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Quantitative trait locus analysis of boll-related traits in an intraspecific population of *Gossypium hirsutum*

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Abstract Quantitative trait locus (QTL) mapping lays the foundation for marker-assisted selection (MAS) for lint yield and fiber quality in cotton (*Gossypium hirsutum*). Boll-related traits affect yield and fiber quality, but few studies have focused on boll-related traits. Here, we detected QTLs related to cotton boll, yield and fiber quality traits using intraspecific F_2 and $F_{2:3}$ populations from the cross AQ × 08-10604. A total of 91 QTLs for 17 traits related to boll, yield and fiber quality in the F_2 and $F_{2:3}$ populations were mapped, including 37 significant QTLs. Six pairs of common QTLs were detected, including two pairs for boll coat weight (BCW) in the same or similar positions on Chr. A10 and D1, two pairs for boll length (BL) in similar positions on Chr. A10 and A13, with a higher percentage of phenotype variation and two pairs for boll diameter (BD) in similar positions on Chr. A10 and D1. These results suggest that the traits BCW, BL and BD have high levels of stability. Five QTL clusters for the same or different traits were also identified on Chr. A10 (2), A13, D1 and D5. We also detected 64 epistatic QTLs for boll- and yield-related traits that play important roles in genetic variation. Correlation analysis revealed significant positive correlations between seed yield and boll number per plant and between boll weight and BCW, BL and BD. The results of this study enhance our understanding of the genetic basis of boll-related traits and will enable further MAS of upland cotton.

Keywords Boll weight · Epistatic QTL · Fiber quality · Major QTL · Upland cotton

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Introduction

Cotton is one of the most important economic crops worldwide. *Gossypium hirsutum* is a tetraploid species, accounting for 95 % of the world cotton yield. The challenge facing cotton breeders is how to meet the increasing demands of the textile industry. Due to the negative genetic correlation between fiber quality and lint yield, performing conventional breeding procedures to further improve fiber quality while simultaneously emphasizing yield has become increasingly difficult. The development of molecular markers has made it possible for crop breeders to employ rapid, precise alternative approaches to conventional selection schemes for improving both economic and agronomic traits of crops (Tanksley and Hewitt 1988).

Genetic linkage maps lay the foundation for exploiting quantitative trait loci (QTLs) conferring yield-, fiber quality- and boll-related traits in cotton.

Since the first genetic map was constructed by Reinisch et al. (1994) using an interspecific cross of *G. hirsutum* × *G. barbadense*, an increasing number of interspecific genetic maps have been constructed throughout the world (Guo et al. 2007; Lacape et al. 2003; Rong et al. 2004; Yu et al. 2011). In addition, many QTLs for lint yield and fiber quality traits have been mapped (Chee et al. 2005; He et al. 2005, 2007; Jiang et al. 1998; Lacape et al. 2010; Mei et al. 2004; Ren et al. 2002; Rong et al. 2007). Numerous genetic studies have shown that both cotton yield traits and fiber quality traits are quantitative traits that are controlled by multiple minor genes, and their phenotypes are affected by hereditary and environmental factors. However, the current interspecific maps and mapped QTLs have very limited use in conventional cotton breeding.

Shappley et al. (1996) first successfully constructed an intraspecific genetic linkage map with molecular markers in upland cotton. Subsequently, several intraspecific genetic linkage maps were constructed for *G. hirsutum* (Lin et al. 2009; Ulloa and Meredith 2000; Ulloa et al. 2002, 2005; Zhang et al. 2005, 2009), which contain 73–604 loci. Using these maps, the precise locations of many QTLs have been determined (Chen et al. 2009; Guo et al. 2006; Li et al. 2014; Liu et al. 2012; Ning et al. 2014; Paterson et al. 2003; Qin et al. 2008, 2009; Shao et al. 2014; Shen et al. 2005, 2007; Sun et al. 2012; Ulloa and Meredith 2000; Ulloa et al. 2005; Wang et al. 2006, 2007; Wu et al. 2009; Zhang et al. 2005, 2009, 2010, 2012a, b). For fiber quality, for example, Qin et al. (2009) discovered eight QTLs for fiber strength (FS), micronaire (MIC) and fiber elongation (FE) simultaneously in two populations. Shen et al. (2005) identified 39 QTLs for fiber quality, including 11 QTLs for FL, 10 for FS, nine for MIC and nine for FE. Zhang et al. (2009) detected 13 QTLs for fiber quality and mapped the QTLs on their corresponding chromosomes, including four for fiber length (FL), two for FS, two for MIC, three for fiber length uniformity (FU) and two for FE, respectively. Zhang et al. (2012a) identified 63 QTLs affecting fiber quality, including 11 for FE, 16 for FL, nine for MIC, 10 for FS and 17 for FU, explaining 8.1–55.8 % of the total phenotypic variance. Using three populations, Shao et al. (2014) detected 77 QTLs, including 19 for FL, 14 for FU, 17 for MIC, 10 for FE and 17 for FS. Sun et al. (2012) identified 50 QTLs for fiber quality, including 10 for FS, 10 for FL, 10 for MIC, eight for FU and 12 for FE. For cotton yield traits, Guo et al. (2006) mapped three QTLs for lint percentage (LP) on the A03 linkage group and chromosome 6. Shen et al. (2007) identified five QTLs for boll weight (BW), six for LP, five for seed index (SI), five for boll number per plant (BN), one for seed cotton yield and four for lint yield (LY), respectively. Zhang et al. (2010) detected seven QTLs for five yield traits, including one for BN, two for BW, one for LP, one for SY and two for LY. Ning et al. (2014) discovered 13 QTLs for SY, nine for LP, 12 for BW and five for SI. These studies have demonstrated that many cotton yield traits are closely related to each other and the corresponding genes may be linked to produce multiple effects on final traits (Mauricio 2001). Since cotton fiber quality is controlled by multiple genes, which are vulnerable to environmental effects, progress to simultaneously improve cotton yield and fiber quality traits using conventional breeding methods has been slow. To date, several hundred QTLs related to fiber quality traits have been mapped, and more new QTLs are still being identified. However, the lower variation present in intraspecific populations versus interspecific populations has limited the development of genetic linkage maps, and the resulting lower-density genetic linkage maps still fail to meet the needs of QTL-assisted crop breeding.

In addition, expression analysis of genes related to cotton fiber development at different stages and in different tissues has shown that this process is regulated in a highly complicated manner involving numerous genes (Taliercio and Boykin 2007; Xu et al. 2008; Al-Ghazi et al. 2009; Paterson et al. 2012), which also suggests that more QTLs should be identified in populations derived from crosses between cotton cultivars with wide genetic backgrounds (Shao et al. 2014). Meanwhile, epistasis, the interaction between alleles from two to more loci, may play an important role in evolutionary and quantitative variation in crops (Lou et al. 2009; Malmberg et al. 2005; Wang et al. 2010; Xing et al. 2002; Xu and Jia 2007; Xu et al. 2009; Yu et al. 1997; Zhang et al. 2001; Zhang et al. 2012a). QTL mapping is increasingly used to explore the role of epistasis in the genetic basis of complex quantitative traits (Li et al. 2009; Mohan et al. 2009). In cotton, QTL mapping analysis of epistatic effects has only been performed to examine a few plant architectural traits in intraspecific populations (Wang et al. 2006; Li et al. 2014). Wang et al.

(2006) identified three epistatic QTLs for plant height (PH), three for fruit branch length (FBL) and three for fruit branch number (FBN). Li et al. (2014) detected a total of 54 pairs of epistatic QTLs (E-QTLs) for ten plant architecture traits, which exhibit additive-by-additive (AA), additive-by-dominant (AD), dominant-by-additive (DA) and dominant-by-dominant (DD) interactions, including five for PH, seven for FBL, eight for FBN and so on.

It is well known that the boll is one of the most important productive organs of cotton, and boll size and boll number are two important yield components; boll shape also affects fiber quality. For instance, Tang and Xiao (2014) recently showed that boll length makes the largest contribution to the largest proportion of phenotypic, additive and dominance variances for fiber length, while boll width makes the largest contribution to phenotypic and additive variances and the second largest contribution to dominance-by-environment interaction variance for micronaire. Ashraf and Ahmad (2000) suggested that boll length plays an important role in cotton breeding. However, few such studies have focused on boll-related traits due to a lack of proper QTL mapping varieties.

In the current study, two extremely distinctive upland cotton lines were crossed to construct F_2 and $F_{2:3}$ populations for QTL mapping. The paternal parent, 08-10604, a highly inbred line from a cross between *G. hirsutum* race *yucatanense* (directly introduced from Mexico) and *G. hirsutum* cv Sumian 8, was developed by our institute and it possesses extremely low boll weight (<2 g), many bolls per plant and low fiber quality (short fiber length, low fiber strength and coarse fibers), while the maternal parent, AQ, exhibits high boll weight (>6 g), fewer bolls per plant and superior fiber quality (high fiber strength and fine fibers). Here, we investigated 17 traits in cotton. Seven boll- and five yield-related traits of the two parents, F_1 population, F_2 individuals and $F_{2:3}$ families were investigated at maturity, except for the first and last plant of each row. Five fiber quality traits were also investigated in the F_2 and $F_{2:3}$ populations. The boll-related traits included boll length (BL), boll diameter (BD), boll coat weight (BCW), locule number per boll (BLN), BW, seed number per boll (BSN), lint weight per boll (BLW). The yield-related traits included SI, LP, SY, LY and BN. The fiber quality traits included FL, FS, MIC, FE and FU. Boll length (BL) represents the longest part of a cotton boll from top to bottom, while BD is measured at the widest part of a cotton boll. The objectives of the present study were to (1) identify new QTLs with major effects on the 17 traits and QTLs with epistatic effects on the 12 boll- and yield-related traits, (2) analyze the common QTLs for boll-related traits and (3) summarize the QTL clusters for boll-related traits. This study provides a theoretical basis for genetic structure analysis and marker-assisted selection for high yield in cotton.

Materials and methods

Materials

Two upland cottons with significant differences in boll-related traits were used to develop F_2 and $F_{2:3}$ populations. The female parent was AQ (*G. hirsutum*), which has superior characters such as tall plants and large (but few) bolls. The male parent was 08-10604, a highly inbred line from a cross between *G. hirsutum* race *yucatanense* (directly introduced from Mexico) and *G. hirsutum* cv Sumian 8, which was then backcrossed with *G. hirsutum* acc. Tai8033. In 2011, 330 F_2 individuals were planted and self-pollinated. The resulting $F_{2:3}$ families were planted in 2012.

Methods

All materials were randomly planted in Jiangpu Breeding Station of Nanjing Agricultural University (Nanjing, China). The plots were 5 m long and 0.8 m apart, with a plant spacing of 40 cm. A total of 285 $F_{2:3}$ family lines, along with P_1, P_2 and F_1, were randomly planted, with two replicates in a single-row plot. The field management measures essentially followed normal agricultural practices.

Boll traits including BL and BD were measured at maturity using a digital caliper (Lugong, Shanghai Jiuliang Hardware Company, Shanghai, China). Fiber samples were collected from bolls at the internal middle parts of plants. F_2 individuals and $F_{2:3}$ family lines in the middle of each row were tagged for scoring, harvested and sent to the Cotton Quality Supervision, Inspection and Testing Center of the Ministry of Agriculture, China for tests of FL (cm), FS (cN/tex), MIC, FU and FE using an Uster HVI 900. The BCW and BW were measured and the BLN was

Table 1 Basic information about each chromosome and the number of QTLs in the SSR linkage map

Chr.	LGs	Markers	Average distance (cM)	Genetic distance (cM)	Segregation loci	Number of QTLs	Number of significant QTLs
A2	1	4	2.62	7.87	0	0	0
A3	1	18	5.93	100.83	8	6	2
A5	1	6	7.06	35.30	4	3	1
A6	1	4	13.35	40.04	0	3	3
A9	2	22	8.40	173.10	1	5	1
A10	2	21	5.78	115.53	2	17	8
A12	2	15	5.68	79.45	0	4	0
A13	1	21	7.02	140.37	2	10	2
At	11	111	6.24	692.48	17	48	17
D1	2	23	8.80	184.82	3	17	12
D5	1	29	5.75	160.92	5	16	9
D6	1	2	21.89	21.89	0	0	0
D7	2	16	27.00	105.03	4	1	0
D8	3	16	7.38	110.65	2	1	0
D9	2	5	4.08	16.32	0	1	0
D10	1	10	6.58	59.22	0	2	1
D13	1	5	14.98	59.91	4	2	0
Dt	13	106	6.78	718.76	18	40	22
LG01	1	2	15.46	15.46	1	0	0
LG02	1	2	15.61	15.61	0	2	0
LG03	1	5	17.10	68.39	1	1	0
LG04	1	4	7.08	21.25	0	0	0
Total	28	230	6.66	1531.94	37	91	39

counted in bolls from the internal, middle parts of the plants for 330 F_2 individuals, and a total of 285 $F_{2:3}$ family lines, along with P_1, P_2 and F_1 in the middle of each row, were tagged for scoring and harvesting.

Genomic DNA was extracted from young leaves of the 330 F_2 individuals, F_1 and two parents using the improved CTAB method (Paterson et al. 1993). A total of 8,200 simple sequence repeat (SSR) primer pairs were chosen according to several cotton 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 polymorphisms. These SSR primer sequences are available at 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).

JoinMap 3.0 (Van Ooijen 2001) was used to construct a complete linkage map. A logarithm of odds (LOD) threshold of 4.0 and a 50 cM maximal distance were used to determine all linkage groups. The major QTLs and their effects were determined with WinQTLCart2.5 software (Wang et al. 2005) using the composite interval mapping (CIM) method (Zeng 1994). QTLs with LOD values between 2.0 and 3.0 were defined as suggestive QTLs (Lander and Kruglyak 1995), and QTLs with LOD values no less than the threshold value (calculated by a permutation test with 1,000 repeats) were defined as significant QTLs (Churchill and Doerge 1994). QTLs for the same trait across different generations were defined as "common" QTLs when their confidence intervals overlapped. Epistatic QTLs (E-QTLs) were also detected using the mapping of additive, dominance and digenic epistasis genes in biparental populations (BIP) functionality of the inclusive composite interval mapping (ICIM) software IciMapping ver. 3.2 (Wang et al. 2012), The ICIM-EPI mapping method in BIP functionality has high detection efficiency and is used specifically for estimating digenic epistasis genes in

biparental populations, even if the effect of a single QTL is minor. The probability in stepwise regression was set at 0.0001 and the scanning step was 5 cM. A LOD threshold score of 5.0 was used to declare significant E-QTLs.

The name of each QTL includes a "q" followed by an abbreviation of the trait name, the population type, the chromosome or linkage group and a serial number to distinguish different QTLs of the same trait on the same chromosome. Linkage groups were assigned to chromosomes based on anchored markers in the dense linkage map (Han et al. 2004; Guo et al. 2007). Linkage groups that could not be assigned to any chromosome were designated as "LGXX" (where LG indicates linkage group and XX is the serial number).

Results

Marker analysis and map construction

We chose 8,200 SSR markers to screen for polymorphisms between the two parents, AQ and 08-10604. Approximately 3.22 % (264/8,200) of the SSR primers showed polymorphisms. These polymorphic primers were then used to screen F_2 individuals, and 284 loci were obtained, including 155 codominant loci (1:2:1) and 129 dominant loci (1:3 or 3:1). There were 45 loci (17.31 %) that showed segregation distortion, and 37 loci were mapped to chromosomes or linkage groups.

A total of 230 loci were successfully assigned to 28 linkage groups on the 16 chromosomes of the cotton genome using JoinMap3.0 software at a LOD $\geq$4. The total length of the map was 1,531.94 cM, with an average inter-marker distance of 6.66 cM. The average distance of adjacent markers was 6.24 cM in the A-subgenome, covering 692.48 cM, and 6.78 cM in the D-subgenome, covering 718.76 cM (Table 1).

Trait performance

A *T* test showed that the boll-, yield- and fiber quality-related traits were significantly different between the two parents, except for the lint percentage trait (Table 2). Among the 17 traits examined, the values of 14 traits were higher in AQ than in 08-10604, except for BN, FE and MIC. There were significant or highly significant differences in traits between AQ and 08-10604, except for LY, suggesting that the parents used in this study were appropriate for searching for genes responsible for boll-related and fiber traits. The variation coefficients of traits such as BLN, BL and BD were lower, indicating that these traits were relatively stable.

Correlations (Tables 3, 4) between boll-related traits and the other traits in the F_2 and $F_{2:3}$ populations were analyzed using SPSS20.0 software. In the $F_{2:3}$ population (Table 4), significant positive correlations were observed between BD, BL, BCW, BLN and BW (0.613**, 0.447**, 0.725**, 0.431**), while significant negative correlations existed between BD, BL, BCW, BLN and BN (−0.232**, −0.202**, −0.230**, −0.203**) and between BW and BN (−0.261**). Furthermore, there were significant positive correlations between FL, FS and BL (0.162**, 0.241**), while significant negative correlations were observed between BD, BL, BCW and MIC (−0.220**, −0.208**, −0.224**). Boll-related traits not only contribute significantly to cotton yield, but they also contribute to fiber quality traits. In the F_2 population, BLN had the highest contribution (12.63 %), followed by BL, BW and BCW. However, in $F_{2:3}$, BL had the highest contribution (15.93 %), followed by LP, BSN and BCW (Table 5). In the F_2 and $F_{2:3}$ populations, BW had notable positive correlations with the traits BCW, BL, SI, BLN and BD, while BW and BLW also had considerable positive correlations. Since it is difficult to accurately deduce the relationships between characters through correlation analysis, BW-related traits should be further analyzed using regression equations (Table 6). According to the analysis of regression equations and path coefficients, BCW had the highest positive contribution to BW. In the F_2 population, BW increased by 0.426 g, which was accompanied by a 1 g increase in BCW. BW increased by 0.230 g as a result of a 1 mm increase in BD. BW increased by 0.136 g, while the BLN increased by 1. However, BW decreased by 0.061 g while SI increased by 1 g. In the $F_{2:3}$ population, BW increased by 0.369 g, which was accompanied by an increase in BCW of 1 g. BW increased by 0.208 g as a result of a 1 mm increase in BD. BW increased by 0.180 g while the BLN increased by 1. Unlike the F_2 population, in the $F_{2:3}$ population, BW increased by 0.197 g while SI increased by 1 g.

Table 2 Performance of boll, yield-related and fiber traits of parents and the F_2 and $F_{2:3}$ populations

Trait	Parents					F_2			$F_{2:3}$		
	AQ		08-10604		P1–P2	Range	Mean ± SD	CV%	Range	Mean ± SD	CV%
	Mean ± SD	CV%	Mean ± SD	CV%							
BCW (g)	2.99 ± 0.13	4.35	0.59 ± 0.06	10.17	2.40**	0.64–2.63	1.49 ± 0.32	21.16	0.94–2.12	1.43 ± 0.23	15.89
BL (mm)	55.30 ± 2.25	4.07	32.03 ± 2.44	7.62	23.27**	35.99–57.06	45.52 ± 3.43	7.54	35.42–51.09	42.20 ± 2.69	6.36
BLN	4.55 ± 0.27	5.93	3.13 ± 0.10	3.19	1.42**	2.60–5.00	3.86 ± 0.34	8.72	2.48–4.32	3.82 ± 0.21	5.42
BLW (g)	2.53 ± 0.35	13.83	0.56 ± 0.13	23.21	1.97**	0.55–2.20	1.43 ± 0.36	25.38	0.69–1.85	1.21 ± 0.18	15.33
BN	16.43 ± 4.27	25.99	39.10 ± 12.11	30.97	−22.67**	3.00–52.00	22.96 ± 10.79	46.98	11.50–59.00	26.03 ± 6.73	25.86
BW (g)	6.92 ± 0.83	11.99	1.62 ± 0.23	14.20	5.30**	1.67–6.74	4.09 ± 0.82	20.01	2.57–5.12	3.69 ± 0.44	11.96
BSN	32.31 ± 2.54	7.86	18.69 ± 1.82	9.74	13.62**	12.00–40.00	26.74 ± 5.10	19.07	17.60–33.20	25.40 ± 2.77	10.91
BD (mm)	40.97 ± 3.52	8.59	21.69 ± 1.16	5.35	19.28**	26.04–38.73	31.69 ± 2.20	6.95	26.86–37.36	31.41 ± 1.89	6.01
FE (%)	6.90 ± 0.58	8.41	7.50 ± 0.65	8.67	−0.60*	4.90–10.00	6.91 ± 1.02	14.73	6.40–8.00	7.13 ± 0.24	3.34
FL (mm)	29.87 ± 0.81	2.71	27.69 ± 0.65	2.35	2.18*	26.78–36.65	31.93 ± 1.80	5.65	24.43–33.33	30.00 ± 1.45	4.82
FS (cN/tex)	33.70 ± 1.87	5.55	27.50 ± 1.66	6.04	6.20**	25.60–53.20	38.42 ± 4.22	10.98	27.00–37.40	31.84 ± 1.74	5.48
FU (%)	85.50 ± 0.96	1.12	82.70 ± 0.93	1.12	2.80*	79.90–91.40	86.09 ± 1.82	2.11	81.00–87.70	85.20 ± 1.17	1.37
LP	0.34 ± 0.02	5.88	0.33 ± 0.02	6.06	0.01	0.20–0.45	0.35 ± 0.05	13.40	0.23–0.41	0.33 ± 0.03	9.01
LY (g)	36.91 ± 6.92	18.75	12.57 ± 2.94	23.39	24.34**	2.38–56.29	19.95 ± 11.35	56.90	6.43–45.73	20.92 ± 6.12	29.24
MIC	4.40 ± 0.32	7.27	5.06 ± 0.21	4.15	−0.66*	3.10–7.60	4.54 ± 0.60	13.17	3.41–5.64	4.77 ± 0.39	8.25
SI (g)	14.92 ± 1.35	9.05	6.08 ± 0.37	6.09	8.84**	6.54–13.63	10.40 ± 1.34	12.88	8.03–12.93	10.31 ± 1.00	9.71
SY (g)	107.32 ± 20.50	19.10	36.97 ± 7.43	20.10	70.35**	3.46–159.37	57.49 ± 32.69	56.87	11.53–142.11	67.28 ± 17.9	26.60

BCW boll coat weight, *BL* boll length, *BLN* locule number per boll, *BN* boll number per plant, *BLW* lint weight per boll, *BW* boll weight, *BSN* Seed number per boll, *BD* boll diameter, *FE* fiber elongation, *FL* fiber length, *FS* fiber strength, *FU* fiber uniformity ratio, *LP* lint percentage, *LY* lint yield, *MIC* micronaire, *SI* seed-index, *SY* seed-cotton yield

* and ** indicate significance levels of $P = 0.05$ and $P = 0.01$, respectively

Table 3 Correlation analysis of boll, yield-related and fiber traits in the F_2 population

	LY	BLW	BD	BL	BN	SI	SY	BW	BCW	BLN	BSN	LP	FL	FS	MIC	FU	FE
LY	1																
BLW	0.253**	1															
BD	0.148*	0.425**	1														
BL	0.153**	0.393**	0.632**	1													
BN	0.648**	0.061	0.151**	0.165**	1												
SI	−0.099	0.059	0.400**	0.321**	−0.022	1											
SY	0.916**	0.037	0.159**	0.159**	0.657**	−0.023	1										
BW	0.132*	0.782**	0.610**	0.553**	0.081	0.279**	0.102	1									
BCW	0.029	0.508**	0.691**	0.627**	0.022	0.423**	0.049	0.763**	1								
BLN	−0.001	0.273**	0.309**	0.143*	0.001	0.088	0.014	0.346**	0.332**	1							
BSN	0.167**	0.407**	0.320**	0.255**	0.199**	0.018	0.162**	0.502**	0.311**	0.255**	1						
LP	0.258**	0.571**	−0.004	−0.035	0.047	−0.324**	−0.014	0.083	−0.080	0.036	0.115	1					
FL	−0.099	−0.089	0.123	0.085	0.016	0.191**	−0.070	−0.014	0.070	−0.049	−0.029	−0.164**	1				
FS	0.026	−0.029	0.210**	0.134*	−0.043	0.083	0.034	0.008	0.142*	0.011	−0.096	−0.026	0.491**	1			
MIC	−0.042	0.076	−0.081	−0.080	−0.043	0.134*	−0.047	0.108	−0.005	0.114	−0.013	−0.038	−0.207**	−0.183**	1		
FU	−0.032	0.026	0.170**	0.107	0.051	0.085	−0.049	0.040	0.125	−0.001	0.009	−0.050	0.534**	0.689**	−0.011	1	
FE	0.009	0.041	−0.195**	−0.087	−0.014	−0.221**	−0.006	−0.031	−0.170**	−0.010	0.044	0.060	−0.521**	−0.537**	0.139*	−0.325**	1

BCW boll coat weight, *BL* boll length, *BLN* locule number per boll, *BN* boll number per plant, *BLW* lint weight per boll, *BW* boll weight, *BSN* Seed number per boll, *BD* boll diameter, *FE* fiber elongation, *FL* fiber length, *FS* fiber strength, *FU* fiber uniformity ratio, *LP* lint percentage, *LY* lint yield, *MIC* micronaire, *SI* seed-index, *SY* seed-cotton yield

* and ** indicate significance levels of $P = 0.05$ and $P = 0.01$, respectively

Table 4 Correlation analysis of boll, yield-related and fiber traits in the $F_{2:3}$ population

	LY	BLW	BD	BL	BN	SI	SY	BW	BCW	BLN	BSN	LP	FL	FS	MIC	FU	FE
LY	1																
BLW	0.258**	1															
BD	−0.030	0.490**	1														
BL	−0.005	0.361**	0.710**	1													
BN	0.456**	−0.228**	−0.232**	−0.202**	1												
SI	−0.164**	0.222**	0.509**	0.432**	−0.236**	1											
SY	0.922**	0.101	−0.036	−0.026	0.547**	−0.114	1										
BW	0.116	0.810**	0.613**	0.447**	−0.261**	0.529**	0.091	1									
BCW	−0.093	0.473**	0.728**	0.606**	−0.230**	0.646**	−0.061	0.725**	1								
BLN	0.026	0.327**	0.411**	0.244**	−0.203**	0.108	0.027	0.431**	0.419**	1							
BSN	0.228**	0.382**	0.231**	0.134*	−0.039	0.020	0.225**	0.488**	0.233**	0.359**	1						
LP	0.277**	0.613**	0.005	0.014	−0.044	−0.337**	0.041	0.037	−0.169**	−0.012	−0.007	1					
FL	−0.059	−0.169**	0.135*	0.162**	0.014	0.275**	0.026	0.019	0.190**	−0.017	−0.078	−0.313**	1				
FS	−0.149*	−0.014	0.290**	0.241**	−0.079	0.400**	−0.078	0.195**	0.387**	0.028	−0.047	−0.279**	0.555**	1			
MIC	0.120	0.124*	−0.220**	−0.208**	0.000	−0.080	0.044	−0.022	−0.224**	−0.198**	−0.005	0.236**	−0.526**	−0.503**	1		
FU	−0.002	0.066	0.160**	0.080	−0.040	0.350**	0.022	0.192**	0.219**	−0.027	−0.069	−0.150*	0.262**	0.341**	−0.035	1	
FE	−0.103	−0.089	0.135*	0.176**	−0.049	0.213**	−0.067	0.039	0.221**	−0.107	−0.061	−0.197**	0.573**	0.578**	−0.215**	0.177**	1

BCW boll coat weight, *BL* boll length, *BLN* locule number per boll, *BN* boll number per plant, *BLW* lint weight per boll, *BW* boll weight, *BSN* Seed number per boll, *BD* boll diameter, *FE* fiber elongation, *FL* fiber length, *FS* fiber strength, *FU* fiber uniformity ratio, *LP* lint percentage, *LY* lint yield, *MIC* micronaire, *SI* seed-index, *SY* seed-cotton yield

* and ** indicate significance levels of $P = 0.05$ and $P = 0.01$, respectively

Table 5 Summary of main-effect quantitative trait loci (QTLs) for boll, yield-related and fiber traits detected in both populations

Trait	QTLs	Position (cM)	LOD	LOD threshold	Flanking markers (99 %)	Additive effect	Dominant effect	Origin	PV (%)
BCW	qBCW-$F_{2:3}$-A10-1#	43.81	5.05	3.73	NAU1297-290-NAU1297-400	0.0948	−0.0674	AQ	13.72
	qBCW-$F_{2:3}$-A10-2#	50.01	5.08	3.73	NAU1297-400-BNL1569-210	0.0902	−0.0576	AQ	12.46
	qBCW-$F_{2:3}$-A10-3	63.41	3.19	3.73	BNL1569-210-Gh236-120	0.0753	−0.0421	AQ	8.09
	qBCW-$F_{2:3}$-A5-1	1.01	2.56	3.73	NAU4106-390-NAU4111-360	0.0492	−0.033	AQ	4.62
	qBCW-$F_{2:3}$-D1-1#	52.61	6.18	3.73	NAU6539-400-MNL2921-180	0.1109	0.0109	AQ	9.74
	qBCW-$F_{2:3}$-D1-2#	60.01	6.27	3.73	MNL2921-180-Gh649-150	0.1043	0.0248	AQ	7.07
	qBCW-F_2-A10-1#	50.01	5.65	3.89	NAU1297-400-BNL1569-210	0.1311	−0.02	AQ	9.51
	qBCW-F_2-A13-1#	48.51	4.46	3.89	NAU1141-210-cgr6359-200	0.1032	−0.0788	AQ	9.37
	qBCW-F_2-A13-2#	58.21	4.61	3.89	NAU1023-290-NAU6122-320	0.1058	−0.0553	AQ	8.45
	qBCW-F_2-D1-1#	53.61	7.34	3.89	NAU6539-400-Gh216-100	0.1414	0.0614	AQ	6.40
	qBCW-F_2-D1-2#	65.81	6.79	3.89	Gh216-100-Gh649-150	0.1395	0.0353	AQ	7.07
	qBCW-F_2-D5-1	145.51	2.74	3.89	cer0148-200-dPL0056-100	0.0883	−0.0622	AQ	6.12
	qBCW-F_2-LG02-1	8.51	2.76	3.89	dc40265-190-Gh246-110	−0.0037	0.1864	08-10604	3.58
BL	qBL-$F_{2:3}$-A10-1#	41.81	7.40	3.81	NAU1297-290-NAU1297-400	1.3897	−0.4285	AQ	15.93
	qBL-$F_{2:3}$-A10-2#	51.01	8.44	3.81	NAU2935-350-BNL1569-210	1.3251	−0.3377	AQ	15.25
	qBL-$F_{2:3}$-A13-1	124.21	2.82	3.81	NAU6699-400-NAU5110-490	0.7491	−0.2181	AQ	5.03
	qBL-$F_{2:3}$-A5-1	3.01	3.17	3.81	NAU4106-390-BNL1878-300	0.6824	−0.4019	AQ	5.85
	qBL-$F_{2:3}$-D1-1#	61.01	4.41	3.81	NAU6539-400-NAU5107-500	0.9432	0.4324	AQ	3.12
	qBL-F_2-A10-1#	35.81	11.74	3.73	NAU1236-200-NAU3122-200	1.8271	0.5807	AQ	8.94
	qBL-F_2-A10-2#	42.81	8.21	3.73	NAU1297-290-NAU1297-400	1.7043	0.2328	AQ	9.91
	qBL-F_2-A13-1	127.61	3.51	3.73	NAU6699-400-NAU5110-490	0.7996	−0.6422	AQ	5.29
	qBL-F_2-A6-1#	8.91	6.24	3.73	dPL0617-150-Gh433-150	1.3905	0.6214	AQ	3.68
	qBL-F_2-D5-1#	113.51	3.89	3.73	CIR062-200-NAU5273-240	1.2124	0.0342	AQ	5.14
	qBL-F_2-D5-2#	126.11	6.37	3.73	HAU1952-500-TMC05-190	1.4326	−0.2546	AQ	9.06
	qBL-F_2-D5-3#	141.81	4.25	3.73	cer0148-200-HAU3109-250	1.1671	−0.2711	AQ	6.54
BLN	qBLN-$F_{2:3}$-A10-1	86.51	3.45	3.57	BNL1569-210-NAU5359-350	0.0713	0.0138	AQ	5.28
	qBLN-$F_{2:3}$-D5-1#	128.11	4.47	3.57	NAU779-600-TMC05-190	0.0815	0.0247	AQ	5.08
	qBLN-$F_{2:3}$-D5-2#	145.01	4.26	3.57	cer0148-200-dPL0056-100	0.0816	0.0123	AQ	6.48
	qBLN-F_2-D10-1	5.71	2.72	3.70	NAU2540-160-BNL946-350	1.6377	0.1366	AQ	3.81
	qBLN-F_2-D1-1	89.31	2.58	3.70	NAU5107-500-HAU3297-300	−0.0604	0.1155	08-10604	7.00
	qBLN-F_2-D1-2	97.01	3.26	3.70	JESPR-243-150-TME03-200	−0.1324	0.1055	08-10604	12.63

Table 5 continued

Trait	QTLs	Position (cM)	LOD	LOD threshold	Flanking markers (99 %)	Additive effect	Dominant effect	Origin	PV (%)
BLW	qBLW-$F_{2:3}$-A10-1	35.91	2.90	3.73	NAU1236-200-NAU1297-400	0.0588	−0.0198	AQ	6.32
	qBLW-$F_{2:3}$-D13-1	2.01	3.07	3.73	NAU2886-270-JESPR-204-170	0.0589	−0.0339	AQ	7.73
	qBLW-$F_{2:3}$-D5-1#	58.71	3.75	3.73	Gh354-150-NAU3096-300	0.0671	−0.0555	AQ	11.65
	qBLW-F_2-A3-1	65.71	3.38	3.70	NAU2440-160-NAU3995-480	−0.008	0.212	08-10604	4.13
	qBLW-F_2-D5-2	142.01	2.93	3.70	cer0148-200-dPL0056-100	0.1177	0.0309	AQ	3.60
BW	qBW-$F_{2:3}$-A10-1	77.71	2.70	3.82	BNL1569-210-NAU5359-350	0.128	−0.1058	AQ	7.19
	qBW-$F_{2:3}$-D13-1	3.01	3.05	3.82	NAU2886-270-JESPR-204-200	0.1525	−0.0469	AQ	7.17
	qBW-F_2-A10-1#	104.01	5.44	3.63	HAU1423-150-NAU5359-350	0.3417	0.2221	AQ	4.76
	qBW-F_2-A13-1	52.91	2.64	3.63	cgr5856-130-NAU1023-290	0.2163	−0.102	AQ	5.02
	qBW-F_2-A13-2	58.21	2.77	3.63	NAU1023-290-BNL1421-200	0.227	−0.0604	AQ	4.65
	qBW-F_2-A9-1	56.51	3.42	3.63	cgr5110-150-NAU6130-200	−0.0322	0.5887	08-10604	3.66
	qBW-F_2-D5-1#	74.11	4.09	3.63	JESPR-204-190-NAU3001-200	0.3452	−0.1007	AQ	9.86
	qBW-F_2-D5-2#	96.91	4.53	3.63	dPL0155-220-NAU3620-240	0.308	0.1253	AQ	3.37
	qBW-F_2-D5-3	142.01	2.58	3.63	NAU5273-240-dPL0056-100	0.2426	−0.0651	AQ	4.89
BSN	qBSN-$F_{2:3}$-A10-1	64.41	2.56	3.71	NAU1297-400-Gh236-120	0.7871	−0.7997	AQ	7.90
	qBSN-$F_{2:3}$-A9-1	7.01	3.64	3.71	Gh247-150-cgr5707-420	−1.0469	1.0185	08-10604	14.30
	qBSN-F_2-A3-1	13.81	3.19	3.64	NAU3016-500-NAU3995-600	−1.4103	0.8252	08-10604	6.50
BD	qBD-$F_{2:3}$-A10-1	51.31	3.34	3.59	NAU1297-400-Gh236-120	0.5665	−0.2155	AQ	6.07
	qBD-$F_{2:3}$-A10-2	105.51	3.04	3.59	HAU1423-150-NAU5359-350	0.6282	0.043	AQ	4.93
	qBD-$F_{2:3}$-A5-1#	5.01	3.76	3.59	NAU4106-390-HAU1384-280	0.6146	0.1593	AQ	4.33
	qBD-$F_{2:3}$-D1-1#	51.61	4.85	3.59	NAU6539-400-MNL2921-180	0.7875	0.083	AQ	7.15
	qBD-$F_{2:3}$-D1-2#	60.01	5.06	3.59	MNL2921-180-Gh216-100	0.7553	0.0441	AQ	6.68
	qBD-F_2-A10-1	101.51	3.42	3.78	NAU456-300-NAU5359-350	0.7669	0.388	AQ	3.65
	qBD-F_2-A3-2#	73.31	4.88	3.78	NAU3995-480-NAU1167-500	0.7838	0.2327	AQ	4.53
	qBD-F_2-D1-1#	53.11	8.43	3.78	NAU6539-400-MNL2921-180	1.0853	0.4799	AQ	6.94
	qBD-F_2-D1-2#	70.41	7.26	3.78	Gh649-150-NAU5107-500	0.9833	0.6223	AQ	4.29
	qBD-F_2-D5-1	150.01	3.51	3.78	cer0148-200-dPL0056-100	0.6952	−0.3777	AQ	7.19
FE	qFE-$F_{2:3}$-A13-1	19.61	2.81	3.67	NAU2300-600-cgr5856-130	−0.0878	0.0434	08-10604	8.49
	qFE-$F_{2:3}$-LG02-1	2.01	3.48	3.67	dc40265-190-Gh246-110	0.0039	0.2015	08-10604	4.90
	qFE-F_2-A10-1	78.61	3.37	3.83	BNL1569-210-HAU1423-150	0.2306	−0.9437	AQ	5.23
	qFE-F_2-A12-1	30.91	2.64	3.83	dc20022-140-NAU3401-260	0.547	−0.1174	AQ	4.99
	qFE-F_2-D5-1	160.01	2.55	3.83	HAU3109-250-cgr5510-150	−0.5228	−0.1084	08-10604	3.08

Table 5 continued

Trait	QTLs	Position (cM)	LOD	LOD threshold	Flanking markers (99 %)	Additive effect	Dominant effect	Origin	PV (%)
FL	qFL-$F_{2:3}$-A3-1	63.81	2.71	3.76	NAU2440-160-NAU3995-480	−0.477	0.1919	08-10604	6.53
	qFL-$F_{2:3}$-A6-1#	15.41	5.26	3.76	NAU3206-170-Gh433-150	−0.4905	0.3415	08-10604	10.89
	qFL-$F_{2:3}$-LG03-1	45.31	2.69	3.76	NAU4030-150-cgr5181-140	0.0127	0.0074	AQ	4.76
	qFL-F_2-A13-1	0.01	2.86	3.84	HAU0539-210-NAU2300-600	−0.5558	−0.04	08-10604	3.96
FS	qFS-$F_{2:3}$-A9-1	29.01	3.24	3.72	NAU1009-200-BNL1672-100	0.6473	−0.2883	AQ	9.11
	qFS-$F_{2:3}$-D1-1#	85.81	4.09	3.72	NAU5107-500-JESPR-243-150	0.6309	0.2533	AQ	3.78
	qFS-$F_{2:3}$-D1-2	52.41	2.76	3.72	TMJ24-190-NAU3736-200	−0.4782	0.2997	08-10604	6.07
	qFS-F_2-A12-1	0.01	2.58	4.96	cgr6439-370-HAU2835-400	−0.3111	−0.0012	08-10604	4.31
	qFS-F_2-D5-1	93.41	4.40	4.96	dc30008-500-HAU3238-150	0.4092	−0.0166	AQ	7.36
FU	qFU-$F_{2:3}$-D1-1	88.81	2.94	3.80	HAU2425-200-JESPR-243-150	0.3666	−0.1054	AQ	6.25
	qFU-$F_{2:3}$-D1-2	100.31	2.76	3.80	JESPR-243-150-JESPR-221-190	0.3783	0.1442	AQ	3.43
	qFU-F_2-A12-1	32.21	2.62	3.69	NAU4089-190-dPL0240-280	1.354	0.0034	AQ	4.53
LP	qLP-$F_{2:3}$-A13-1	0.01	3.02	3.85	HAU0539-210-cgr5331-170	−0.0089	0.0001	08-10604	4.36
	qLP-$F_{2:3}$-A13-2	16.61	2.91	3.85	cgr5331-170-dPL0308-190	−0.01	0.0043	08-10604	7.40
	qLP-$F_{2:3}$-A6-1#	15.41	4.91	3.85	dPL0617-150-Gh433-150	0.0116	0.0024	AQ	6.02
	qLP-$F_{2:3}$-A9-1	26.71	3.41	3.85	cgr6692-150-cgr5867-200	−0.01	0.003	08-10604	7.03
	qLP-$F_{2:3}$-D5-1	18.11	2.53	3.85	NAU4907-1000-JESPR-236-130	0.0039	−0.0099	AQ	4.60
	qLP-$F_{2:3}$-D5-2#	52.01	5.98	3.85	NAU5121-180-JESPR-204-220	0.009	−0.0156	AQ	15.19
LY	qLY-$F_{2:3}$-D10-1	2.81	2.60	3.73	NAU6360-350-BNL946-350	−1.6177	1.482	08-10604	6.72
MIC	qMIC-$F_{2:3}$-A12-1	40.51	3.36	3.57	HAU1081-170-HAU0545-250	−0.1053	0.1259	08-10604	8.00
	qMIC-$F_{2:3}$-A9-1#	0.01	3.59	3.57	JESPR-110-250-Gh247-150	−0.114	0.0679	08-10604	7.14
	qMIC-$F_{2:3}$-D1-1#	55.41	5.22	3.57	TMJ24-190-NAU3736-200	0.1634	−0.0711	AQ	11.30
	qMIC-$F_{2:3}$-D8-1	18.11	2.84	3.57	NAU3201-220-NAU3954-490	−0.1306	0.0715	08-10604	7.41
	qMIC-F_2-D7-1	9.11	4.05	6.14	NAU4030-170-HAU1129-230	0.1442	−0.2534	AQ	9.85
SI	qSI-$F_{2:3}$-A3-1	70.31	2.95	3.62	TML04-220-NAU5035-250	0.3568	−0.1124	AQ	7.00
	qSI-$F_{2:3}$-A3-2	81.71	2.85	3.62	NAU5035-250-NAU1167-500	0.3657	0.064	AQ	4.74
	qSI-$F_{2:3}$-D1-1#	60.01	5.32	3.62	MNL2921-180-NAU5107-500	0.4158	0.2262	AQ	3.79
	qSI-F_2-D9-1	3.01	2.86	3.75	BNL686-170-NAU3100-640	−0.1245	1.1479	08-10604	3.41

Origin: indicates the parent that provides genes facilitating plant architecture

BCW boll coat weight, *BL* boll length, *BLN* locule number per boll, *BN* boll number per plant, *BLW* lint weight per boll, *BW* boll weight, *BSN* seed number per boll, *BD* boll diameter, *FE* fiber elongation, *FL* fiber length, *FS* fiber strength, *FU* fiber uniformity ratio, *LP* lint percentage, *LY* lint yield, *MIC* micronaire, *SI* seed-index, *SY* seed-cotton yield, *PV%* phenotypic variation explained by a QTL

Significant QTLs

Table 6 Regression equations and path coefficients of yield-component traits related to boll weight

Generation	Regression equations	Path coefficient			
		Px_1-y	Px_2-y	Px_3-y	Px_4-y
F_2	$Y = -2.743 + 0.085X_1 + 1.021X_2 + 0.307\ X_3 - 0.036X_4$	0.230	0.426	0.136	−0.061
$F_{2:3}$	$Y = -0.959 + 0.049X_1 + 0.667X_2 + 0.383X_3 + 0.087X_4$	0.208	0.369	0.180	0.197

Y boll weight (g), X_1 boll diameter (mm), X_2 boll coat weight (g), X_3 locule number per boll, X_4 seed-index (g)

QTLs for boll-, fiber quality- and yield-related traits

We performed QTL analysis using CIM via WinQTLCart2.5. Many QTLs related to almost all traits were detected in the F_2 and $F_{2:3}$ populations. A total of 91 M-QTLs were detected in the F_2 and $F_{2:3}$ populations for 17 traits using CIM, including 37 significant QTLs with LOD values greater than or equal to the threshold value calculated by a permutation test with 1,000 repeats. We detected 18 and 19 significant QTLs in the F_2 and $F_{2:3}$, respectively (Fig. 1; Table 5). Moreover, six pairs of common QTLs and five QTL clusters affecting boll-related traits were found in both populations (Table 7). A total of 64 pairs of E-QTLs exhibiting additive-by-additive (AA), additive-by-dominant (AD), dominant-by-additive (DA) and dominant-by-dominant (DD) interactions were detected for all measured traits in both populations (Table 8), namely, 39 for boll- and 25 for yield-related traits, but no interaction for fiber quality traits was detected. The phenotype variation (PV) explained by all E-QTLs ranged from 7.852 to 34.251 %.

Boll-related traits

A total of 58 M-QTLs were detected in the F_2 and $F_{2:3}$ populations for seven boll-related traits using CIM, including 30 significant QTLs with LOD values greater than or equal to the threshold value calculated by a permutation test with 1,000 repeats. We detected 17 and 13 significant QTLs in the F_2 and $F_{2:3}$, respectively (Fig. 1; Table 5). Only common QTLs and QTL clusters for boll-related traits were found in both populations (Table 7).

Boll coat weight

Thirteen M-QTLs (nine significant QTLs) were detected in the F_2 and $F_{2:3}$ populations. In the F_2 population, among seven M-QTLs affecting BCW, five significant QTLs were detected, including *qBCW-F_2-A10-1*, *qBCW-F_2-A13-1*, *qBCW-F_2-A13-2*, *qBCW-F_2-D1-1* and *qBCW-F_2-D1-2*, which explained 6.40–9.51 % of PV, with LOD scores of 4.46–7.34. In the $F_{2:3}$ population, among six M-QTLs, four significant QTLs were detected, namely, *qBCW-$F_{2:3}$-A10-1*, *qBCW-$F_{2:3}$-A10-2*, *qBCW-$F_{2:3}$-D1-1* and *qBCW-$F_{2:3}$-D1-2*, which explained 7.07–13.72 % of PV, with LOD scores of 5.05–6.27. The favorable alleles of all 13 M-QTLs originated from AQ. Among the 13 QTLs, two pairs of QTLs for BCW, *qBCW-$F_{2:3}$-A10-2* and *qBCW-F_2-A10-1* and *qBCW-$F_{2:3}$-D1-1* and *qBCW-F_2-D1-1*, were found on Chr. A10 and Chr. D1, respectively, in both populations at the same (50.01 cM) or similar positions (52.61, 53.61 cM) in the same marker interval. These two pairs of common QTLs contributed positive additive effects from AQ. In addition, seven pairs of E-QTLs for BCW were also detected, which are distributed on nine chromosomes or linkage groups and displayed −0.082 to 0.090 AA effects, −0.224 to 0.428 AD effects, −0.218 to 0.210 DA effects and −0.767 to 0.210 DD effects, explaining 14.745–33.718 % of PV.

Boll length

Twelve M-QTLs (nine significant QTLs) were detected in the F_2 and $F_{2:3}$ populations. In the F_2 population, among seven M-QTLs affecting boll length, six significant QTLs were detected, namely, *qBL-F_2-A10-1*, *qBL-F_2-A10-2*, *qBL-F_2-A6-1*, *qBL-F_2-D5-1*, *qBL-F_2-D5-2* and *qBL-F_2-D5-3*, which explained 3.68–9.91 % of PV, with LOD scores of 3.89–11.74. In the $F_{2:3}$ population, among five M-QTLs, three significant QTLs were detected, namely, *qBL-$F_{2:3}$-A10-1*, *qBL-$F_{2:3}$-A10-2* and *qBL-$F_{2:3}$-D1-1*, which explained 3.12–15.93 % of PV, with LOD scores of 4.41–8.44. Among of 12 M-QTLs from AQ, two common pairs of QTLs, including *qBL-$F_{2:3}$-*

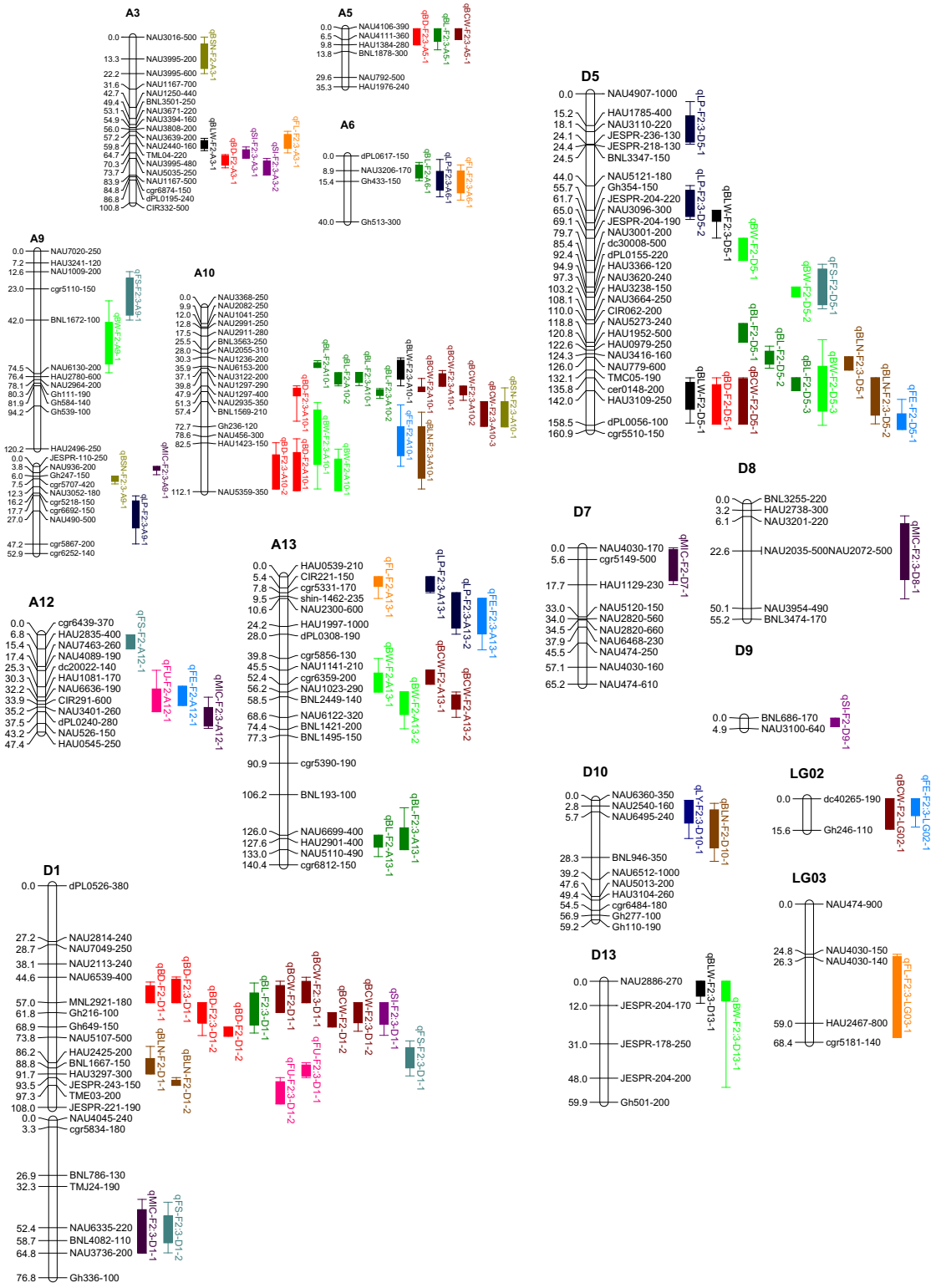

Fig. 1 The locations of 91 M-QTLs on the linkage map

A10-1 and *qBL-F_2-A10-2* (in the same marker interval, NAU1297-290-NAU1297-400) and *qBL-$F_{2:3}$-A13-1* and *qBL-F_2-A13-1* (in the same marker interval, NAU6699-400-NAU5110-490), were detected in both populations. Meanwhile, six pairs of E-QTLs were detected. These E-QTLs, which are distributed on nine chromosomes or linkage groups, displayed −0.670 to 1.556 AA effects, −0.874 to 3.104 AD effects, −2.230 to 2.256 DA effects and −1.608 to 4.876 DD effects, accounting for 7.852–27.413 % of PV.

Boll diameter

Ten M-QTLs (six significant QTLs) were detected in the F_2 and $F_{2:3}$ populations. In the F_2 population, among five M-QTLs affecting BD, three significant QTLs were detected, namely, *qBD-F_2-A3-2*, *qBD-F_2-D1-1* and *qBD-F_2-D1-2*, which explained 4.29–6.94 % of PV, with LOD scores of 4.88–8.43. In the $F_{2:3}$ population, among five M-QTLs, three significant QTLs were detected, namely, *qBD-$F_{2:3}$-A5-1*, *qBD-$F_{2:3}$-D1-1* and *qBD-$F_{2:3}$-D1-2*, which explained 4.33–7.15 % of PV, with LOD scores of 3.76–5.06. Among the 10 M-QTLs from AQ, two common pairs of QTLs, *qBD-$F_{2:3}$-A10-2* and *qBD-F_2-A10-1* (in very close positions, 105.51 and 101.51 cM, respectively) and *qBD-$F_{2:3}$-D1-1* and *qBD-F_2-D1-1* (in the same marker interval, NAU6539-400-MNL2921-180), were detected in both populations. In addition, five pairs of E-QTLs, which are distributed on eight chromosomes or linkage groups, displayed −0.630 to 0.547 AA effects, −0.257 to 2.343 AD effects, −1.400 to 1.284 DA effects and −4.165 to 3.649 DD effects, accounting for 9.244–28.680 % of PV (Table 8).

Locule number per boll

Six M-QTLs (two significant QTLs) were detected in the F_2 and $F_{2:3}$ populations. Among three M-QTLs affecting BLN, two significant QTLs were detected in the $F_{2:3}$ population, namely, *qBLN-$F_{2:3}$-D5-1* and *qBLN-$F_{2:3}$-D5-2*, which explained 5.08 and 6.48 % of PV, respectively, with LOD scores of 4.26 and 4.47, originating from AQ. In the F_2 population, no significant QTL for BLN was detected, although three M-QTLs, *qBLN-F_2-D10-1*, *qBLN-F_2-D1-1* and *qBLN-F_2-D1-2*, were detected, which explained 3.81–12.63 % of PV, with LOD scores of 2.58–3.26. Four M-QTLs contributed positive effects from AQ while the other two M-QTLs (*qBLN-F_2-D10-1* and *qBLN-F_2-D10-2*) contributed positive additive effects from 08-10604. Moreover, five pairs of E-QTLs for BLN were detected. These E-QTLs, which are distributed on six chromosomes or linkage groups, displayed −0.104 to 0.067 AA effects, −0.108 to 0.685 AD effects, −0.108 to 0.685 DA effects and −1.629 to 1.246 DD effects, explaining 15.359–31.953 % of PV.

Lint weight per boll

Five M-QTLs (two significant QTLs) were detected in the F_2 and $F_{2:3}$ populations. In the F_2 population, of the two M-QTLs, one significant QTL was detected, *qBLW-F_2-A3-1*, which explained 4.13 % of PV, with a LOD score of 3.38. In the $F_{2:3}$ population, among the three M-QTLs, one significant QTL was detected, *qBLW-$F_{2:3}$-D5-1*, which explained 11.65 % of PV, with a LOD score of 3.75. Five M-QTLs contributed positive effects from AQ while the other M-QTL (*qBLW-F_2-A3-1*) contributed positive additive effects from 08-10604. Two pairs of E-QTLs for BLW, including interactions between two loci on Chr. A10 and Chr. A9 and between two loci on Chr. A10 and Chr. D1, were also detected in the F_2 population. These E-QTL pairs demonstrated 0.133 and −0.076 AA effects, −0.197 and 0.390 AD effects, 0.121 and −0.403 DA effects and −0.268 and 0.603 DD effects, explaining 26.070 and 29.861 % of PV, respectively.

Boll weight

Nine M-QTLs (three significant QTLs) were detected in the F_2 and $F_{2:3}$ populations. Among seven M-QTLs, three significant QTLs were detected in the F_2 population, *qBW-F_2-A10-1*, *qBW-F_2-D5-1* and *qBW-F_2-D5-2*, which explained 3.37–9.86 % of PV, with LOD scores of 4.09–5.44. In the $F_{2:3}$ population, no significant QTL was detected for this trait, although two M-QTLs, *qBW-$F_{2:3}$-A10-1* and *qBW-$F_{2:3}$-D13-1*, were detected, which explained 7.19 and 7.17 % of PV, with LOD scores of 2.70 and 3.05, respectively. Eight M-QTLs had alleles with positive effects from AQ while the other M-QTL (*qBW-F_2-A9-1*) contributed positive additive effect from 08-10604. Six pairs of E-QTLs for BW were also detected. These E-QTLs, which are distributed on six chromosomes or linkage groups, displayed −0.249 to 0.288 AA effects, −0.886

to 0.321 AD effects, −0.571 to 0.877 DA effects and −0.814 to 0.694 DD effects, explaining 13.849–33.539 % of PV.

Seed number per boll

Three M-QTLs were detected in the F_2 and $F_{2:3}$ populations. There were no significant QTLs for this trait. One M-QTL, *qBSN-F$_2$-A3-1*, was detected in the F_2 population, which explained 6.50 % of PV, with a LOD score of 3.19, originating from 08-10604. In the $F_{2:3}$ population, two M-QTLs were detected, including *qBSN-F$_{2:3}$-A10-1*, with the favorable alleles originating from AQ, and *qBSN-F$_{2:3}$-A9-1*, with the favorable alleles originating from 08-10604, which explained 7.89 and 14.30 % of PV, with LOD scores of 2.56 and 3.64, respectively. Eight pairs of E-QTLs for BSN were also found. These E-QTLs, which are distributed on ten chromosomes or linkage groups, displayed −2.321 to 2.074 AA effects, −1.989 to 6.707 AD effects, −1.296 to 4.359 DA effects and −10.173 to 3.793 DD effects, explaining 11.101–34.351 % of PV.

Meanwhile, QTL clusters of boll-related traits were also observed in this study. A total of five QTL clusters of boll-related traits were found on Chr. A10, A13, D1 and D5 (Table 7). For example, Chr. A10 contains two QTL clusters, i.e., A10-cluster-1 at 35.81–77.71 cM and A10-cluster-1 at 86.51–105.51 cM, carrying 12 and four QTLs, respectively. Chr. A13 contains one QTL cluster carrying four QTLs, i.e., A13-cluster at 48.51–58.21 cM. Chromosome D1 contains one QTL cluster carrying 11 QTLs, i.e., D1-cluster at 51.61–97.01 cM. Finally, Chr. D5 contains one QTL cluster carrying ten QTLs, namely, D5-cluster at 96.91–150.01 cM. These results suggest that genes controlling boll-related traits may be linked or may exhibit pleiotropy.

Fiber quality-related traits

CIM revealed a total of 22 M-QTLs in the F_2 and $F_{2:3}$ populations for five traits, including four significant QTLs with LOD values greater than or equal to the threshold value calculated by a permutation test with 1,000 repeats; these QTLs were only detected in the $F_{2:3}$ (Fig. 1; Table 5).

Fiber elongation

Five M-QTLs for FE were detected in the F_2 and $F_{2:3}$ populations. There were no significant QTLs for this trait. Three M-QTLs were detected in the F_2 population, including *qFE-F$_2$-A10-1*, *qFE-F$_2$-A12-1* and *qFE-F$_2$-D5-1*, which explained 3.08–5.27 % of PV, with LOD scores of 2.55–3.37; the positive additive effects originated from AQ, except for *qFE-F$_2$-D5-1*. In the $F_{2:3}$ population, two M-QTLs were detected, *qFE-F$_{2:3}$-A13-1* and *qFE-F$_{2:3}$-LG02-1*, which explained 4.90 and 8.49 % of PV, respectively, with LOD scores of 2.81–3.48; the favorable alleles of two M-QTLs originated from 08-10604.

Fiber length

Four M-QTLs (one significant QTL) were detected in the F_2 and $F_{2:3}$ populations. Among three M-QTLs, one significant QTL, *qFL-F$_{2:3}$-A6-1*, was detected in the $F_{2:3}$ population, which explained 10.89 % of PV, with a LOD score of 5.26. In the F_2 population, one M-QTL, *qFL-F$_2$-A13-1*, was detected, which explained 3.96 % of PV, with a LOD score of 2.86. The favorable alleles of three M-QTLs originated from 08-10604, except for *qFL-F$_{2:3}$-LG03-1*, where it originated from AQ.

Fiber strength

Five M-QTLs (one significant QTL) were detected in the F_2 and $F_{2:3}$ populations. Among three M-QTLs, one significant QTL, *qFS-F$_{2:3}$-D1-1*, was detected in the $F_{2:3}$population, which explained 3.78 % of PV, with a LOD score of 4.09. In the F_2 population, two M-QTLs, *qFS-F$_2$-A12-1* and *qFS-F$_2$-D5-1*, were detected, which explained 4.31–7.36 % of PV, with a LOD score of 2.58–4.96. Three M-QTLs had alleles with positive effects from AQ while the other two M-QTLs (*qFS-F$_{2:3}$-D1-2* and *qFS-F$_2$-A12-1*) contributed positive additive effects from 08-10604.

Fiber uniformity

Three M-QTLs were detected in the F_2 and $F_{2:3}$ populations. There were no significant QTLs for this trait. One QTL, *qFU-F$_2$-A12-1*, was detected in the F_2 population, which explained 4.53 % of PV, with a

Table 7 Distribution of clusters of boll-related traits

Cluster name	Approximate position on chromosome (cM)	Number of QTLs	Name of QTLs		
A10					
A10-cluster-1	35.81–77.71	12	qBCW-$F_{2:3}$-A10-1	qBD-$F_{2:3}$-A10-1	qBL-F_2-A10-2
			qBCW-$F_{2:3}$-A10-2	qBL-$F_{2:3}$-A10-1	qBLW-$F_{2:3}$-A10-1
			qBCW-$F_{2:3}$-A10-3	qBL-$F_{2:3}$-A10-2	qBSN-$F_{2:3}$-A10-1
			qBCW-F_2-A10-1	qBL-F_2-A10-1	qBW-$F_{2:3}$-A10-1
A10					
A10-cluster-2	86.51–105.51	4	qBLN-$F_{2:3}$-A10-1		
			qBW-F_2-A10-1		
			qBD-$F_{2:3}$-A10-2		
			qBD-F_2-A10-1		
A13					
A13-cluster	48.51–58.21	4	qBCW-F_2-A13-1		
			qBCW-F_2-A13-2		
			qBW-F_2-A13-1		
			qBW-F_2-A13-2		
D1					
D1-cluster	51.61–97.01	11	qBCW-$F_{2:3}$-D1-1	qBD-$F_{2:3}$-D1-1	qBL-$F_{2:3}$-D1-1
			qBCW-$F_{2:3}$-D1-2	qBD-$F_{2:3}$-D1-2	qBLN-F_2-D1-1
			qBCW-F_2-D1-1	qBD-F_2-D1-1	qBLN-F_2-D1-2
			qBCW-F_2-D1-2	qBD-F_2-D1-2	
D5					
D5-cluster	96.91–150.01	10	qBCW-F_2-D5-1	qBL-F_2-D5-3	qBW-F_2-D5-3
			qBD-F_2-D5-1	qBLN-$F_{2:3}$-D5-1	qBW-F_2-D5-4
			qBL-F_2-D5-1	qBLN-$F_{2:3}$-D5-2	
			qBL-F_2-D5-2	qBLW-F_2-D5-2	

LOD score of 2.62, originating from AQ. In the $F_{2:3}$ population, two M-QTLs, *qFU-$F_{2:3}$-D1-1* and *qFU-$F_{2:3}$-D1-2*, were detected, which explained 6.52 and 3.43 % of PV, with LOD scores of 2.76 and 2.94, respectively, originating from AQ.

Micronaire

Five M-QTLs (two significant QTLs) were detected in the F_2 and $F_{2:3}$ populations. Among four M-QTLs, two significant QTLs were detected in the $F_{2:3}$ population, including *qMIC-$F_{2:3}$-A9-1*, which originated from 08-10604, and *qMIC-$F_{2:3}$-D1-1*, which originated from AQ, which explained 7.14 % and 11.3 % of PV, respectively, with LOD scores of 3.59–5.22. In the F_2 population, one M-QTL, *qMIC-F_2-D7-1*, was detected, which explained 9.85 % of PV, with a LOD score of 4.05, originating from AQ.

Yield-related traits

Eleven QTLs related to three yield-related traits were detected in the F_2 and $F_{2:3}$ populations, except for BN and SY, using CIM, including three significant QTLs with LOD values greater than or equal to the threshold value calculated by a permutation test with 1,000 repeats, which were detected only in the $F_{2:3}$ (Fig. 1; Table 5). However, 25 pairs of E-QTLs exhibiting AA, AD, DA and DD interactions were detected for yield-related traits in both populations (Table 8).

Table 8 Characteristics of epistatic quantitative trait loci (E-QTLs) for boll and yield-related traits detected in both populations

Trait	Generation	Loci1			Loci2			LOD	AA	AD	DA	DD	PVE (%)
		Chromosome1	Left Marker	Right Marker	Chromosome2	Left Marker	Right Marker						
BCW	F_2	A9	BNL1672-100	NAU6130-200	A9	cgr6692-150	NAU490-500	6.161	0.090	−0.080	−0.218	−0.767	33.718
	F_2	D5	NAU4907-1000	HAU1785-400	D1	cgr5834-180	BNL786-130	6.442	−0.082	0.320	−0.122	0.576	14.745
	F_2	D1	NAU3736-200	Gh336-100	D6	HAU2367-300	NAU6347-700	5.420	0.075	0.428	0.210	−0.227	26.291
	$F_{2:3}$	A10	NAU2935-350	BNL1569-210	D10	NAU6495-240	BNL946-350	6.073	0.034	−0.180	0.112	−0.407	20.787
	$F_{2:3}$	D5	BNL3347-150	NAU5121-180	A5	BNL1878-300	NAU792-500	5.816	0.050	−0.126	−0.192	0.099	25.403
	$F_{2:3}$	A3	NAU5035-250	NAU1167-500	A9	cgr6692-150	NAU490-500	5.010	0.081	−0.224	−0.103	−0.194	28.798
	$F_{2:3}$	D1	NAU6335-220	BNL4082-110	A6	NAU3206-170	Gh433-150	5.353	0.080	0.180	0.094	−0.067	15.010
BL	F_2	D10	NAU2540-160	NAU6495-240	D8	Gh146-200	TML21-300	5.881	1.556	3.058	2.256	4.876	27.413
	F_2	D10	NAU6512-1000	NAU5013-200	D1	NAU7049-250	NAU2113-240	5.704	1.349	3.104	−0.314	−1.608	20.786
	F_2	D1	TMJ24-190	NAU6335-220	LG03	NAU4030-150	NAU4030-140	6.317	0.802	1.848	−2.230	4.838	15.025
	$F_{2:3}$	D13	JESPR-204-170	JESPR-178-250	A5	BNL1878-300	NAU792-500	5.014	−0.465	1.093	1.553	0.184	11.702
	$F_{2:3}$	A3	cgr6874-150	dPL0195-240	D8	NAU2631-200	NAU2631-150	5.896	0.991	1.293	0.153	−1.423	7.852
	$F_{2:3}$	D13	NAU2886-270	JESPR-204-170	A9	NAU2964-200	Gh111-190	5.064	−0.670	−1.874	0.826	3.162	18.789
BLN	F_2	A13	HAU1997-1000	dPL0308-190	D1	NAU5107-500	HAU2425-200	6.050	0.067	−0.190	−0.040	0.976	31.953
	F_2	D5	CIR062-200	NAU5273-240	A9	Gh539-100	HAU2496-250	5.288	−0.097	−0.124	0.226	−1.629	30.865
	F_2	D5	NAU4907-1000	HAU1785-400	D1	cgr5834-180	BNL786-130	5.184	−0.104	−0.455	−0.108	1.246	23.318
	$F_{2:3}$	A3	NAU1167-700	NAU1250-440	D7	NAU2974-180	NAU3911-230	5.245	0.047	0.064	0.051	−0.487	15.359
	$F_{2:3}$	A3	NAU5035-250	NAU1167-500	D1	BNL1667-150	HAU3297-300	5.065	0.039	−0.048	0.685	0.419	20.690
BLW	F_2	A10	BNL1569-210	Gh236-120	D1	NAU5107-500	HAU2425-200	6.429	−0.076	0.390	−0.403	0.603	29.861
	F_2	A10	NAU2935-350	BNL1569-210	A9	NAU6130-200	HAU2780-600	5.859	0.133	−0.197	0.121	−0.268	26.070
BN	F_2	A12	cgr6439-370	HAU2835-400	D7	NAU2820-660	NAU6468-230	5.436	0.157	9.478	3.923	14.007	27.921
	F_2	D7	cgr5149-500	HAU1129-230	A12	NAU3519-600	dPL0917-220	5.380	2.819	9.625	−2.942	11.097	13.617
	F_2	A12	HAU2835-400	NAU7463-260	LG01	Gh379-140	CIR187-230	6.410	0.363	−9.241	−1.535	−1.803	12.511
	$F_{2:3}$	D5	NAU4907-1000	HAU1785-400	D5	BNL3347-150	NAU5121-180	7.379	−0.908	−1.103	−11.910	−13.810	26.543
	$F_{2:3}$	D5	NAU4907-1000	HAU1785-400	D13	NAU2886-270	JESPR-204-170	8.056	−0.181	−4.597	−9.838	−12.428	33.610
	$F_{2:3}$	D5	BNL3347-150	NAU5121-180	A3	NAU5035-250	NAU1167-500	7.019	−1.159	16.104	−6.921	−17.228	27.668
	$F_{2:3}$	D5	BNL3347-150	NAU5121-180	D8	Gh146-200	TML21-300	7.436	0.401	−16.753	−7.573	−18.791	27.660
	$F_{2:3}$	D5	NAU4907-1000	HAU1785-400	D1	NAU6539-400	MNL2921-180	8.810	0.460	−5.444	−11.135	−9.361	33.108
	$F_{2:3}$	A12	NAU526-150	HAU0545-250	A9	JESPR-110-250	NAU936-200	7.437	0.174	−3.693	2.101	−15.883	28.845
BW	F_2	A10	NAU2935-350	BNL1569-210	A13	cgr5856-130	NAU1141-210	7.134	0.192	−0.886	0.877	0.274	25.861
	F_2	A10	NAU2911-280	BNL3563-250	D1	dPL0526-380	NAU2814-240	5.429	0.196	−0.546	−0.403	0.539	13.849
	F_2	A13	shin-1462-235	NAU2300-600	D1	NAU3736-200	Gh336-100	5.841	0.288	0.321	0.646	−0.814	18.223
	$F_{2:3}$	A13	HAU0539-210	CIR221-150	A13	NAU6122-320	BNL1421-200	5.208	−0.052	−0.621	0.385	−0.386	33.539
	$F_{2:3}$	A3	TML04-220	NAU3995-480	D1	NAU5107-500	HAU2425-200	5.265	0.111	−0.663	0.222	−0.739	20.773
	$F_{2:3}$	D7	NAU2974-180	NAU3911-230	LG02	dc40265-190	Gh246-110	5.334	−0.249	−0.424	−0.571	0.694	24.469

Table 8 continued

Trait	Generation	Loci1			Loci2			LOD	AA	AD	DA	DD	PVE (%)
		Chromosome1	Left Marker	Right Marker	Chromosome2	Left Marker	Right Marker						
BSN	F_2	D13	JESPR-204-170	JESPR-178-250	A12	NAU526-150	HAU0545-250	5.613	−1.932	6.707	−1.296	0.704	25.023
	F_2	D1	MNL2921-180	Gh216-100	LG03	NAU4030-140	HAU2467-800	6.146	−2.321	2.864	−0.043	−8.161	21.843
	F_2	A9	HAU3241-120	NAU1009-200	LG03	HAU2467-800	cgr5181-140	5.613	−1.792	3.557	2.269	−6.831	17.638
	$F_{2:3}$	A12	HAU2835-400	NAU7463-260	D1	NAU2113-240	NAU6539-400	5.603	1.028	3.176	0.732	−0.697	34.251
	$F_{2:3}$	A10	NAU1297-290	NAU1297-400	A6	dPL0617-150	NAU3206-170	5.203	0.617	−1.989	−0.382	3.793	19.506
	$F_{2:3}$	A10	NAU2082-250	NAU1041-250	LG01	Gh379-140	CIR187-230	5.319	0.069	−1.581	1.454	−10.173	23.754
	$F_{2:3}$	D5	NAU3001-200	dc30008-500	LG02	dc40265-190	Gh246-110	5.368	−0.348	−1.278	−0.522	−6.341	11.101
	$F_{2:3}$	LG01	Gh379-140	CIR187-230	LG02	dc40265-190	Gh246-110	5.173	2.074	−1.580	4.359	2.613	32.517
BD	F_2	A13	NAU2300-600	HAU1997-1000	D5	NAU5121-180	Gh354-150	5.689	−0.496	2.343	0.459	−0.981	15.089
	F_2	D8	NAU2631-150	NAU2665-1000	D6	HAU2367-300	NAU6347-700	6.404	0.547	2.099	−1.400	0.902	25.428
	$F_{2:3}$	A3	NAU5035-250	NAU1167-500	D7	cgr6680-200	NAU5439-230	5.660	0.204	1.467	1.284	3.649	28.680
	$F_{2:3}$	A3	TML04-220	NAU3995-480	LG02	dc40265-190	Gh246-110	5.370	−0.630	−0.257	0.479	−2.883	9.244
	$F_{2:3}$	A3	NAU3995-200	NAU3995-600	LG04	NAU6966-310	NAU4057-210	5.281	0.170	0.287	−0.584	−4.165	25.042
LP	F_2	D13	NAU2886-270	JESPR-204-170	LG02	dc40265-190	Gh246-110	5.040	−0.030	−0.043	0.014	0.020	20.773
LY	F_2	A10	NAU3368-250	NAU2082-250	A5	NAU792-500	HAU1976-240	5.318	−6.949	−3.010	−0.239	−1.670	10.586
	F_2	A3	NAU3995-200	NAU3995-600	A9	NAU1009-200	cgr5110-150	5.789	2.180	−11.178	9.525	−16.669	31.429
	$F_{2:3}$	A13	shin-1462-235	NAU2300-600	A12	NAU4089-190	dc20022-140	5.954	1.879	1.930	9.879	−7.495	23.969
	$F_{2:3}$	D1	MNL2921-180	Gh216-100	D1	TME03-200	JESPR-221-190	5.941	−3.820	5.798	−11.122	10.229	28.982
	$F_{2:3}$	D13	JESPR-204-170	JESPR-178-250	D8	NAU3201-220	NAU2035-500	5.838	1.974	−1.114	−1.751	14.745	23.122
	$F_{2:3}$	A13	dPL0308-190	cgr5856-130	LG03	NAU474-900	NAU4030-150	9.223	−1.798	−12.855	6.908	−11.509	33.594
SI	F_2	D5	Gh354-150	JESPR-204-220	D5	NAU779-600	TMC05-190	5.633	−0.450	−0.576	0.944	−2.661	28.186
	F_2	D10	NAU6495-240	BNL946-350	A9	cgr5707-420	NAU3052-180	5.616	0.366	0.299	−0.231	−2.595	27.293
	$F_{2:3}$	A13	NAU2300-600	HAU1997-1000	D5	NAU5121-180	Gh354-150	5.205	−0.549	0.372	−0.206	0.246	13.962
	$F_{2:3}$	D10	NAU6512-1000	NAU5013-200	D5	NAU3664-250	CIR062-200	5.924	0.153	−0.340	−0.257	1.573	21.632
	$F_{2:3}$	D13	NAU2886-270	JESPR-204-170	D8	NAU2072-500	NAU3954-490	5.465	−0.108	−1.312	−0.396	−0.767	18.679
	$F_{2:3}$	D1	NAU5107-500	HAU2425-200	A6	Gh433-150	Gh513-300	5.496	−0.262	0.912	−0.636	−0.129	26.698
	$F_{2:3}$	D13	JESPR-178-250	JESPR-204-200	A10	NAU2508-150	HAU2147-250	5.192	−0.354	−0.282	−0.232	1.076	22.682
SY	$F_{2:3}$	A3	NAU5035-250	NAU1167-500	D8	HAU2738-300	NAU3201-220	5.114	11.502	2.727	3.003	10.370	13.692
	$F_{2:3}$	D1	TMJ24-190	NAU6335-220	D8	NAU3201-220	NAU2035-500	5.282	−12.416	−19.917	14.343	8.181	21.831

AA, AD, DA and DD are effects of additive-by-additive, additive-by-dominant, dominant-by-additive and dominant-by-dominant interactions, respectively

PVE % phenotypic variation explained by a pair of E-QTLs, *BCW* boll coat weight, *BL* boll length, *BLN* locule number per boll, *BN* boll number per plant, *BLW* lint weight per boll, *BW* boll weight, *BSN* seed number per boll, *BD* boll diameter, *LP* lint percentage, *LY* lint yield, *SI* seed-index, *SY* seed-cotton yield

Lint percentage

Six M-QTLs (two significant QTLs) were detected in the $F_{2:3}$ population. Two significant QTLs, *qLP-$F_{2:3}$-A6-1* and *qLP-$F_{2:3}$-D5-2*, were detected, which explained 6.02 and 15.19 % of PV, with LOD scores of 4.91 and 5.98, respectively. All QTLs from AQ were responsible for the increase in LP. One pair of E-QTLs was detected. These E-QTLs are distributed on two chromosomes or linkage groups and displayed −0.030 AA effects, −0.043 AD effects, 0.014 DA effects and 0.020 DD effects, accounting for 20.773 % of PV.

Seed cotton yield

Two pairs of E-QTLs, including interactions between two loci on Chr. A3 and Chr. D8 and between two loci on Chr. D1 and Chr. D8, were detected in the $F_{2:3}$. These E-QTLs demonstrated 11.502 and −12.416 AA effects, 2.727 and −19.917 AD effects, 3.003 and 14.343 DA effects and 10.370 and 8.181 DD effects, explaining 13.692 and 21.831 % of PV, respectively.

Lint yield

One M-QTL, *qLY-$F_{2:3}$-D10-1*, was detected in the $F_{2:3}$ population, which explained 6.72 % of PV, with a LOD score of 2.60. The favorable alleles originated from 08-10604. In addition, six pairs of E-QTLs were found, which are distributed on ten chromosomes or linkage groups and displayed −6.949 to 2.180 AA effects, −12.855 to 5.798 AD effects, −11.122 to 9.879 DA effects and −16.669 to 14.745 DD effects, explaining 10.586–33.594 % of PV.

Seed index

Four M-QTLs (one significant QTL) were detected in the F_2 and $F_{2:3}$ populations. Among three M-QTLs, one significant QTL, *qSI-$F_{2:3}$-D1-1*, was detected in the $F_{2:3}$ population, which explained 3.79 % of PV, with a LOD score of 5.32; the favorable alleles of the three M-QTLs originated from AQ. In the F_2 population, one M-QTL, *qSI-F_2-D9-1*, was detected, which explained 3.41 % of PV, with a LOD score of 2.86, originating from 08-10604. Meanwhile, seven pairs of E-QTLs were detected, which are distributed on nine chromosomes or linkage groups and displayed −0.549 to 0.366 AA effects, −1.312 to 0.912 AD effects, −0.626 to 0.912 DA effects and −2.661 to 1.573 DD effects, explaining 13.962–28.186 % of PV.

Boll number per plant

Nine pairs of E-QTLs were detected, which are distributed on 10 chromosomes or linkage groups and displayed −1.159 to 2.819 AA effects, −16.753 to 16.104 AD effects, −11.910 to 3.923 DA effects and −18.791 to 14.007 DD effects, accounting for 12.511–33.610 % of PV.

Epistasis-QTLs for interactions between boll and yield-related traits

In addition, we further observed two groups of interacting marker intervals, each of which simultaneously controlled two traits. The interacting marker intervals NAU2300-600-HAU1997-1000 on Chr. A13 and NAU5121-180-Gh354-150 on Chr. D5 influenced both SI and BD. The interacting marker intervals NAU4907-1000-HAU1785-400 on Chr. D5 and cgr5834-180-BNL786-130 on Chr. D1 influenced both BCW and BLN. Five groups of interacting marker intervals were detected, each of which had interactions on the same chromosome. Chr. A9 contains one pair of interacting marker intervals for BCW, BNL1672-100-NAU6130-200 and cgr6692-150-NAU490-500. Chr. A13 contains one pair of interacting marker intervals for BW, HAU0539-210-CIR221-150 and NAU6122-320-BNL1421-200. Chr. D1 contains one pair of interacting marker intervals for LY, MNL2921-180-Gh216-100 and TME03-200-JESPR-221-190. Chr. D5 contains two pairs of interacting marker intervals, including one for SI, Gh354-150-JESPR-204-220 and NAU779-600-TMC05-190 and one for BN, NAU4907-1000-HAU1785-400 and BNL3347-150-NAU5121-180. In addition, some marker intervals had interactions with other multiple marker intervals to control different traits. For example, the marker interval NAU5035-250-NAU1167-500 had interactions with multiple marker intervals including cgr6692-150-NAU490-500, BNL1667-150-HAU3297-300, cgr6680-200-NAU5439-230 and HAU2738-300- NAU3201-220 to control four traits, BCW, BLN, BD and SY, respectively.

Discussion

The F_2 population has the most complete genetic composition of all populations and can provide the most abundant genetic information; theoretically, this population can be applied to QTL and genetic effect analysis. However, the F_2 represents a temporarily separating population, and its trait performance cannot be repeated among generations, which greatly limits the application of the F_2 population to QTL mapping. Although the genetic compositions of the F_2 and $F_{2:3}$ populations differ, a highly positive correlation exists between these populations (Xu and Zhu 1994). The use of the average value of each line in the $F_{2:3}$ population to estimate the phenotypes of F_2 individuals can reduce the environmental error and improve the accuracy of QTL location. However, this technique underestimates the dominance and over-dominance effects of QTLs. Considering the advantages of the F_2 and $F_{2:3}$ populations, it is essential to use both populations for QTL analysis. Hence, both F_2 and $F_{2:3}$ populations were employed for QTL mapping in this study, and common QTLs were simultaneously detected in the same or similar positions, suggesting that these QTLs can be used for further verification and analysis and thus, for marker-assisted breeding. However, many previous studies have focused on QTL mapping of cotton yield and fiber quality traits, but few studies have examined traits related to cotton bolls, especially for boll weight-related traits such as BD, BL, BLN and BCW (except for BW), despite the fact that these traits play important roles in cotton breeding (Ashraf and Ahmad 2000; Tang and Xiao 2014). In this study, we detect 58 M-QTLs in the F_2 and $F_{2:3}$ populations for boll-related traits, including 13 BCW, 12 BL, 10 BD, six BLN, five BLW, nine BW and three BSN QTLs. Moreover, we also found six pairs of common QTLs conferring boll-related traits (including two pairs each for BCW, BL and BD, respectively), suggesting that these common QTLs have high reliability and can be utilized for MAS to improve boll weight.

In addition, we detected several boll-related QTL-rich regions with QTLs conferring yield-related or fiber traits on a few chromosomes. For instance, a region on Chr. A10 contains 17 M-QTLs (eight significant QTLs) controlling BCW, BL, BLN, BLW, BW, BSN, BD and FE. A region on Chr. A13 contains 10 M-QTLs (two significant QTLs), including those controlling BCW, BL, BW, FE, FL and LP. A region on Chr. D1 contains 17 M-QTLs (12 significant QTLs) controlling BCW, BL, BLN, BD, FS, FU, MIC and SI. A region on Chr. D5 contains 16 M-QTLs (nine significant QTLs) controlling BCW, BL, BLN, BLW, BW, BD, FE, FS and LP. The clustering of QTLs within linkages indicates that genes for different traits on the same chromosome are linked or that the phenotypes are due to pleiotropic effects of a single QTL, especially QTLs for boll weight traits, which is consistent with the results of correlation analysis. The synergistic alleles of QTLs of boll-related traits mainly came from AQ. For example, we found that the additive effect of the traits BL and BD originated from the same parent, AQ. Therefore, AQ can play an important role in improving boll weight. In this study, five QTL clusters for boll-related traits were found on Chr. A10, A13, D1 and D5. Unlike those for boll-related traits, the M-QTLs for fiber quality traits detected in this study were not clustered, although QTL clusters for fiber quality or plant architecture traits were previously been reported in cotton (Chen et al. 2009; Mei et al. 2004; Wang et al. 2006; Zhang et al. 2005, 2009, 2012a). Said et al. (2013) also detected QTL clusters comprising regions containing four or more QTLs for various traits (including fiber quality and others). Said et al. (2013) ascribed the different results from various studies to the use of different genetic populations, markers and marker densities, and testing environments.

Many previous studies have focused on QTL mapping for fiber quality and yield traits using intraspecific maps (Chen et al. 2009; Guo et al. 2006; Qin et al. 2008, 2009; Shao et al. 2014; Shen et al. 2005, 2007; Sun et al. 2012; Ulloa et al. 2005; Wang et al. 2007; Wu et al. 2009; Zhang et al. 2010, 2012a, 2005, 2009). However, it is difficult to compare the QTLs detected in these studies because few common markers exist in the diverse intraspecific populations employed, and the maps produced in these studies cover different chromosome regions of the cotton genome. Nonetheless, both the present study and the previous studies have revealed many common characteristics for QTLs conferring fiber quality and yield traits, and these QTLs for fiber traits were mapped to the same chromosomes in different populations. For example, some QTLs for fiber quality and yield traits detected in the current study were also mapped to the same chromosomes in previous studies,

including three QTLs for FS (Shao et al. 2014; Sun et al. 2012; Wu et al. 2009), two QTLs for FL (Liang et al. 2013; Shao et al. 2014; Shen et al. 2005; Zhang et al. 2005, 2009, 2012a), four QTLs for MIC (Liang et al. 2013; Qin et al. 2008, 2009; Shao et al. 2014; Shen et al. 2005, 2007; Zhang et al. 2012a, 2013), two QTLs for FU (Shao et al. 2014; Zhang et al. 2012a), three QTLs for FE (Liang et al. 2013; Qin et al. 2008; Shao et al. 2014; Shen et al. 2005; Sun et al. 2012; Wang et al. 2007; Zhang et al. 2012a, 2013), six QTLs for BW (Ning et al. 2014; Shen et al. 2007; Xia et al. 2014; Zhang et al. 2010), four QTLs for LP (Liu et al. 2012; Wang et al. 2007; Wu et al. 2009; Zhang et al. 2009, 2013), one QTL for LY (Xia et al. 2014) and three QTLs for SI (Liu et al. 2012; Shen et al. 2007; Wang et al. 2007; Wu et al. 2009; Xia et al. 2014). These QTLs may be common QTLs for fiber quality and yield traits in upland cotton, which may be verified through the use of many more common markers in the future.

Furthermore, in the present study, some QTLs were not mapped to the same chromosomes as those of previous studies. For example, six QTLs for yield traits were detected on different chromosomes, including three QTLs (qBW-F_2-A13-1, qBW-F_2-A13-2 and qBW-F_2-A9-1) for BW on Chr. A9 and A13, two QTLs (qLP-$F_{2:3}$-A13-1 and qLP-$F_{2:3}$-A13-2) for LP on Chr. A13 and one QTL (qSI-$F_{2:3}$-D1-1#) for SI on Chr. D1. Moreover, one QTL (qFE-F_2-A12-1) for fiber quality (FE) was also detected on Chr. A12. Our results indicate that these seven positive additive QTLs were from the elite parent AQ, and they are distributed on different chromosomes, implying that these QTLs are unique to upland cotton and may be useful for cotton improvement.

Finally, epistasis, or interlocus interaction, is a type of gene interaction whereby one gene interferes with the phenotypic expression of another non-allelic gene. A considerable body of evidence from classical studies strongly suggests the prevalence of an epistatic effect on quantitative traits in genetic populations (Zhang et al. 2001). Based on heterosis research in rice, Yu et al. (1997) found that epistasis plays an important role in the inheritance of quantitative traits and heterosis. Xing et al. (2002) further reported that epistasis, in the form of additive-by-additive interactions, plays a highly important role in controlling the expression of yield and yield-component traits. Some studies have demonstrated that E-QTLs play an important role in the genetic control of plant architectural traits in cotton (Wang et al. 2006; Song and Zhang 2009) and other crops such as maize (Xu et al. 2009) and wheat (Wang et al. 2010). In this study, we identified 64 pairs of E-QTLs for 12 boll weight-related traits in both populations examined, including seven for BCW, six for BL, five for BLN, two for BLW, nine for BN, six for BW, eight for BSN, five for BSN, one for LP, six for LY, seven for SI and two for SY. Notably, two pairs of interacting marker intervals simultaneously control two traits. Moreover, some marker intervals have interactions with other multiple marker intervals to control different traits. However, no E-QTLs detected in the current study were mapped to the same chromosomes as those of previous studies. In addition, no E-QTLs for fiber quality were detected in the current study, which is inconsistent with a previous report employing different populations (Wang et al. 2013).

In conclusion, in the F_2 and $F_{2:3}$ populations, common QTLs were detected in the same and similar positions simultaneously, suggesting that these are major QTLs that can be used for further verification and analysis and thus, for marker-assisted breeding. QTL clusters were inferred and identified using the positions and distribution of QTLs along the *Gossypium* genome. The presence of QTL clusters indicates that genes pertaining to certain traits are more heavily concentrated in certain regions of the genome than in others. The markers associated with E-QTLs identified in the current study will be important for future breeding programs aimed at developing cotton cultivars.

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