). Some studies have shown that more QTLs occurred on the Dt subgenome than on the At subgenome for fiber quality traits (Jiang et al. 1998; Paterson et al. 2003; Rong et al. 2007; Shen et al. 2007; Lacape et al. 2010). However, whether the difference was significant has not been statistically tested. In the present study, among the 28 QTLs affecting fiber quality traits, we observed a numeric difference in the numbers of QTLs distributed between the two subgenomes, i.e. 10 versus 18 on the At and Dt subgenomes, respectively, and the difference was significant based on a Chi-square test. Therefore, our research does support the notion that the Dt subgenome exerted a higher contribution to the genetic control of the fiber quality traits than the At subgenome. However, for yield and yield component traits, almost an equal number of QTLs (19 on the At subgenome and 20 on the Dt subgenome) was detected and the difference was insignificant based on a Chi-square test. Overall, more QTLs were detected on the Dt subgenome than on the At subgenome (38 vs. 29), and the QTLs on the two subgenomes appears unevenly distributed. However, the number of QTLs detected in the current study will not allow a genomewide analysis of QTL distributions.

Comparison of QTLs with other reports

It was not easy to compare different QTL studies among different populations in cotton because of the lack of sufficient common markers. However, some relative stable and common QTLs on the same chromosomes in different populations were reported. Lacape et al. (2005) reported that 20 % of the QTLs were common between at least two of the three backcross segregating populations and only 30 % of the QTLs detected in their studies putatively agreed with at least one QTL report in the literature for both chromosome locations and parental species origin. One major QTL for fiber strength was identified in $F_2/F_{2:3}$ and RIL populations of 7,235 × TM-1 (Shen et al. 2005, 2007). Chen et al. (2009) further identified five tightly linked and/or clustered QTLs on c24 in three populations generated using three RIL lines, which overlapped with their previously identified major QTL region. In the present study, almost 1/2 of the QTLs (13 of 28) affecting fiber quality traits were found to be located on the same chromosomes through a comparative analysis with the previous studies, including three QTLs for fiber length on c5, c12 and c21 (Chee et al. 2005b; Shen et al. 2007; Wu et al. 2009; Zhang et al. 2009; Lacape et al. 2010); two QTLs for fiber strength on c20 and c21 (Wu et al. 2009; Lacape et al. 2010); five QTLs for fiber elongation on c5, c9, c14, c15 and c20 (Chee et al. 2005a; Lacape et al. 2005, 2010; Wu et al. 2009; Zhang et al. 2009); and three QTLs for fiber uniformity on c19, c22 and c26 (Shen et al. 2007; Lacape et al. 2010). However, we were unable to compare QTLs for fiber fineness because of different measurements in different tests. There were also seven QTLs for yield components mapped to the same chromosomes as others, including two QTLs for LY on c7 (He et al. 2007) and c24 (Shen et al. 2007); three QTLs for SCY on c14 (He et al.

2007), c24 (Shen et al. 2007) and c26 (Wu et al. 2009); and two QTLs for BW on c24 (Shen et al. 2007) and c26 (Wu et al. 2009). These QTLs may be common QTLs or closely linked for fiber quality or yield components.

However, it also should be pointed out that the population size of BILs in the current study is relatively small, considering its imbalanced genotype nature (55aa: 2Aa: 7AA). The introgressed allele (A) and genotype (AA) from *G. barbadense* are far fewer than these from the recurrent Upland cotton parent, which could limit the resolution power in QTL mapping and estimation of QTL parameters including effects and map locations. Furthermore, only two replicates in each environment were implemented in the current study, which may also affect QTL mapping. However, BILs tested in multiple environments helped in detecting more QTLs responding to various environmental conditions.

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