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ORIGINAL PAPER

Construction of a high-density genetic map and lint percentage and cottonseed nutrient trait QTL identification in upland cotton (*Gossypium hirsutum* L.)

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Abstract Upland cotton plays a critical role not only in the textile industry, but also in the production of important secondary metabolites, such as oil and proteins. Construction of a high-density linkage map and identifying yield and seed trait quantitative trail loci (QTL) are prerequisites for molecular marker-assisted selective breeding projects. Here, we update a high-density upland cotton genetic map from recombinant inbred lines. A total of 25,313 SSR primer pairs were screened for polymorphism between Yumian 1 and T586, and 1712 SSR primer pairs were used to genotype the mapping population and construct a map. An additional 1166 loci have been added to our previously published map with 509 SSR markers. The updated genetic map spans a total recombinant length of 3338.2 cM and contains 1675 SSR loci and nine morphological markers, with an average interval of 1.98 cM between adjacent markers. Green lint (Lg) mapped on chromosome 15 in a previous report is mapped in an interval of 2.6 cM on chromosome 21. Based on the map and phenotypic data from multiple environments, 79 lint percentage and seed nutrient trait QTL are detected. These include 8 lint percentage, 13 crude protein, 15 crude oil, 8 linoleic, 10 oleic, 13 palmitic, and 12 stearic acid content QTL. They explain 3.5–62.7 % of the phenotypic variation observed. Four morphological markers identified have a major impact on lint percentage and cottonseed nutrients traits. In this study, our genetic map provides new sights into the tetraploid cotton genome. Furthermore, the stable QTL and morphological markers could be used for fine-mapping and map-based cloning.

Keywords Genetic map · Lint percentage · Nutrient traits · Quantitative trait loci (QTL) · Upland cotton · *Gossypium hirsutum* L.

Introduction

As a leading global fiber crop, cotton provides most of the natural fiber for the textile industry. Furthermore, the cottonseed by-product is also a good natural source of oil and protein, and plays important roles in world oil and livestock feed product markets. Four species of the *Gossypium* genus are cultivated, including two diploid species, *G. arboreum* and *G. herbaceum*, and two allotetraploid species, *G. barbadense* and *G. hirsutum* (Wendel and Cronn 2003). *G. hirsutum* (upland cotton) is the most widely grown worldwide, accounting for 95 % of both acreage and fiber production (Chen et al. 2007).

Cotton fiber, the most important product of the cotton plant, is a highly elongated single cell derived from the ovule epidermis; its development synchronizes with and depends on seed development. Cottonseed development is a highly programmed and regulated process, shaping cotton fiber yield, quality, and seed nutrients. Lint percentage (LP), a component of lint yield and a critical economic index for cotton cultivars, is closely related to lint yield

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improvement (Culp and Harrell 1975; Meredith, 1984; Zeng and Meredith 2009). Previous research has demonstrated that lint percentage is a quantitative, stably inherited trait (Meredith 1984). Many quantitative trait loci (QTL) conferring lint percentage have been identified and mapped with molecular markers in different populations (Zhang et al. 2005; Shen et al. 2007; Wang et al. 2007; Qin et al. 2008; Wu et al. 2009; An et al. 2010; Yu et al. 2013; Zhe et al. 2014). Although the QTL identified have helped reveal the landscape of genetic factors controlling lint percentage, these QTL, which are either only detected in a single environment or have small effects, exhibit low reliability and stability, thus limiting their application.

Although cottonseed nutrients are not as important as fiber yield or quality traits, they are of interest to researchers. The major concerns in terms of cottonseed nutrient traits are oil and protein content. Generally, cottonseed has an oil content ranging from 13.6 to 24.7 % and a protein content ranging from 12 to 23 % (Lukonge et al. 2007; Dowd et al. 2010). Significant relationships have been detected between cotton fiber yield and seed nutrient traits (Dani and Pundarikakshudu 1986; Ashokkumar and Ravikesavan 2013). The relationship of most concern is the negative relationship between seed oil content and fiber yield (Turner et al. 1976), which indicates competition for carbohydrates made from photosynthesis. However, cottonseed oil content is also negatively related to seed protein content (Hanny et al. 1978; Kohel and Cherry 1983; Sun et al. 1987). Cottonseed nutrient traits are also quantitative and mainly affected by genotype (Anderson and Worthington 1971; Dowd et al. 2010). However, few studies on QTL mapping for cottonseed nutrient traits have been reported to date (Song and Zhang 2007; Liu et al. 2010; Yu et al. 2012).

In this study, we aimed to comprehensively map the loci associated with lint percentage and cottonseed nutrient traits based on a recombinant inbred line mapping population. The results will help us further understand the genetic mechanism of lint percentage and cottonseed nutrient traits and the relationship between them. The QTL identified as particularly stable, and co-located QTL will further facilitate mining of the genetic factors underlying lint percentage and cottonseed nutrient traits and provide a means for molecular marker-assisted selective breeding.

Materials and methods

Mapping population

Cultivar Yumian 1, bred by our laboratory, is characterized by high lint yield and high fiber strength. T586, known as the multiple dominant gene line, has nine morphological markers (R_1, red plant; T_1, pubescent; L_2, okra leaf; R_2, petal spot; Y_1, yellow flower; P_1, yellow pollen; Lc_1, brown fiber; N_1, naked seed; Lg, green lint) (Endrizzi et al. 1984). The population was developed from the two parent cultivars in summer 2000 in Southwest University (SWU), Chongqing, China. F_1 individual plants were self-pollinated, and F_2 seeds were harvested in winter 2000 in Hainan Island (Zhang et al. 2005). Two hundred and seventy F_2 individuals were hand-harvested randomly and planted to obtain $F_{2:3}$ family lines. One individual of each $F_{2:3}$ family line was randomly selected to produce the next generation. This procedure was continued in the following generations until an $F_{2:7}$ recombinant inbred line population was obtained. A completely randomized design was used to arrange the lines in the field. Parents and recombination inbred lines were planted in single-row plots 0.7 m wide and 5 m long, planted in April and harvested in October in Chongqing from 2004 to 2012.

Trait examination

All naturally opened bolls were hand-harvested to gin fiber. Delinted seeds were dried at 105 °C for 2 h in a forced-air oven, and then deshelled and ground into powder to detect the crude oil (CO) and crude protein (CP) content. CO and CP content (on a dry weight of kernel powder basis) was measured following the methods described by Ye et al. (2003). A GC 2010 gas chromatography system (Shimadzu Co., Ltd., Tokyo, Japan) was used to analyze fatty acid components, as described by Dowd et al. (2010). LP of a given line was measured by the weight ratio of lint to cottonseed. CO and CP percentages were determined by dividing delinted seed CO or CP percentage by embryo percentage. Cottonseed oil consists of four major fatty acids, which were expressed as a percentage (%) of CO; these include linolenic acid (18:3, LA), stearic acid (18:0, SA), oleic acid (18:1, OA) and palmitic acid content (16:0, PA).

SSR analysis and genetic map construction

Genomic DNA from the parents and the RIL population was isolated from leaf tissue by the CTAB method (Zhang et al. 2005). PCR was conducted in a total volume of 10 μl with 50 ng of cotton DNA, 1 × PCR buffer, 2.0 mM $MgCl_2$, 0.2 mM dNTPs, 0.5 μM concentrations of each primer, and 0.5 units of Taqase (Shanghai Sangon, China). The PCR conditions were as follows: 94 °C for 5 min; 35 cycles of 94 °C for 30 s, 55 °C for 30 s, 72 °C for 1 min; 72 °C for 10 min; 4 °C for preservation. After amplification, the PCR products were mixed with loading buffer (2.5 mg/ml bromophenol blue, 2.5 mg/ml diphenylamine blue) and then kept at 4 °C. The PCR products were separated on 10 % (w/v) polyacrylamide gels and visualized by silver staining.

A total of 25,313 pairs of microsatellite marker primers, including 18,358 pairs from the cotton marker database (http://www.cottonmarker.org/) and 6955 pairs from our laboratory (Tang et al. 2015), were synthesized by Shanghai Invitrogen and Shanghai Sangon. The primer pairs showing polymorphism between the mapping parents were used to genotype 270 recombinant inbred lines. Marker nomenclature was the same as the primer name. For multiple polymorphic loci revealed by the same primer pair, marker nomenclature consisted of the primer name and a letter a/b/c indicating the polymorphic fragment size from the smallest to the largest.

JoinMap 4.0 (Van Ooijen 2006) was used to group and order loci with a log of odds (LOD) threshold range of 4–8. Locus localization derived from previous maps (Zhang et al. 2009; Yu et al. 2011; Blenda et al. 2012) was used to assign linkage groups to putative chromosomes. Linkage groups known to a given chromosome were then treated as separate data sets and grouped and ordered at LOD values between 1 and 4. Map distances were calculated using Kosambi's mapping function.

QTL analysis

MapQTL 6.0 (Van Ooijen 2009) was used to identify QTL for LP and seed nutrient traits. LOD $\geq$2.0 was used to declare suggestive QTL, as suggested by Lander and Kruglyak (1995), which has been used previously in cotton QTL identification (Shen et al. 2007; Qin et al. 2008). Graphic representation of the linkage groups and QTL was created in MapChart 2.2. QTL names start with "q", followed by the trait abbreviation (e.g., LP for lint percentage), the name of the chromosome and then the number of QTL affecting the trait on the same chromosome.

Results

Phenotypic data analysis

Descriptive statistics for LP data across ten environments and seed nutrient trait data across three environments are summarized in Table 1. Significant differences were observed between parents for all of the traits, except for stearic acid content. For the recombinant inbred line population, all of the traits presented transgressive segregation in different environments and the skewness and kurtosis values revealed that these traits were all approximately normally distributed. The correlation analysis based on data from three environments for the recombinant inbred line population for the tested traits is shown in Table 2. The most obvious and stable relationship was that for all the three environments. First of all, LP was significantly positively correlated with CP content but negatively correlated with CO content. In addition, CP content was significantly negatively correlated with CO content and oil components. At the last, linoleic acid content was significantly negatively correlated with oleic acid and palmitic acid content. All other correlations were neither significant nor stable, showing low reliability.

Updated genetic map

A total of 25,313 microsatellite marker primer pairs were employed to screen for polymorphisms between the parents and 1712 primer pairs revealed clear polymorphism, accounting for 6.8 % of the total primers. The polymorphic primers were used to genotype the recombinant inbred line population, and 1792 loci were obtained, including 509 SSR (Zhang et al. 2009) and 32 SSR from transcription factors (Li et al. 2012). Among the polymorphic primers, 70 primer pairs amplified two loci, two amplified three loci, and two amplified four loci. Among the 1801 loci, 320 (17.7 %) exhibited segregation distortion ($P < 0.05$) with 226 (70.6 %) favoring the Yumian 1 alleles and 94 (29.4 %) favoring the T586 alleles. All of the 1801 loci and nine morphological marker loci were applied to construct the genetic map. We mapped 1675 SSR and nine morphological marker loci onto 26 upland cotton chromosomes. Generally, all of the loci were evenly distributed along the genome, but some chromosomes had more markers than others, for example Chr08 had 120 loci while Chr04 only had 27. The total recombinant length of this map was 3338.2 cM with an average of 1.98 cM between adjacent markers (Table 3; Fig. 1). The average chromosome recombinant length was 128.39 cM, with the longest chromosome (Chr19) spanning 172.6 cM and the shortest (Chr01) spanning 90.9 cM. Loci on Chr06 were densest, being 0.6 cM between adjacent markers, while the scarcest was Chr04, being 2.94 cM apart. The At-subgenome spanned 1446.7 cM, containing 726 markers with an average marker interval of 2.02 cM. The Dt-subgenome spanned 1871.5 cM, containing 958 markers with an average marker interval of 1.95 cM. There were 13 gaps (marker interval >10 cM) on this genetic map, with eight on At-subgenome and five on Dt-subgenome. The largest gap on Chr11 spanned 22.9 cM. More detailed information of the genetic map is depicted in Table 3 and Fig. 1.

A total of 279 segregation-distorted loci, accounting for 16.6 % of the mapped loci, were unevenly distributed on the 26 cotton chromosomes with 2–27 loci on each chromosome. More distorted loci were located on the At-subgenome than on the Dt-subgenome (163 versus 116) (Table 3). A total of 19 segregation distortion regions (SDRs) were found on the 14 cotton chromosomes with 12 SDRs on the At-subgenome and seven SDRs on the

Table 1 Phenotypic variation in lint percentage and seed nutrient traits in the recombinant inbred line population

	Years	Parents		Recombinant inbred line population				
		T586	Yumian 1	Mean	Max.	Min.	Skewness	kurtosis
LP	2004	6.28	42.52	22.64	43.76	0	−0.33	−0.99
	2005	5.46	41.53	24.92	47.97	0.48	−0.23	−1.13
	2005H	7.88	42.30	26.68	49.5	0.26	−0.04	−1.12
	2006	6.42	43.46	19.4	43.71	0	0.07	−1.38
	2007	7.41	42.57	21.93	48.26	0.28	0.09	−1.22
	2008	5.85	41.49	21.1	47.23	0.94	0.16	−1.29
	2009	6.24	42.91	22.96	42.43	1.3	−0.26	−1.13
	2010	5.6	41.29	24.4	47.52	0.64	−0.07	−1.13
	2011	7.73	41.87	21.45	43.27	1.48	0.03	−0.98
	2012	6.62	43.54	21.11	45.5	0.81	−0.11	−1.13
	Average	6.55	42.22	22.68	46.15	0.69	−0.04	−1.17
CP	2006	36.83	50.36	45.33	51.6	39.2	0.01	−0.73
	2007	36.02	50.19	45.47	51.47	38.09	−0.19	−0.49
	2011	44.49	50.37	46.66	53.12	41.29	0.06	0.71
	Average	39.11	50.31	45.82	52.06	39.53	−0.04	−0.17
CO	2006	35.82	24.45	27.9	34.1	23.4	0.13	−0.65
	2007	37.87	24.34	28.38	34.49	23.82	0.27	−0.44
	2011	30.64	25.76	29.81	33.49	25.3	−0.16	0.01
	Average	34.78	24.85	28.7	34.03	24.17	0.08	−0.36
LA	2006	49.52	52.2	50.57	60.62	38.95	−0.24	10.4
	2007	53.05	54.52	55.64	63.28	48.44	−0.30	0.76
	2011	45.94	49.95	49.43	55.36	39.2	−0.75	0.29
	Average	49.5	52.22	51.88	59.75	42.2	−0.43	3.82
OA	2006	19.43	16.58	18.91	30.05	13.57	1.50	3.48
	2007	19.32	18.41	17.65	30.37	12.94	0.14	0.26
	2011	24.72	18.60	19.69	30.37	15.28	0.93	0.84
	Average	21.16	17.86	18.75	30.26	13.93	0.86	1.53
PA	2006	23.68	26.99	26.27	29.33	21.21	−0.57	−0.04
	2007	25.24	27.82	24.04	28.5	20.22	0.23	0.02
	2011	26.70	28.6	28.1	31.44	25.47	0.24	−0.35
	Average	25.21	27.8	26.14	29.76	22.3	−0.03	−0.12
SA	2006	2.12	2.76	2.64	3.84	1.64	0.17	−0.20
	2007	2.41	2.8	2.61	5.56	1.82	1.85	6.68
	2011	2.67	2.81	2.76	3.58	2.1	0.13	−0.66
	Average	2.40	2.61	2.67	4.33	1.85	0.72	1.94

Dt-subgenome (Fig. 1). Chr05 had the most distorted loci with the highest proportion, forming the largest SDRs.

LP QTL

Eight QTL, explaining 3.4–63.4 % of the total phenotypic variation, were detected across 10 environments. The nearest loci and confidence interval of these QTL are shown in Table 4 and Fig. 1. Among the eight non-over lapping QTL, qLP06.1, qLP07.1, qLP09.1, qLP12.1, qLP21.1, and qLP26.1, detected in 6–10 environments were stable. Four QTL, qLP06.1, qLP07.1, qLP12.1, and qLP21.1, were associated with the dominant morphological markers T_1, Lc1, N_1, and Lg, respectively. Three major QTL, qLP07.1, qLP21.1, and qLP12.1, explained >10 % variation; all of the favorable QTL effects were conferred by Yumian 1 alleles. Parent Yumian 1 alleles confer favorable effects for most QTL, except qLP06.1 and qLP26.1, which is consistent with parental LP.

Seed nutrient trait QTL

Sixty-four significant QTL for six seed nutrient traits were identified, including four detected in three environments

Table 2 Correlation coefficients among all traits

Trait	Years	LP	CP	CO	LA	OA	PA
CP	2006	0.74**					
	2007	0.67**					
	2011	0.53**					
CO	2006	−0.74**	−0.89**				
	2007	−0.70**	−0.91**				
	2011	−0.53**	−0.74**				
LA	2006	0.12	0.10	−0.14*			
	2007	0.01	0.00	0.02			
	2011	−0.04	−0.03	−0.09			
OA	2006	0.30**	−0.24**	0.24**	−0.81**		
	2007	0.10	−0.19**	0.18*	−0.70**		
	2011	0.00	−0.05	0.16	−0.93**		
PA	2006	0.17**	0.13*	−0.07	−0.66**	0.21**	
	2007	0.10	0.22**	−0.20**	−0.53**	−0.15*	
	2011	0.10	0.17	−0.13	−0.46**	0.14	
SA	2006	0.15*	0.09	0.02	−0.23**	−0.07	0.39**
	2007	−0.06	−0.10	0.06	−0.30**	0.17*	−0.13
	2011	0.06	0.10	−0.16	0.20	−0.25*	−0.15

*, ** Indicate significance differences with a probability level of 0.05 and 0.01, respectively

and four detected in two environments. These QTL were mapped on different chromosomes (Fig. 1).

For the CP content, 13 QTL were identified and located on 13 chromosomes, explaining 5.2–48.1 % of the phenotypic variation (Table 5). Of these, 12 Yumian 1 alleles increased coarse protein content. qCP07.1 (at locus Lc_1) and qCP12.1 (at locus N_1) were identified in three environments, had large additive effects, and explained a lot of the phenotypic variation; these are major QTL. With the exception of QTL qCP01.1 identified in two environments, all the other ten QTL were identified only in one environment.

For the CO content, 15 QTL were identified and mapped on 15 chromosomes, explaining 2.0–39.8 % of the phenotypic variation. Of these, 11 alleles from T586 increased coarse oil content. qCO07.1 (at locus Lc_1) and qCO12.1 (at locus N_1) were detected in three environments and qCO21.1 (at locus Lg) and qCO23.1 were detected in two. All of the other 11 QTL were detected in only one environment.

For the LA content, eight QTL were identified and located on seven chromosomes, explaining 2.2–8.0 % of the phenotypic variation, and no QTL was identified in two or three environments. Four alleles from T586 and four alleles from Yumian 1 increased the LA content

For the OA content, 10 QTL were identified and located on ten chromosomes, explaining between 2.0 and 15.4 % of the phenotypic variation. qOA18.1 was detected in 2006 and 2007, and the other nine QTL were detected in only one environment. Five alleles from T586 and five alleles from Yumian 1 increased the OA content.

For the PA content, 13 QTL were detected on 12 chromosomes, explaining between 4.2 and 13.3 % of the phenotypic variation. All of the QTL were detected in only one environment. Three alleles from T586 and nine alleles from Yumian 1 increased the PA content.

For the SA content, 12 QTL were detected on 10 chromosomes, which explained between 4.4 and 22.7 % of the phenotypic variation. qSA14.1 was detected in 2006 and 2011, and the other nine QTL were detected in only one enviroment. Eight alleles from T586 and four from Yumian 1 increased the SA content.

Co-localization QTL

A number of QTL controlling different traits were found to co-localize to the same region of the chromosomes. For example, eight regions (on Chr06, Chr07, Chr12, Chr14, Chr15, Chr16, Chr21, and Chr26) controlling three or more traits were detected in the RIL population. QTLs for LP, CP, and CO content were identified and mapped in the same confidence intervals on Chr06, Chr07, Chr12, Chr21, and Chr26. CO content had an opposite additive effect with LP and CP content, but LP and CP content had positive additive effects. QTL for CO and OA content were identified at the Lc1 loci on Chr07 with positive additive effects. QTL for CO and SA content identified on Chr06, Chr07 and Chr14 had opposite additive effects. QTL for CO and PA content identified on Chr15 and Chr26 had opposite additive effects. QTL for LA and OA content identified on Chr12 and Chr18 had opposite additive effects.

The co-localization QTL may serve to explain some correlations and the common genetic basis among the involved traits. Meanwhile, this result indicated that increasing LP may increase the CP content but reduces the CO content in cottonseed. Furthermore, it appeared that the four major fatty acids could not be simultaneously increased because of the different biochemical synthesis pathways of seed fatty acids.

Fig. 1 QTL for lint percentage, seed protein, oil, and fatty acid components in upland cotton (T586 × Yumian1) recombinant inbred line population. Morphological loci are shown in **bold** and *italics*. Map distances are given in centimorgans (cM). Markers showing segregation distortion are indicated by *asterisks* ($^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$) for markers skewed toward the Yumian 1 alleles or plus signs ($^{+}P < 0.05$; $^{++}P < 0.01$; $^{+++}P < 0.001$) for markers skewed toward the T586 alleles. *Bars* along the linkage groups indicate 1-LOD likelihood intervals for QTL. QTL are shown as lint percentage (*LP*), crude protein content (*CP*), crude oil content (*CO*), linoleic acid content (*LA*), oleic acid content (*OA*), palmitic acid content (*PA*), and stearic acid content (*SA*). Favorable QTL alleles contributed by Yumian 1 are represented by *black bars*, and those contributed by T586 are represented by *empty bars*. Segregation distortion regions (*SDRs*) are named as "chromosome + no". For example, SDR01.1 refers to the first SDR on Chr01

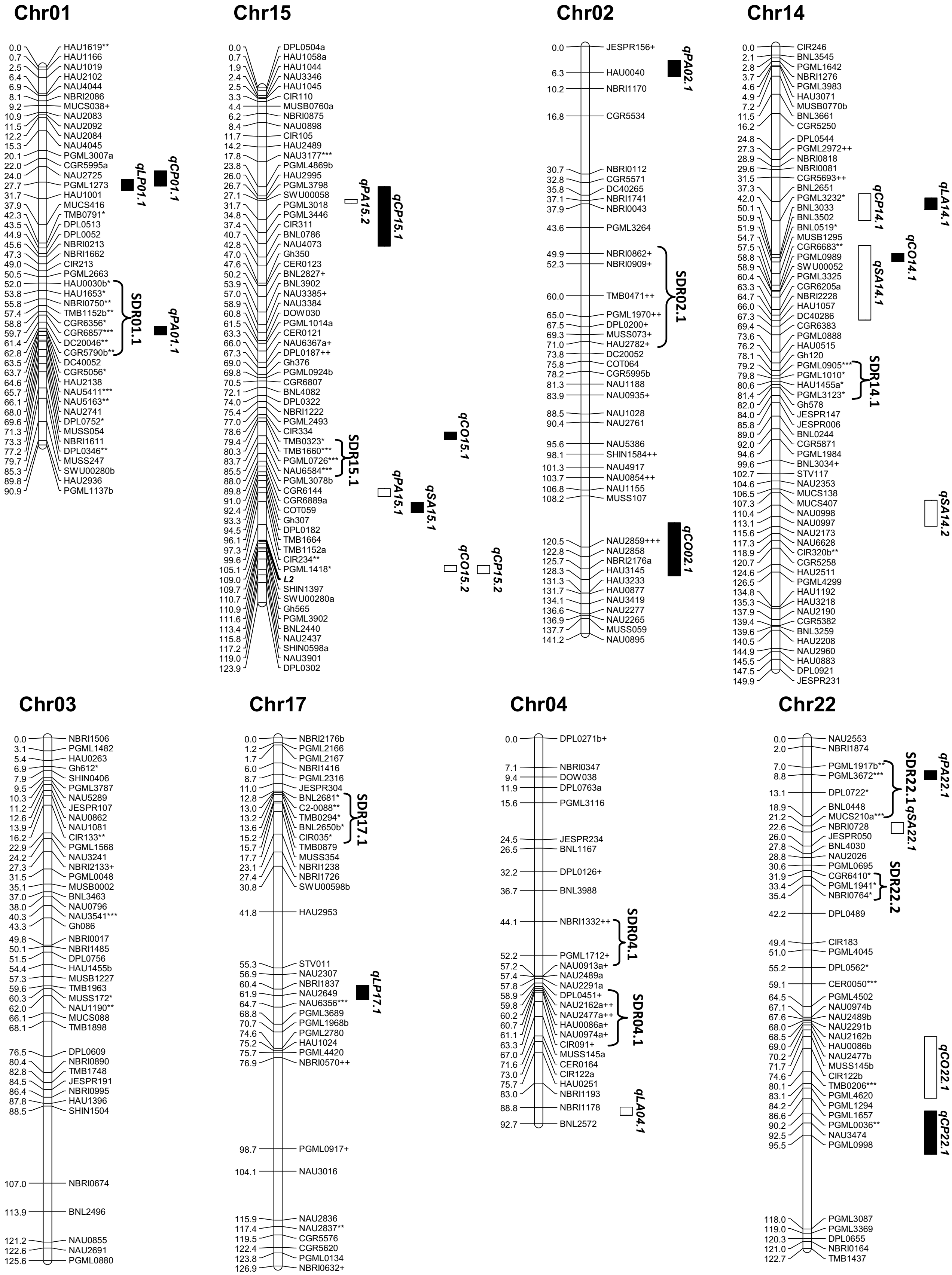
Discussion

Genetic map

The updated genetic map contained 1675 SSR and nine morphological loci spanning 3338.2 cM with an average interval of 1.98 cM between adjacent loci. Because of the narrow genetic background (Linos et al. 2002; Lacape et al. 2007; Zhang et al. 2009), this is the densest intraspecific upland cotton genetic map to date. Compared with the tetraploid cotton interspecific genetic map (Rong et al. 2004; Yu et al. 2011; Zhao et al. 2012), this map is still far from being saturated. We had used 25,313 SSR primer pairs, including almost all of the publicly available ones. We only

Table 3 Marker distribution on chromosomes in the map developed from the recombinant inbred line population

Chromosome	Loci	Length (cM)	Gap >10 cM	Distorted loci	Distorted rate (%)	Interval
Chr01	46	90.9	0	17	37.0	2.01
Chr02	41	141.2	2	12	29.3	2.49
Chr03	42	125.6	1	6	14.3	2.46
Chr04	27	92.7	0	10	37.0	2.94
Chr05	74	114.8	0	27	36.5	2.54
Chr06	116	156.4	0	15	12.9	0.6
Chr07	47	161.3	1	13	27.7	2.93
Chr08	120	120.2	0	20	16.7	0.77
Chr09	52	118.3	1	4	7.7	2.63
Chr10	46	118.5	1	10	21.7	2.28
Chr11	62	121.9	2	6	9.7	2.38
Chr12	53	104.9	0	16	30.2	1.87
Chr13	67	123.4	0	7	10.4	1.04
A subgenome	726	1466.7	8	163	22.5	2.02
Chr14	65	149.9	0	11	16.9	1.59
Chr15	64	123.9	0	11	17.2	1.95
Chr16	63	116.1	0	5	7.9	1.8
Chr17	36	126.9	3	10	27.8	2.31
Chr18	65	105.5	0	5	7.7	1.85
Chr19	89	172.6	0	6	6.7	1.72
Chr20	108	171.3	0	15	13.9	1.63
Chr21	97	170.1	1	20	20.6	1.8
Chr22	41	122.7	1	11	26.8	1.98
Chr23	85	101.8	0	9	10.6	1.09
Chr24	55	169.8	0	7	12.7	2.86
Chr25	65	99.7	0	2	3.1	1.39
Chr26	58	117.8	0	4	6.9	2.58
D subgenome	958	1871.5	5	116	12.1	1.95
Total	1684	3338.2	13	279	16.6	1.98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Chr15
Chr02
Chr14
Chr03
Chr17
Chr04
Chr22
qCP01.1
qLP01.1
SDR01.1
qPA01.1
qPA15.2
qCP15.1
qCO15.1
SDR15.1
qPA15.1
qSA15.1
qCO15.2
qCP15.2
qPA02.1
SDR02.1
qCO02.1
qCP14.1
qLA14.1
qCO14.1
qSA14.1
SDR14.1
qSA14.2
SDR17.1
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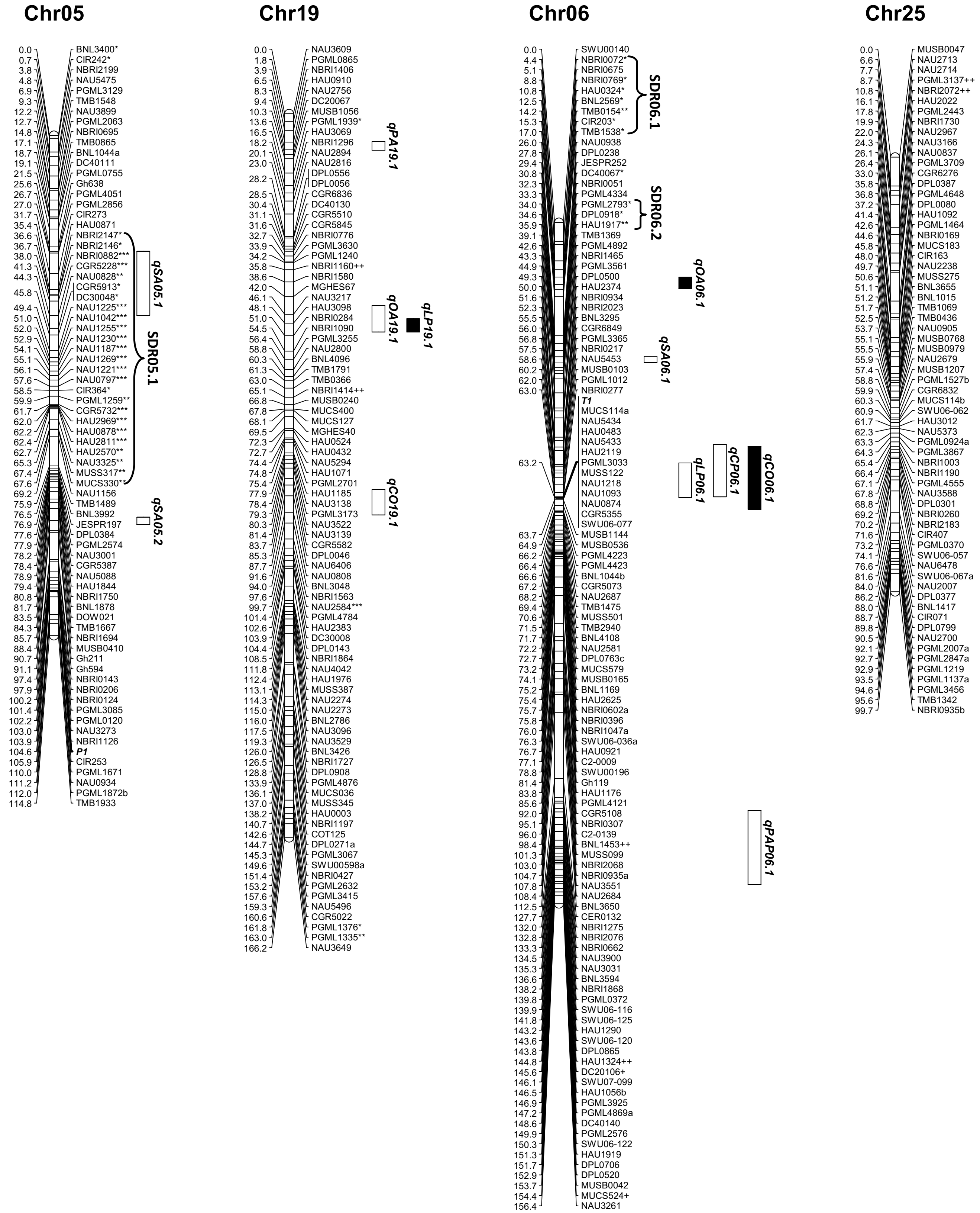

Fig. 1 continued

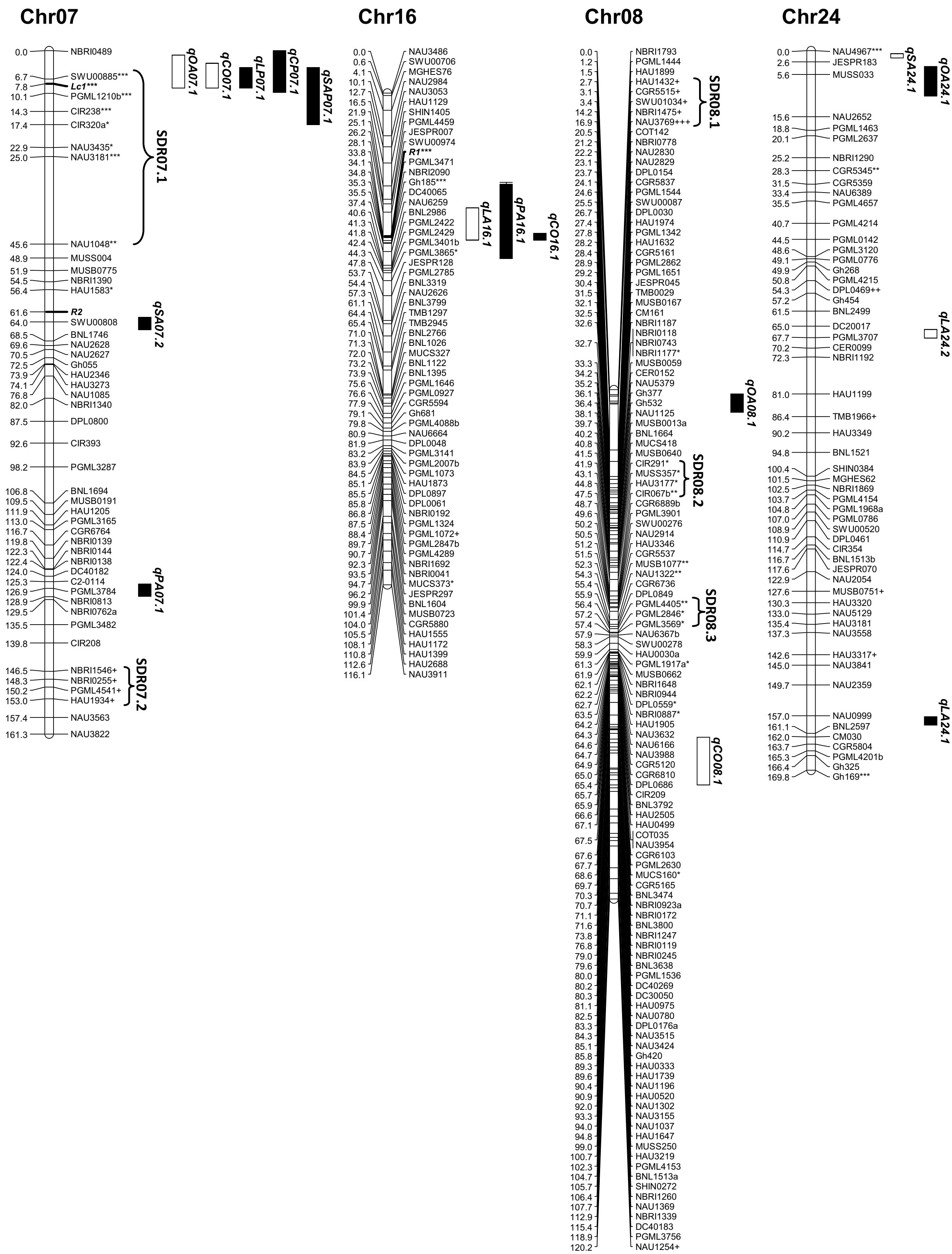

Fig. 1 continued

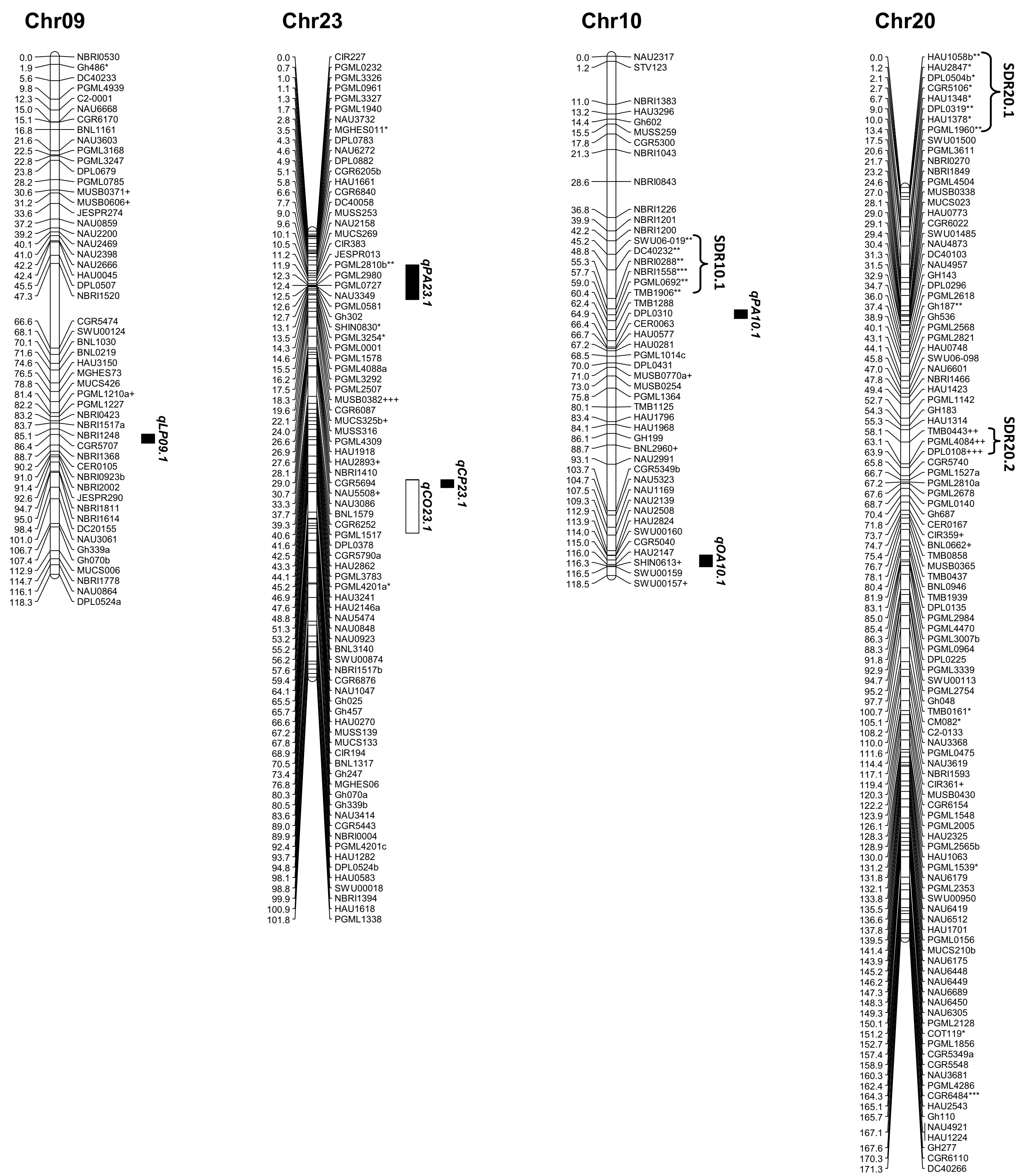

Fig. 1 continued

obtained 1712 primers with a polymorphism rate of 6.8 %, indicating that the potential of the publicly available SSR loci to construct a saturated upland cotton genetic map is very limited. Therefore, for saturated upland cotton genetic map construction, development of new markers from the genome databases, such as the *G. arboreum* and *G. raimondii* genomes, is necessary (Paterson et al. 2012; Wang et al. 2012; Li et al. 2014). However, the large number of SSR loci

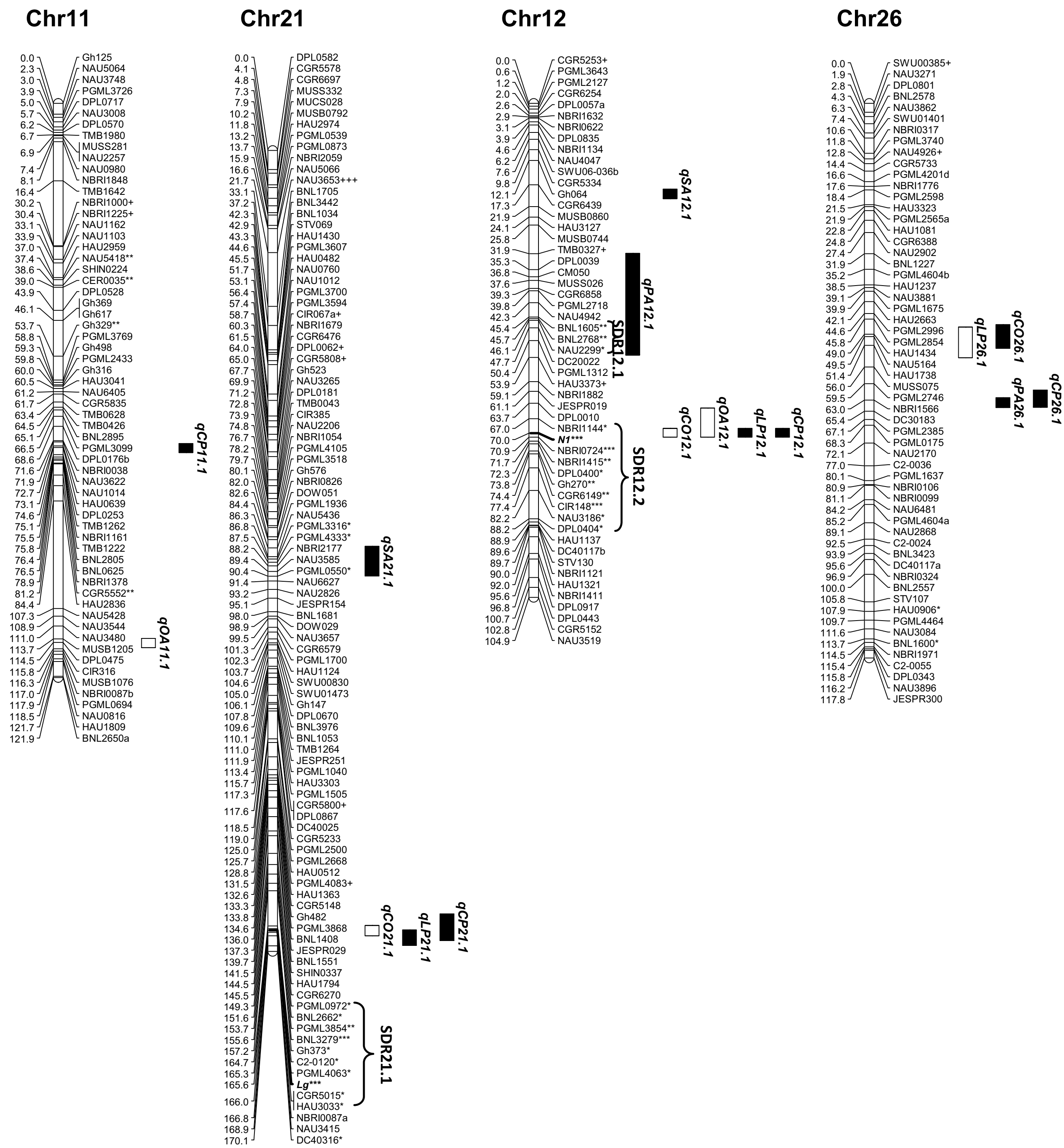

Fig. 1 continued

and even loci distribution make ours a good skeleton map to understand and exploit the tetraploid *Gossypium* genome.

Relationship between LP and cottonseed nutrient traits

The correlation analysis in this study presents the overall network of relationships between LP and cottonseed nutrient traits. The most important correlations were detected between LP, CO, and CP content, which revealed the proportion of carbohydrates flowing to different molecular types and how cottonseed nutrient traits have impacted on fiber yield. LP was positively correlated with CP content, whereas it was negatively correlated with CO content, which is consistent with previous reports

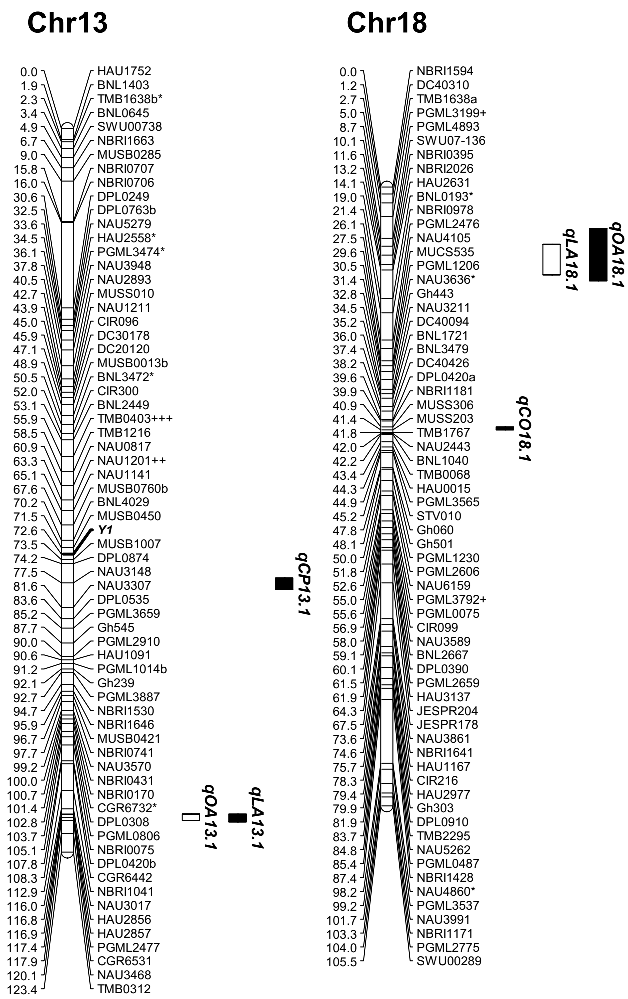

Fig. 1 continued

(Bechere et al. 2009; An et al. 2010). A negative correlation between CO and CP content had also been reported by other researchers (Song and Zhang 2007; Yu et al. 2012). Our study provides further evidence that it is impossible to increase all three in breeding projects. However, there were no significant unfavorable correlations between LP and fatty acid content; similar correlations were observed between CP content and fatty acid components, except for oleic acid content. This means that breeders could increase a given fatty acid component content while increasing LP and CP content. Among the fatty acid components, the correlations were very complicated and the most significant were the negative correlations between linoleic acid and other fatty acid component content. Considering the high linoleic acid content in crude fatty acid content, it is obvious that the linoleic acid biosynthetic pathway is far more competitive.

Major QTL identified at morphological loci

Endrizzi et al. (1984) reported that T586 includes R_1, T_1, L_2, R_2, Y_1, P_1, Lc_1, N_1, and Lg, which were mapped on seven genetic linkage groups (Kohel et al. 1965). All nine morphological markers located in the present report were consistent with previous genetic maps, expect for Lg (Kohel et al. 1965; Guo et al. 2006). Green fiber (Lg) controlled by an incomplete dominance gene was located on Chr15 in previous studies (Stephens 1955; Kohel et al. 1965; Kohel 1985). In the present study, Lg is mapped on the end of Chr21 flanked by loci C2-0120 and CGR5015. Based on the *G. raimondii* reference genome (Paterson et al. 2012), the loci (C2-120, NAU3415, and DC340316) closely linked to Lg are physically aligned to Chr07 (corresponding to Chr11 and Chr21 of tetraploid cotton) rather than Chr02 (corresponding to Chr01 and Chr15 of

Table 4 Fiber lint percentage QTL identified

QTL	Chr	Years	Locus	LOD	Additive	% Expl.
qLP01.1	Chr01	2005	PGML1273	2.1	−3.25	5.3
	Chr01	2006	PGML1273	2.4	−3.27	5.7
qLP17.1	Chr17	2005H	NAU2649	2.3	−2.68	4.0
	Chr17	2006	NBRI1837	2.6	−2.92	5.1
	Chr17	2009	NAU2649	2.2	−2.15	3.7
	Chr17	2010	NAU2649	2.4	−2.66	4.0
qLP06.1	Chr06	2004	T_1	3.6	+2.94	6.0
	Chr06	2005	T_1	3.2	+3.17	5.7
	Chr06	2005H	T_1	4.7	+3.89	8.6
	Chr06	2009	T_1	2.7	+2.46	4.9
	Chr06	2010	T_1	4.1	+3.71	7.6
	Chr06	2012	T_1	2.2	+2.39	4.2
qLP07.1	Chr07	2004	Lc1	5.9	−3.80	9.6
	Chr07	2005	Lc1	8.4	−4.98	13.5
	Chr07	2005H	Lc1	20.9	−8.33	36.7
	Chr07	2006	Lc1	13.8	−6.03	21.1
	Chr07	2007	Lc1	17.1	−7.13	29.2
	Chr07	2008	Lc1	6.3	−7.53	10.3
	Chr07	2009	Lc1	11.0	−4.75	17.4
	Chr07	2010	Lc1	16.4	−7.30	28.3
	Chr07	2012	Lc1	11.7	−4.98	18.3
	Chr07	2011	Lc1	15.4	−5.34	23.6
qLP09.1	Chr09	2004	CGR5707	2.1	−2.24	3.5
	Chr09	2005	CGR5707	2.6	−2.76	4.4
	Chr09	2005H	CGR5707	2.4	−2.66	4.0
	Chr09	2006	CGR5707	2.6	−2.68	4.4
	Chr09	2009	CGR5707	2.5	−2.30	4.3
	Chr09	2010	CGR5707	2.7	−2.79	4.5
	Chr09	2012	CGR5707	2.3	−2.21	3.8
qLP21.1	Chr21	2004	Lg	11.5	−5.17	18.3
	Chr21	2005	Lg	12.6	−5.99	19.9
	Chr21	2005H	Lg	15.6	−6.63	24.3
	Chr21	2006	Lg	13.3	−5.93	21.0
	Chr21	2007	Lg	14.8	−6.17	23.0
	Chr21	2008	Lg	5.0	−6.70	8.3
	Chr21	2009	Lg	14.0	−5.28	22.0
	Chr21	2010	Lg	12.3	−6.25	21.2
	Chr21	2011	Lg	12.0	−4.78	19.4
	Chr21	2012	Lg	13.4	−5.26	21.0
qLP12.1	Chr12	2004	N_1	57.3	−9.91	62.7
	Chr12	2005	N_1	58.2	−11.04	63.4
	Chr12	2005H	N_1	30.3	−8.91	41.0
	Chr12	2006	N_1	54.4	−10.45	60.9
	Chr12	2007	N_1	47.3	−9.91	55.7
	Chr12	2008	N_1	12.2	−10.48	19.2
	Chr12	2009	N_1	52.0	−9.02	59.4
	Chr12	2012	N_1	43.4	−8.64	52.7
	Chr12	2011	N_1	33.3	−7.53	44.2
qLP26.1	Chr26	2004	NAU5164	3.0	+2.98	5.7
	Chr26	2005	NAU5164	3.0	+3.31	5.7

Table 4 continued

QTL	Chr	Years	Locus	LOD	Additive	% Expl.
	Chr26	2005H	HAU1738	3.9	+3.89	8.0
	Chr26	2006	NAU5164	2.4	+2.90	4.7
	Chr26	2007	HAU1738	2.5	+2.97	5.1
	Chr26	2009	HAU1738	2.5	+2.59	5.1
	Chr26	2010	HAU1738	2.6	+3.25	5.7
	Chr26	2011	NAU5164	2.2	+2.28	4.2
	Chr26	2012	NAU5164	2.2	+2.43	4.2

− Indicates T586 allele and + indicates Yumian 1 allele; both increase the phenotype value

tetraploid cotton), which further confirms that our result is reliable.

In this and our previous studies (Zhang et al. 2009), some of the major morphological markers (N_1, Lc_1, T_1, and Lg) exhibited pleiotropic effects on fiber yield, fiber quality, and CO and CP content. Three of the morphological markers (N_1, Lc_1, and Lg) significantly impacted LP with very high phenotypic variation; in particular, QTL on loci N_1 accounted for >60 %. N_1 were fuzzless and had a significantly negative effect on LP. Abdurakhmonov (2007) detected two highly significant fiber percentage QTL that explained approximately 23–59 % of phenotypic variation around the regions TMB0471 and MGHES-31 on Chr12, and one parent was L-70 (fuzzless/lintless with 0 % lint percentage on cottonseed). Rong et al. (2005) reported that a major QTL, which explain 33.6 % of LP variation (LOD = 7.50), were mapped at the region where N_1 is located. N_1, as a dominant gene, could have pleiotropic effects on fiber development inhibition, in terms of both fuzz and lint. N_1 may also be associated with a major gene affecting fiber development.

Both brown and green fibers were negatively correlated with fiber yield and quality (Richmond 1943). Zhang et al. (2005, 2009) reported that stable QTL affecting fiber length, uniformity, fineness, and strength were identified at locus Lc_1 and that T586 alleles decrease the phenotypic value of traits. In this study, major QTL for LP, CP content, and CO content are identified at loci N_1, Lc_1, and Lg, which indicates that these loci affect multiple traits. Meanwhile, the T586 alleles at these loci decrease LP and CP content but increase CO content. This result shows that these loci are very important for cottonseed development, and partly explains the correlations among LP, CP, and CO content.

Simpson (1947) first reported that pilose (T_1) produced short dense trichomes on the vegetative parts of upland cotton plants. Yi et al. (2001) and Guo et al. (2006) reported that T_1 was associated with an LP QTL and with the favorable from T586 allele, which was further confirmed in this study. Zhang et al. (2005, 2009) and Wan et al. (2007) reported that the T_1 locus might contain the candidate gene underlying QTL controlling fiber length, uniformity, strength, and fineness. The T_1 region on Chr06 may carry a QTL with pleiotropic effects or a QTL cluster controlling plant trichomes and seed fibers (Said et al. 2014). In summary, the T_1 locus in T586 increases LP and fiber micronaire but decreases fiber length and strength. QTL identified at locus T_1 provide further evidence that trichomes and cotton fiber likely share common regulatory mechanisms (Suo et al. 2003; Lee et al. 2007).

Common QTL across populations

In the present study, eight LP QTL were detected, but only qLP26.1 was found near locus NAU5164 on Chr26 (Yu et al. 2013) in previous studies, except for the QTL common to the morphological markers. Among the 71 seed nutrient trait QTL in this study, three were also reported in other studies on different populations; these included qCO07.1 sharing a common marker NAU1302 (Song and Zhang 2007), qCO12.1, and qCP12.1 closely linked to marker BNL3867 (Yu et al. 2012). The reason that a few of the QTL identified in the present study were also detected in other populations are inferred as following. First, parent T586 has several morphological loci that contribute to most of the phenotypic variation. The other population, in which T856 was not a parent, did not contain the alleles that T586 had at the morphological loci. Therefore, the QTL identified at these loci were not detected. Second, most of the QTL have little effect and are mainly affected by environmental factors, so they are not easy to detect across populations planted under different environments. Third, not a lot of QTL mapping work has been carried out on cottonseed nutrient traits to date. Only 29 protein- and 16 oil-related QTL have been identified, which is far fewer than the number of fiber quality QTL (Said et al. 2013). Last, less common markers were found in the upland cotton genetic map because of relatively low levels of DNA marker polymorphism.

Knowledge on fiber growth and development at the molecular level and its integration with QTL mapping is essential in designing next-generation breeding strategies. The present map will provide a highly dense

Table 5 QTL affecting seed protein content, oil, and fatty acid component percentage

Trait	QTL	Chr	Years	Locus	LOD	Additive	PV (%)
CP	q CP01.1	Chr01	2006	PGML1273	2.3	−0.61	5.3
			2007	HAU1001	2.1	−0.78	6.9
	q CP15.1	Chr15	2006	PGML3018	2.8	−0.65	6.5
	q CP15.2	Chr15	2011	NAU2437	2.2	−0.64	10.2
	q CP14.1	Chr14	2006	BNL2651	2.4	+0.58	5.3
	q CP22.1	Chr22	2007	PGML1657	2.8	−0.79	7.4
	q CP06.1	Chr06	2007	BNL3295	4.1	+1.01	11.9
	q CP07.1	Chr07	2006	Lc1	4.6	−0.71	7.7
			2007	Lc1	5.9	−1.03	12.8
			2011	Lc1	2.2	−0.76	13.5
	q CP23.1	Chr23	2007	NBRI1517b	2.6	−0.77	7.3
	q CP11.1	Chr11	2007	HAU0639	2.2	−0.67	5.2
	q CP21.1	Chr21	2006	Lg	9.8	−1.02	16.2
	q CP12.1	Chr12	2006	N_1	37.3	−1.82	48.1
			2007	N_1	13.2	−1.67	34.1
			2011	N_1	7.3	−1.16	30.5
	q CP26.1	Chr26	2011	NBRI1566	3	−0.94	20.2
	q CP13.1	Chr13	2011	NAU3148	2.3	−0.66	10.8
CO	qCO15.1	Chr15	2006	PGML0726	2.2	+0.49	4.8
	qCO15.2	Chr15	2011	NAU2437	2.5	+0.54	11.8
	qCO02.1	Chr02	2007	NAU2858	3.5	−0.70	8
	qCO14.1	Chr14	2011	BNL3502	2.1	−0.51	9.5
	qCO22.1	Chr22	2007	PGML4620	2.6	+0.65	7.2
	qCO19.1	Chr19	2006	NAU6406	2.8	+0.52	5.6
	qCO06.1	Chr06	2007	T_1	3	−0.62	6.7
	qCO07.1	Chr07	2006	Lc1	2.5	+0.45	4.3
			2007	Lc1	5.5	+0.92	14.8
			2011	Lc1	2.8	+0.58	12.7
	qCO16.1	Chr16	2007	R_1	2.3	−0.57	5.1
	qCO08.1	Chr08	2006	NAU1302	2.7	+0.50	5.2
	qCO23.1	Chr23	2007	NBRI1517b	2.1	+0.58	6.1
			2011	MUCS133	2.2	+0.52	10.2
	qCO21.1	Chr21	2006	Lg	12.7	+0.97	20.3
			2007	Lg	2.5	+0.70	8.9
	qCO12.1	Chr12	2006	N_1	32.1	+1.46	42.8
			2007	N_1	16	+1.41	35.9
			2011	N_1	4.1	+0.70	18.5
	qCO26.1	Chr26	2007	HAU1738	2.4	−0.60	6.1
	qCO18.1	Chr18	2006	MUSS306	2.3	−0.43	3.9
LA	qLA14.1	Chr14	2007	BNL2651	2.3	−0.52	5.4
	qLA04.1	Chr04	2007	NBRI1178	2.2	+0.76	11.3
	qLA19.1	Chr19	2011	HAU3098	3.3	−1.33	15.1
	qLA16.1	Chr16	2006	R_1	3.5	+0.96	7.7
	qLA24.1	Chr24	2011	NBRI1290	2.1	−1.13	11.5
	qLA24.2	Chr24	2007	PGML3707	2.1	+0.52	5.5
	qLA13.1	Chr13	2011	PGML2477	2.8	−1.22	12.9
	qLA18.1	Chr18	2007	HAU2631	2.7	+0.66	8.4

Table 5 continued

Trait	QTL	Chr	Years	Locus	LOD	Additive	PV (%)
OA	qOA19.1	Chr19	2011	HAU3098	3.6	+1.28	16.6
	qOA06.1	Chr06	2011	TMB0154	2.1	−0.99	9.8
	qOA07.1	Chr07	2006	Lc1	5.8	+0.82	10.5
	qOA08.1	Chr08	2006	HAU1432	2.2	−0.65	6.9
	qOA24.1	Chr24	2011	MUSS033	2.7	−1.13	14.6
	qOA10.1	Chr10	2011	SHIN0613	2.1	−0.98	9.9
	qOA11.1	Chr11	2007	DPL0475	2.2	+0.41	5.7
	qOA12.1	Chr12	2006	N_1	3.4	+0.64	6.5
	qOA13.1	Chr13	2011	PGML2477	2.3	+1.02	10.8
	qOA18.1	Chr18	2006	NBRI0395	2.8	−0.67	7.3
			2007	NBRI0395	4.8	−0.66	15.3
PA	qPA01.1	Chr01	2011	DC40052	2.1	−0.39	10
	qPA15.1	Chr15	2011	TMB1152a	2.1	+0.40	10
	qPA15.2	Chr15	2007	SWU00058	2.2	+0.39	6.8
	qPA02.1	Chr02	2007	HAU0040	2.4	−0.39	6.4
	qPA22.1	Chr22	2006	PGML3672	2.7	−0.38	5.5
	qPA19.1	Chr19	2011	NAU2756	2.1	+0.45	13.3
	qPA06.1	Chr06	2007	SWU06-120	2.3	+0.41	7.1
	qPA07.1	Chr07	2006	PGML3784	2.1	−0.33	4.2
	qPA16.1	Chr16	2006	SHIN1405	2.8	−0.42	6.8
	qPA23.1	Chr23	2011	MUCS269	3.2	−0.49	14.8
	qPA10.1	Chr10	2011	PGML0692	2.2	−0.41	10.6
	qPA12.1	Chr12	2007	PGML1312	3.3	−0.53	12.3
	qPA26.1	Chr26	2006	NAU1738	2.9	−0.48	8.6
SA	qSA15.1	Chr15	2006	CIR234	2.3	−0.09	4.5
	qSA14.1	Chr14	2006	BNL3033	5.5	+0.13	9.2
			2011	NBRI2228	2.6	+0.12	12.8
	qSA14.2	Chr14	2011	NAU0998	2.5	+0.12	11.6
	qSA22.1	Chr22	2011	NBRI0728	2.1	+0.11	10.2
	qSA05.1	Chr05	2006	PGML2856	2.9	+0.11	6.8
	qSA05.2	Chr05	2006	MUSB0410	2.5	+0.09	4.4
	qSA06.1	Chr06	2011	NBRI0051	2.3	+0.12	11.5
	qSA07.1	Chr07	2006	Lc1	3.7	−0.12	7.7
	qSA07.2	Chr07	2011	SWU00808	2.1	−0.11	11.5
	qSA24.1	Chr24	2011	Gh325	2.1	+0.12	12.1
	qSA21.1	Chr21	2006	NAU5436	3.7	−0.12	7.5
	qSA12.1	Chr12	2011	MUSB0860	2.4	−0.16	22.7
	qSA07.1	Chr07	2006	Lc1	3.7	−0.12	7.7
	qSA07.2	Chr07	2011	SWU00808	2.1	−0.11	11.5
	qSA24.1	Chr24	2011	Gh325	2.1	+0.12	12.1
	qSA21.1	Chr21	2006	NAU5436	3.7	−0.12	7.5
	qSA12.1	Chr12	2011	MUSB0860	2.4	−0.16	22.7

LOD was larger than the significant LOD threshold calculated by permutation test. − Indicates T586 alleles and + indicates Yumian 1 alleles; both increase the phenotype value. PV indicates the percentage of phenotypic variation explained

genetic linkage map for molecular marker-assisted selection. The QTL identified for LP and seed nutrient traits at loci T_1, N_1, Lc_1, and Lg provide a means for further study on the molecular mechanisms of fiber and cottonseed development through map-based cloning and functional analysis.

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