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QTL analysis for early-maturing traits in cotton using two upland cotton (*Gossypium hirsutum* L.) crosses

Chengqi Li[1)], Xiaoyun Wang[2)], Na Dong[1)], Haihong Zhao[1)], Zhe Xia[2)], Rui Wang[1)], Richard L. Converse[3)] and Qinglian Wang*[1)]

[1)] *Henan Institute of Science and Technology, Key Discipline Open Lab on Crop Molecular Breeding of Henan Institute of Higher Learning, Cotton Research Institute*, Xinxiang Henan 453003, China
[2)] *College of Life Sciences, Henan Normal University*, Xinxiang Henan 453003, China
[3)] *University of Cincinnati Blue Ash College*, 9555 Plainfield Rd, Blue Ash, OH 45236, USA

Making use of the markers linked closely to QTL for early-maturing traits for MAS (Marker-assisted selection) is an effective method for the simultaneous improvement of early maturity and other properties in cotton. In this study, two F_2 populations and their $F_{2:3}$ families were generated from the two upland cotton (*Gossypium hirsutum* L.) crosses, Baimian2 × TM-1 and Baimian2 × CIR12. QTL for early-maturing traits were analyzed using $F_{2:3}$ families. A total of 54 QTL (31 suggestive and 23 significant) were detected. Fourteen significant QTL had the LOD scores not only > 3 but also exceeding permutation threshold. At least four common QTL, *qBP-17* for bud period (BP), *qGP-17a/qGP-17b* (*qGP-17*) for growth period (GP), *qYPBF-17a/qYPBF-17b* (*qYPBF-17*) for yield percentage before frost (YPBF) and *qHFFBN-17* for height of first fruiting branch node (HFFBN), were found in both populations. These common QTL should be reliable and could be used for MAS to facilitate early maturity. The common QTL, *qBP-17*, had a LOD score not only > 3 but also exceeding permutation threshold, explaining 12.6% of the phenotypic variation. This QTL should be considered preferentially in MAS. Early-maturing traits of cotton are primarily controlled by dominant and over-dominant effects.

Key Words: short-season upland cotton, early-maturing traits, QTL, common QTL, MAS.

Introduction

Short-season upland cotton (*Gossypium hirsutum* L.), which is also called early-maturing cotton, generally exhibits a dwarf, compact phenotype with fewer leaves, shorter internodes and fruiting branches, and shorter growth period than middle-late-maturing cotton (Yu and Huang 1990). The selection and popularization of short-season cotton has significant value in alleviating the contradiction presented when occupying farmlands with either cotton or cereals, while optimizing cropping system. Early maturity of cotton is a comprehensive trait, encompassing growth period, individual growth stages, yield percentage before frost, first fruiting branch node and height of first fruiting branch node. These components that contribute to early maturity are all complex quantitative traits (White 1966), which are controlled by both QTL (quantitative trait locus/loci) and environment and manifest a variety of genetic modes in different combinations (Dong *et al.* 2010, Song *et al.* 2005). In addition, many researchers believe that a significant negative correlation exists between early maturity and yield, and between early maturity and quality (Fan *et al.* 2006b, Song *et al.* 2005). Obtaining a satisfactory yield and quality in a short growing season is likely to exacerbate the conflict between early maturity and yield and between early maturity and quality, so it is increasingly difficult to improve upon these agriculturally desirable traits in short-season cotton simultaneously by means of traditional breeding.

Since the first elaborated RFLP map of allotetraploid cotton was published (Reinisch *et al.* 1994), genetic mapping in cotton, especially interspecific genetic mapping for *Gossypium hirsutum* × *G. Barbadense*, has made remarkable progress (Guo *et al.* 2007, Lacape *et al.* 2009, Nguyen *et al.* 2004). However, interspecific genetic maps are hard to apply directly to the genetic improvement of upland cotton (*Gossypium hirsutum* L.). At present, intraspecific genetic maps in cotton are relatively less advanced because of limited genetic diversity and low polymorphism (Shappley *et al.* 1998, Shen *et al.* 2005, Ulloa *et al.* 2002, Zhang *et al.* 2009). To take advantage of markers linked closely to target genes for marker-assisted selection (MAS), a highly saturated intraspecific genetic map in upland cotton covering the entire genome is a necessity. Yu *et al.* (2010) constructed a comprehensive reference map that contained 7,424 markers

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*Corresponding author (e-mail: cottonmol@yahoo.cn)

and represented over 93% of the combined information from 28 individual maps, which laid an important foundation for exploration and utilization of cotton gene resources.

Construction of a genetic linkage map in short-season upland cotton and identification of QTL for early-maturing traits, as well as making use of the markers linked closely to target genes for MAS, is an effective method for the simultaneous improvement of early maturity and other properties. The first genetic linkage map in short-season upland cotton was constructed by using a F_2 population obtained from the cross between the short-season upland cotton cultivar, CIR36 and the genetic standard line of *Gossypium hirsutum* L., TM-1 (Fan *et al.* 2006a). The map contained five linkage groups and 43 markers, representing a total length of 1,174 cM covering 23.48% of the cotton genome, with 12 QTL for early-maturing traits detected. Guo *et al.* (2008) reported another genetic map that contained 70 molecular markers and three morphological markers distributed in 17 linkage groups covering 650.8 cM, approximately 14.5% of the cotton genome. Ultimately, five QTL for first fruiting branch node were detected. Zhang *et al.* (2008) used a recombinant inbred line (RIL) population raised from the cross between the upland cotton Acala 1517 (ZM-06339) and Dezhou 047 to construct a genetic map; 51 SSR markers were assigned to 15 linkage groups, about 504.05 cM (10.08% of the cotton genome) was covered and three significant QTL for growth period were detected.

From above studies, it can be concluded that only preliminary progress of the genetic map construction in short-season upland cotton has been made; few QTL for early-maturing traits have been identified and their reliability has yet to receive further verification. In this study, the short-season upland cotton cultivar, Baimian2, was used as the common parent to cross respectively with TM-1 and CIR12 and two F_2 populations and their $F_{2:3}$ families were generated. $F_{2:3}$ families were used to analyze QTL for early-maturing traits based on the maps constructed from the F_2 populations. Our objective was to provide a theoretical basis for the genetic structure analysis and marker-assisted selection for early maturity of cotton.

Materials and Methods

Mapping population

Three upland cotton cultivars of varying maturity were chosen as the parents to generate two mapping populations: F_2 population (Pop I) and its $F_{2:3}$ families raised from Baimian2 × TM-1 and F_2 population (Pop II) and its $F_{2:3}$ families raised from Baimian2 × CIR12. Baimian2 is a Chinese commercial short-season cotton bred by Henan Institute of Science and Technology using the pedigree method and characterized by the desirable features of early maturity, high quality, disease resistance and wide adaptability (Zhu *et al.* 2008). TM-1 is a genetic standard line of upland cotton in the United States and exhibits a late-maturing phenotype in the Yangtze River basin, Yellow River basin and northwestern inland of China (Ai *et al.* 2010, Kohel *et al.* 1970, Li *et al.* 2011). CIR12 is a Chinese commercial multiple-hybrid line bred by Cotton Research Institute of Chinese Agricultural Academy exhibiting a middle-maturing phenotype in China (Tan and Liu 1990). In the summer of 2008, Baimian2 was crossed with both TM-1 and CIR12 to obtain F_1 seeds in the Henan Institute of Science and Technology experimental field. In the winter of 2008, F_1 individual plants were self-pollinated and F_2 seeds were harvested in Hainan Province of China. In 2009, F_2 individual plants were self-pollinated and $F_{2:3}$ family seeds were harvested; in 2010, parents and $F_{2:3}$ families (numbering 220 and 208, respectively) for the two F_2 populations were grown in a single-row plot (0.8 m wide, 5 m long) with two replicates and a random complete block design.

Phenotypic data collection and statistical analysis

To reduce the environmental error, the average value of every $F_{2:3}$ family row was used as the estimated value of the corresponding F_2 individual plant. Seven early-maturing traits of both $F_{2:3}$ families were investigated. These traits comprised: seedling period (SP; the period from seedling emergence to flower bud); bud period (BP; the period from flower bud emergence to flowering); flower and boll period (FBP; the period from flowering to boll opening); growth period (GP; the period from seedling emergence to boll opening); yield percentage before frost (YPBF); first fruiting branch node (FFBN; the node from cotyledon node to first fruiting branch node) and height of first fruiting branch node (HFFBN; the distance between cotyledon node and NFFB). Ten plants of each family row were investigated and the average of two replicates was recorded as the last phenotypic value. The phenotypic data were analyzed using statistical software SPSS 17.0 (SPSS, Chicago, USA).

DNA marker Assays

Genomic DNA of individual plants of both F_2 populations was extracted using a modified CTAB method (Paterson *et al.* 1993). A total of 4,083 SSR primers were used to screen for polymorphism. These primers including the series of BNL, CER, CGR, CIR, CM, COT, DPL, DC, GH, HAU, JESPR, MUCS, MUSB, MUSS, MGHES, NAU, SHIN, STV and TMB, were mainly selected from the published cotton interspecific and intraspecific maps (Guo *et al.* 2007, Nguyen *et al.* 2004, Qin *et al.* 2008, Zhang *et al.* 2012), as well as reported markers linked to QTL for agriculturally significant traits of cotton (Jiang *et al.* 2009, Lacape *et al.* 2005, Li *et al.* 2008, Mei *et al.* 2004, Qin *et al.* 2008, Zhang *et al.* 2003, Zhang *et al.* 2012). The primer sequences were obtained from the Cotton Marker Database (http://www.cottonmarker.org) and synthesized by Nanjing Jinsirui Biology Engineering Co., Ltd. The protocol for PCR amplification and examination followed that of Zhang *et al.* (2002). A *chi*-square test was performed to determine if the allele frequency at each individual marker locus segregated normally.

Map construction and QTL detection

Map construction were performed for the two F_2 populations by JoinMap 3.0 (Van Ooijen and Voorrips 2001) with a LOD score of 3.0 and a recombination frequency of 0.50. $F_{2:3}$ families for Pop I and Pop II were used to identify QTL. QTL were detected by composite interval mapping (Zeng 1994) using Windows QTL Cartographer 2.5 (Wang *et al.* 2006). The QTL with a LOD value between 2.0 and 3.0 was defined as a suggestive QTL (Lander and Kruglyak 1995) and the QTL with a LOD value ≥ 3.0 (Jiang *et al.* 1998), or ≥ the threshold value calculated by a permutation test with 1000 times, was defined as a significant QTL (Churchill and Doerge 1994). QTL confidence intervals (90% and 95%) were set as map intervals corresponding to one and two LOD declines on either side of the peak. The absolute value of the ratio of dominant effect to additive effect (D/A) was used to classify the gene action mode. If the absolute value was ≤ 1, it was regarded as additive effect (A), if the absolute value > 1, it was regarded as dominant effect (D); if > 3, it was regarded as over-dominant effect (OD) (Paterson *et al.* 2003).

QTL nomenclature followed the protocol used in rice (McCouch *et al.* 1997). The QTL name begin with 'q', followed by an abbreviation of the trait, then the name of the Chr. (subgenome) or linkage group. If there was more than one QTL for the same trait on a linkage group, lowercase letters were used to distinguish them. Maps were drawn using MapChart 2.2 (Voorrips 2006). Linkage groups were localized to Chr. (subgenomes) by using the markers that had been previously anchored (Guo *et al.* 2007, Han *et al.* 2006, Mei *et al.* 2004). LGX was used to designate linkage groups not localized to Chr. (subgenomes).

Results

Performance of early-maturing traits for parents and $F_{2:3}$ families

Statistical analysis of early-maturing traits for parents and $F_{2:3}$ populations are listed in Table 1. The differences in all the seven early-maturing traits were significant or highly significant between the parents of both populations, suggesting that the parents we selected are ideal to search for the genes responsible for early maturity. In Pop I, the difference in first fruiting branch node (FFBN) was significant between Baimian2 and TM-1; in Pop II, the difference in seedling period (SP) was significant between Baimian2 and CIR12; the differences in all the other early-maturing traits were highly significant in the two populations. Statistical analysis of early-maturing traits for $F_{2:3}$ families showed that most of the traits for both $F_{2:3}$ families displayed transgressive segregation; of all traits, the standard deviation (SD) of growth period (GP) was at a maximum (3.39 and 3.13) and that of yield percentage before frost (YPBF) was at a minimum (0.04 and 0.05); skewness of all traits was < 1, which is consistent with the normal distribution characteristics of quantitative traits.

Correlation among early-maturing traits

Correlation analysis among early-maturing traits is given in Table 2. Correlations among most traits showed high consistency in $F_{2:3}$ families of both populations. To illustrate, seedling period (SP) was significant or highly significant positively correlated with bud period (BP), flower and boll period (FBP) and growth period (GP) and was significant or highly significant negative correlated with yield percentage before frost (YPBF) and was non-significant positively correlated with first fruiting branch node (FFBN). Obviously, correlations among some traits showed differences in $F_{2:3}$ families of both populations. Notably, the correlations between yield percentage before frost (YPBF) and first fruiting branch node (FFBN) and between yield percentage before frost (YPBF) and height of first fruiting branch node (HFFBN) displayed non-significant negative correlations in $F_{2:3}$ families of Pop I, but the correlation between them was non-significant positive and highly significant negative in $F_{2:3}$ families of Pop II, respectively.

Genetic map construction

A total of 295 and 169 polymorphic marker loci from the 4,083 SSR primers were obtained for Pop I and Pop II,

Table 1. Statistical analysis of early-maturing traits for parents and $F_{2:3}$ families

Trait	Pop I/Baimian2 (P_2) × TM-1 (P_1)							Pop II/Baimian2 (P_2) × CIR12 (P_1)						
	Parents			$F_{2:3}$ family				Parents			$F_{2:3}$ family			
	P_1	P_2	P_1–P_2	Range	Mean	SD	Skewness	P_1	P_2	P_1–P_2	Range	Mean	SD	Skewness
SP (d)	37.71	35.07	2.64**	34.38–38.11	36.08	0.51	0.79	35.50	34.82	0.68*	35.00–37.36	35.94	0.36	0.95
BP (d)	23.14	19.28	3.86**	18.69–24.91	22.12	1.17	–0.22	22.71	19.27	3.44**	17.77–23.71	20.92	1.06	0.02
FBP (d)	49.71	39.79	9.92**	41.00–50.18	46.29	2.25	0.59	47.30	43.09	4.21**	39.58–50.08	44.21	2.15	0.23
GP (d)	110.57	93.86	16.71**	96.00–115.82	104.55	3.39	0.19	105.60	97.18	8.42**	94.23–109.86	101.11	3.13	0.19
YPBF	0.61	1.00	–0.39**	0.83–1.00	0.96	0.04	–0.98	0.89	1.00	–0.11**	0.76–1.00	0.95	0.05	–0.92
FFBN	5.67	5.00	0.67*	4.20–6.80	5.59	0.53	–0.3	4.78	3.70	1.08**	3.30–7.40	5.25	0.94	0.19
HFFBN (cm)	13.80	8.76	5.04**	8.47–18.02	12.22	1.71	0.35	18.91	10.50	8.41**	11.00–19.60	14.63	1.8	0.44

SP = seedling period, BP = bud period, FBP = flower and boll period, GP = growth period, YPBF = yield percentage before frost, FFBN = first fruiting branch node, HFFBN = height of first fruiting branch node.

*,** Indicate significance at 0.05 and 0.01 levels, respectively.

Table 2. Correlation analyses among early-maturing traits

Trait	SP	BP	FBP	GP	YPBF	FFBN	HFFBN
SP		0.466**	0.289**	0.520**	–0.230**	0.046	0.137
BP	0.595**		0.512**	0.776**	–0.390**	0.264**	0.334**
FBP	0.272**	0.533**		0.893**	–0.313**	0.153*	0.352**
GP	0.567**	0.818**	0.892**		–0.397**	0.210**	0.383**
YPBF	–0.246**	–0.305**	–0.423**	–0.432**		–0.129	–0.115
FFBN	0.035	0.200**	0.058	0.123	0.004		0.512**
HFFBN	0.173*	0.325**	0.358**	0.380**	–0.303**	0.302**	

Correlation coefficients among early-maturing traits in $F_{2:3}$ family of Pop I above the diagonal and in $F_{2:3}$ family of Pop II under the diagonal.
*,** Indicate significance at 0.05 and 0.01 levels, respectively.
See Table 1 for abbreviations.

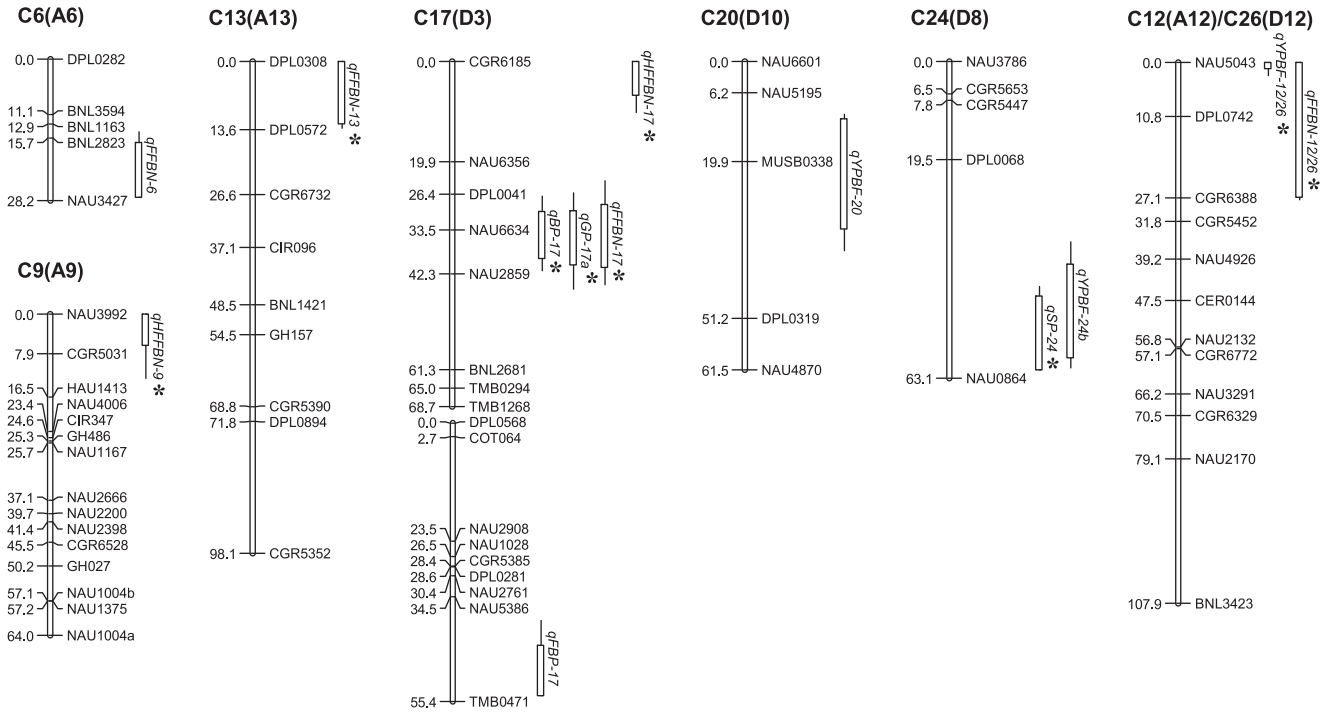

Fig. 1. Location of significant QTL for early-maturing traits in Pop I (Baimian2 × TM-1). 13 significant QTL are shown as seedling period (SP), bud period (BP), flower and boll period (FBP), growth period (GP), yield percentage before frost (YPBF), first fruiting branch node (FFBN) and height of first fruiting branch node (HFFBN). * indicates the QTL had a LOD score not only > 3 but also exceeding permutation threshold.

respectively. A chi-square test indicated that eight and 10 polymorphic loci displayed a segregation distortion (data not shown). All polymorphic loci were used to construct the genetic map. Map I (Pop I) included 269 loci localized into 43 linkage groups that span 1,837.8 cM (approximately 36.76% of the cotton genome) with an average distance of 6.8 cM between markers. Map II (Pop II) included 127 loci localized into 33 linkage groups that span 1,244.3 cM (approximately 24.89% of the cotton genome) with an average distance of 9.7 cM between markers. Taking into account the objective of this study, only those linkage groups associated with the detected QTL were presented.

QTL analysis

A total of 54 QTL, with 31 suggestive and 23 significant, for early-maturing traits were detected (Table 3). They were distributed in 24 Chr. (subgenomes) or linkage groups (Figs. 1, 2, only significant QTL were displayed). Fourteen significant QTL had the LOD scores not only > 3 but also exceeding permutation threshold. They might truly exist in cotton genome.

Seedling period (SP): Six QTL for SP were detected in six Chr. (subgenomes) or linkage groups. In Pop I, one suggestive QTL and one significant QTL were detected in C6 (A6) and C24 (D8), explaining 5.4–42.0% of the phenotypic variation; the significant QTL *qSP-24* had a LOD score not only > 3 but also exceeding permutation threshold. In Pop II, two suggestive and two significant QTL were detected in C8 (A8), C14 (A14), LG5 and LG6, explaining 5.8–46.3% of the phenotypic variation; the significant QTL *qSP-LG5* had a LOD score not only > 3 but also exceeding permutation threshold. Among these six QTL, two represented additive

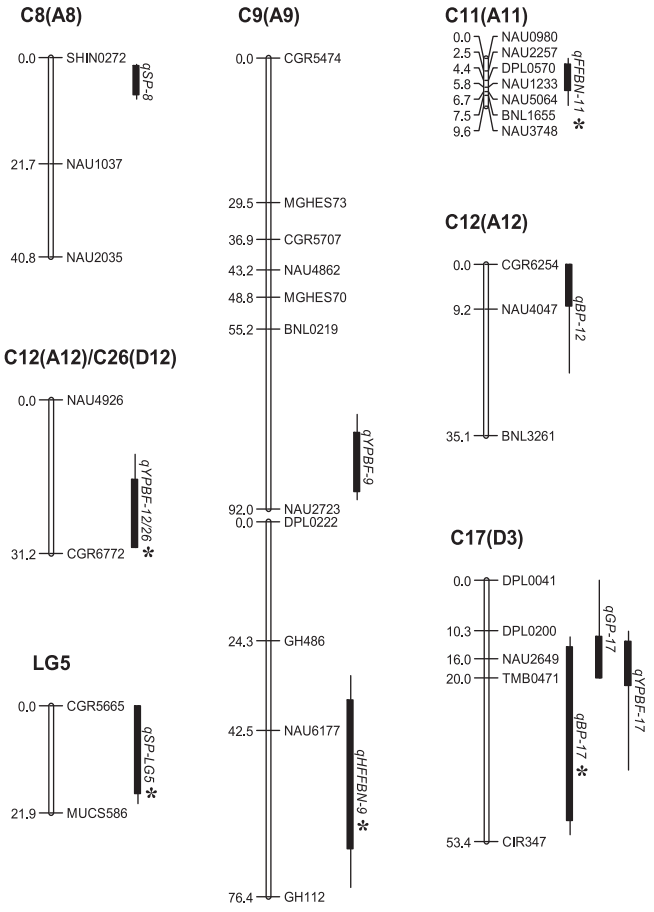

Fig. 2. Location of significant QTL for early-maturing traits from Pop II (Baimian2 × CIR12). Ten significant QTL are shown as seedling period (SP), bud period (BP), growth period (GP), yield percentage before frost (YPBF), first fruiting branch node (FFBN) and height of first fruiting branch node (HFFBN). * indicates that the QTL had a LOD score not only > 3 but also exceeding permutation threshold.

effects and four represented dominant effects; decreased seedling period was conferred by Baimian2 allele in all instances.

Bud period (BP): Seven QTL for BP were detected in six Chr. (subgenomes) or linkage groups. In Pop I, four suggestive and one significant QTL were detected in C1 (A1), C10 (A10), C17 (A17), C12 (A12)/26 (D12) and LG2, explaining 4.6–12.6% of the phenotypic variation; the significant QTL *qBP-17* had a LOD score not only > 3 but also exceeding permutation threshold. In Pop II, two significant QTL was detected in C12 (A12), C17 (D3), explaining 6.5–12.6% of the phenotypic variation; the significant QTL *qBP-17* had a LOD score not only > 3 but also exceeding permutation threshold. Among these seven QTL, four represented additive effects and three represented dominant or over-dominant effects; decreased bud period was conferred by Baimian2 allele at six QTL and by CIR12 allele at one QTL.

Flower and boll period (FBP): Eight QTL for FBP were detected in eight Chr. (subgenomes) or linkage groups. In Pop I, four suggestive and one significant QTL were detected in C9 (A9), C16 (D7), C17 (D3), C22 (D4) and LG2, explaining 4.7–14.6% of the phenotypic variation. In Pop II, three suggestive QTL were detected in C3 (A3), C7 (A7), C8 (A8)/C24 (D8), explaining 6.5–12.1% of the phenotypic variation. Among these eight QTL, five represented additive effects while three represented dominant or over-dominant effects; decreased flower and boll period was conferred by Baimian2 allele at 6 QTL and by TM-1 or CIR12 allele at 2 QTL.

Growth period (GP): Five QTL were detected for GP on three Chr. (subgenomes) or linkage groups. In Pop I, three suggestive and one significant QTL were detected on C13 (A13), C17 (D3) and C24 (D8), explaining 5.7–13.8% of the phenotypic variation. Notably, the significant QTL *qGP-17a* had a LOD score not only > 3 but also exceeding permutation threshold. In Pop II, one significant QTL was detected on C17 (D3), explaining 20.0% of the phenotypic variation. Among these five QTL, two represented additive effects and three represented dominant or over-dominant effects; decreased growth period was entirely conferred by Baimian2 allele.

Yield percentage before frost (YPBF): Fourteen QTL for YPBF were detected in nine Chr. (subgenomes) or linkage groups. In Pop I, five suggestive and three significant QTL were detected on C10 (A10), C11 (A11), C17 (D3), C20 (D10), C24 (D8) and C12 (A12)/26 (D12) and explaining 5.3–46.7% of the phenotypic variation. It should be noted that the significant QTL *qYPBF-12/26* had a LOD score not only > 3 but also exceeding permutation threshold. In Pop II, three suggestive and three significant QTL were detected in C9 (A9), C17 (D3), C12 (A12)/26 (D12), LG5 and LG6, explaining 8.0–42.3% of the phenotypic variation. Note that the significant QTL *qYPBF-12/26* had a LOD score not only > 3 but also exceeding permutation threshold. Among these 14 QTL, six represented additive effects and eight represented dominant or over-dominant effects; increased yield percentage before frost was conferred by Baimian2 allele at 13 QTL and by CIR12 allele at one QTL.

First fruiting branch node (FFBN): Eight QTL were detected for FFBN on eight Chr. (subgenomes) or linkage groups. In Pop I, two suggestive and four significant QTL were detected in C1 (A1), C6 (A6), C9 (A9), C13 (A13), C17 (D3) and C12 (A12)/26 (D12), explaining 4.7–19.1% of the phenotypic variation. Here we note that the significant QTL *qFFBN-13*, *qFFBN-17* and *qFFBN-12/26* had the LOD scores not only > 3 but also exceeding permutation threshold. In Pop II, one suggestive and one significant QTL were detected in C5 (A5), C11 (A11), explaining 6.1–7.5% of the phenotypic variation. Notably, the significant QTL *qFFBN-11* had a LOD score not only > 3 but also exceeding permutation threshold. Among these eight QTL, five represented additive effects and three represented dominant or over-dominant effects; decreased first fruiting branch node was conferred by Baimian2 allele at six QTL and by CIR12 allele at two QTL.

Height of first fruiting branch node (HFFBN): Six QTL

Table 3. Characteristics of QTL for early-maturing traits detected in both populations

Trait	QTL	Pop	Chr. (Subgenome) or linkage group	Position (cM)	Nearest marker	LOD	Permutation threshold	A[a]	D[b]	D/A	Mode	R^2 (%)[c]	Favorable gene[d]
SP	*qSP-6*	I	C6(A6)	15.7	BNL2823	2.08	3.28	–0.16	–0.15	0.99	A	5.4	Baimian2
	qSP-24	I	C24(D8)	55.1	NAU0864	3.74*	3.28	–0.56	–0.64	1.14	D	42.0	Baimian2
	qSP-8	II	C8(A8)	4.1	SHIN0272	4.91	7.27	–0.60	–0.67	1.12	D	46.3	Baimian2
	qSP-14	II	C14(D2)	0.1	SHIN1339	2.37	7.27	–0.10	0.17	–1.75	D	5.8	Baimian2
	qSP-LG5	II	LG5	2.1	CGR5665	10.16*	7.27	–0.82	–0.71	0.87	A	41.9	Baimian2
	qSP-LG6	II	LG6	19.8	MUCS127	2.05	7.27	–0.26	–0.32	1.23	D	26.8	Baimian2
BP	*qBP-1*	I	C1(A1)	73.7	BNL2827	2.11	2.66	–0.34	–0.09	0.26	A	4.6	Baimian2
	qBP-10	I	C10(A10)	0.1	NAU2935	2.63	2.66	0.25	0.36	1.48	D	5.4	TM-1
	qBP-17	I	C17(D3)	33.6	NAU6634	5.68*	2.66	–0.58	–0.03	0.04	A	12.6	Baimian2
	qBP-12/26	I	C12(A12)/C26(D12)	70.6	CGR6329	2.22	2.66	–0.18	0.45	–2.48	D	4.9	Baimian2
	qBP-LG2	I	LG2	1.1	NAU2811	2.08	2.66	–0.78	0.13	–0.16	A	17.1	Baimian2
	qBP-12	II	C12(A12)	0.1	CGR6254	2.43	2.38	–0.10	0.53	–5.13	OD	6.5	Baimian2
	qBP-17	II	C17(D3)	16.2	NAU2649	5.21*	2.38	–0.51	–0.17	0.34	A	12.6	Baimian2
FBP	*qFBP-9*	I	C9(A9)	63.3	NAU1004a	2.56	2.64	–0.73	–0.40	0.54	A	6.5	Baimian2
	qFBP-16	I	C16(D7)	82.5	NAU6078	2.02	2.64	–0.31	0.86	–2.82	D	4.7	Baimian2
	qFBP-17	I	C17(D3)	54.2	TMB0471	2.78	2.64	–0.52	–0.89	1.70	D	8.2	Baimian2
	qFBP-22	I	C22(D4)	8.1	NAU5046	2.56	2.64	0.60	–0.81	–1.36	D	6.8	TM-1
	qFBP-LG2	I	LG2	21.9	BNL1044	2.44	2.64	–0.90	–1.04	1.16	D	14.6	Baimian2
	qFBP-3	II	C3(A3)	0.1	DPL0209	2.03	2.41	0.52	–1.03	–1.99	D	7.5	CIR12
	qFBP-7	II	C7(A7)	0.1	NAU1043	2.11	2.41	–0.32	1.03	–3.27	OD	6.5	Baimian2
	qFBP-8/24	II	C8(A8)/C24(D8)	3.1	CGR5202	2.22	2.41	–1.11	–0.72	0.65	A	12.1	Baimian2
GP	*qGP-13*	I	C13(A13)	0.3	CIR096	2.02	2.68	–0.07	–1.58	22.54	OD	5.7	Baimian2
	qGP-17a	I	C17(D3)	35.5	NAU6634	4.84*	2.68	–1.74	0.20	–0.11	A	13.8	Baimian2
	qGP-17b	I	C17(D3)	50.9	TMB0471	2.34	2.68	–0.80	–1.59	2.00	D	9.5	Baimian2
	qGP-24	I	C21(D11)	8.1	CGR5447	2.56	2.68	–0.97	–0.69	0.71	A	5.7	Baimian2
	qGP-17	II	C17(D3)	18.1	TMB0471	2.88	2.37	–1.41	–1.96	1.39	D	20.0	Baimian2
YPBF	*qYPBF-10*	I	C10(A10)	33.2	NAU0904	2.48	4.63	–0.02	–0.01	0.31	A	7.4	Baimian2
	qYPBF-11	I	C11(A11)	11.3	NAU5064	2.08	4.63	–0.01	0.01	–0.38	A	5.3	Baimian2
	qYPBF-17a	I	C17(D3)	39.6	NAU2859	2.73	4.63	0.02	0.02	0.75	A	10.9	Baimian2
	qYPBF-17b	I	C17(D3)	38.5	NAU5386	2.19	4.63	0.01	–0.20	–21.78	OD	7.2	Baimian2
	qYPBF-20	I	C20(D10)	22.7	MUSB0338	3.09	4.63	0.00	0.03	270.00	OD	10.9	Baimian2
	qYPBF-24a	I	C24(D8)	10.3	TMB0555	2.37	4.63	0.01	–0.01	–0.69	A	6.2	Baimian2
	qYPBF-24b	I	C24(D8)	49.6	NAU0864	3.79	4.63	0.03	0.05	1.96	D	46.7	Baimian2
	qYPBF-12/26	I	C12(A12)/C26(D12)	0.1	NAU5043	10.60*	4.63	0.04	0.04	1.13	D	9.0	Baimian2
	qYPBF-9a	II	C9(A9)	3.3	CGR5474	2.08	4.85	0.01	0.02	1.50	D	7.0	Baimian2
	qYPBF-9b	II	C9(A9)	83.1	NAU2723	3.87	4.85	0.05	0.04	0.71	A	40.7	Baimian2
	qYPBF-17	II	C17(D3)	16.1	NAU2649	3.34	4.85	0.02	0.00	0.06	A	8.0	Baimian2
	qYPBF-12/26	II	C12(A12)/C26(D12)	27.5	CGR6772	5.11*	4.85	0.02	0.02	1.60	D	12.1	Baimian2
	qYPBF-LG5	II	LG5	0.1	CGR5665	2.68	4.85	0.01	0.08	5.92	OD	42.3	Baimian2
	qYPBF-LG6	II	LG6	29.9	MUCS127	2.03	4.85	–0.02	0.04	–2.00	D	19.6	CIR12
FFBN	*qFFBN-1*	I	C1(A1)	23.6	NAU5411	2.50	2.70	0.13	–0.07	–0.56	A	4.7	TM-1
	qFFBN-6	I	C6(A6)	24.2	NAU3427	2.77	2.70	0.17	–0.25	–1.41	D	8.6	TM-1
	qFFBN-9	I	C9(A9)	11.9	CGR5031	2.52	2.70	–0.01	–0.35	44.13	OD	12.0	Baimian2
	qFFBN-13	I	C13(A13)	0.1	DPL0308	3.17*	2.70	–0.15	–0.19	1.23	D	7.2	Baimian2
	qFFBN-17	I	C17(D3)	34.7	NAU6634	6..83*	2.70	–0.34	–0.09	0.26	A	19.1	Baimian2
	qFFBN-12/26	I	C12(A12)/C26(D12)	12.8	DPL0742	4.33*	2.70	–0.24	–0.08	0.33	A	10.6	Baimian2
	qFFBN-5	II	C5(A5)	37.5	DPL0417	2.27	2.94	–0.35	0.25	–0.73	A	6.1	Baimian2
	qFFBN-11	II	C11(A11)	4.4	DPL0570	3.11*	2.94	–0.33	–0.18	0.53	A	7.5	Baimian2
HFFBN	*qHFFBN-9*	I	C9(A9)	0.1	NAU3992	3.02*	2.83	–0.46	–0.59	1.28	D	7.1	Baimian2
	qHFFBN-17	I	C17(D3)	0.1	CGR6185	5.38*	2.83	–0.89	–0.40	0.46	A	13.3	Baimian2
	qHFFBN-25	I	C25(D6)	69.1	DPL0702	2.82	2.83	–0.49	–0.59	1.22	D	6.2	Baimian2
	qHFFBN-9	II	C9(A9)	54.4	NAU6177	3.76*	2.69	0.97	–0.19	–0.20	A	13.9	CIR12
	qHFFBN-17	II	C17(D3)	15.9	NAU2649	2.33	2.69	–0.59	0.12	–0.21	A	5.2	Baimian2
	qHFFBN-LG3	II	LG3	6.1	CGR5576	2.17	2.69	–0.47	–1.31	2.77	D	11.1	Baimian2

* LOD score is not only > 3 but also exceeds permutation threshold.

[a] A = additive effect.

[b] D = dominant effect.

[c] R^2 = phenotypic variation explained.

[d] Favorable gene means the parent provides gene facilitating early maturity.

See Table 1 for abbreviations.

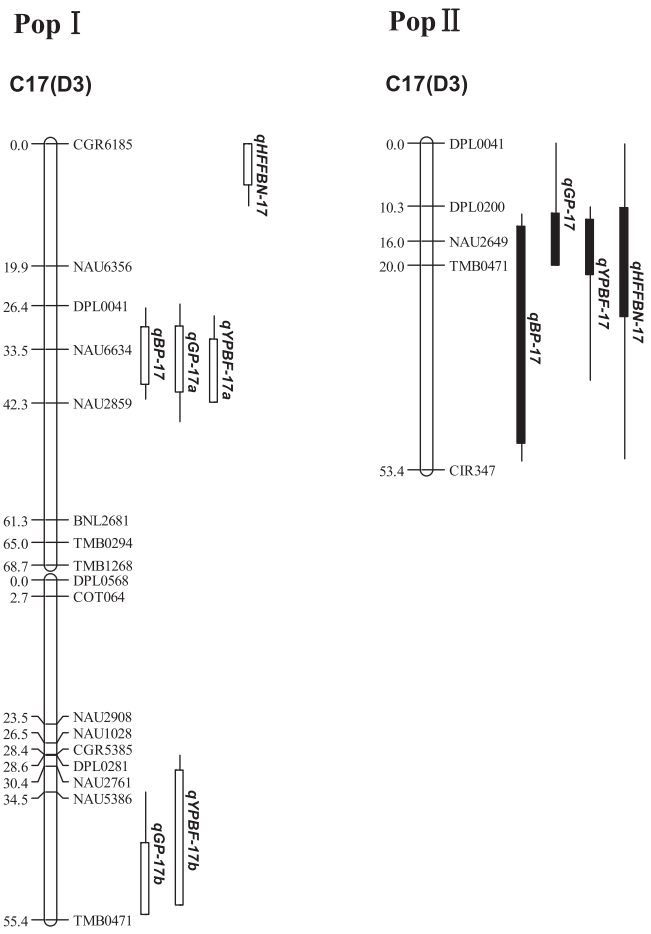

Fig. 3. Location of common QTL in the two populations: Pop I (Baimian2 × TM-1) and Pop II (Baimian2 × CIR12). Four common QTL for four traits are shown as bud period (BP), growth period (GP), yield percentage before frost (YPBF) and height of first fruiting branch node (HFFBN).

for HFFBN were detected in four Chr. (subgenomes) or linkage groups. In Pop I, one suggestive and two significant QTL were detected in C9 (A9), C17 (D3) and C25 (D6), explaining 6.2–13.3% of the phenotypic variation. The significant QTL *qHFFBN-9* and *qFFBN-17* had the LOD scores not only > 3 but also exceeding permutation threshold. In Pop II, two suggestive and one significant QTL were detected in C9 (A9), C17 (D3) and LG3, explaining 5.2–13.9% of the phenotypic variation. Here we note that the significant QTL *qHFFBN-9* had a LOD score not > 3 but also exceeding permutation threshold. Among all the six QTL, three represented additive effects and three represented dominant or over-dominant effects; decreased height of first fruiting branch node was conferred by Baimian2 allele at five QTL and by CIR12 allele at one QTL.

Common QTL

It was found from the comparison of QTL across different populations that at least four QTL (significant or suggestive) were common in both populations (Fig. 3). Of these QTL, *qBP-17* for bud period (BP), *qGP-17a/qGP-17b* (*qGP-17*) for growth period (GP), *qYPBF-17a/qYPBF-17b* (*qYPBF-17*) for yield percentage before frost (YPBF) and *qHFFBN-17* for height of first fruiting branch node (HFFBN) were always localized close to the bridge markers DPL0041 and/or TMB0471 in C17 in the two populations. Moreover, the favorable genes for these QTL always originated from the same parent (Baimian2), indicating that they are respectively common QTL. In addition, *qYPBF-12/26* for yield percentage before frost (YPBF) was detected in C12/C26 with the four bridge markers NAU4926, CGR6772, NAU3921 and NAU2170 in both populations. We should note that *qYPBF-12/26* was tagged at different marker intervals (Figs. 1, 2). Although this pair of QTL have not been confirmed to be common, the favorable genes for them also originated from the same parent (Baimian2) (Table 3), it is supposed to be a common QTL. It is worth noting that *qHFFBN-9* for height of first fruiting branch node (HFFBN) was always detected close to the bridge marker GH486 in C9 in both populations (Figs. 1, 2). However, the favorable genes for this pair of QTL originated from Baimian2 in Pop I and from CIR12 in Pop II (Table 3), whether they belong to a common QTL requires further experimentation.

Discussion

Construction of a detailed genetic linkage map is necessary for QTL discovery. However, the low primer polymorphism in intraspecific cotton accessions makes it difficult to expand the number of markers (Li *et al.* 2008, Iqbal *et al.* 2001, Wendel *et al.* 1992). In this study, a total of 4,083 SSR primers were selected from the published interspecific and intraspecific genetic maps in tetraploid cotton (Guo *et al.* 2007, Nguyen *et al.* 2004, Qin *et al.* 2008, Zhang *et al.* 2012), as well as reported markers linked to QTL for agriculturally significant traits of cotton (Jiang *et al.* 2009, Lacape *et al.* 2005, Li *et al.* 2008, Mei *et al.* 2004, Qin *et al.* 2008, Zhang *et al.* 2003, Zhang *et al.* 2012). Because the primers derived from the published maps are themselves polymorphic and the markers linked to the genes responsible for agriculturally relevant traits can easily identify genotypic differences among different phenotypes, the polymorphic primer rates of the two populations in this study were relatively higher and respectively reached 7.20% and 4.14% by calculation. This feature is useful for the construction of a high-density genetic map and QTL detection.

With regard to the distribution of QTL in A and D subgenomes, Zhang *et al.* (2008) concluded that more QTL for growing period, yield and fiber quality were distributed in D subgenome than in A subgenome. However, Lin *et al.* (2005) and Shen *et al.* (2005) reported that more QTL for fiber quality were located in A subgenome than in D subgenome. In this study, more QTL for early-maturing traits were stably distributed in D subgenome (16) than in A subgenome (12) in Pop I, whereas more QTL were stably

distributed in A subgenome (9) than in D subgenome (5) in Pop II. The differences in the distribution of QTL in A and D subgenomes might be associated with the cultivars employed, the number of marker, and the particular QTL identified for different traits. Therefore, whether the agronomically useful genes are more frequently distributed in A or D subgenome should be established in subsequent studies.

Classical genetics has promulgated the opinion that the genetic action pattern of most early-maturing traits corresponds to an additive dominant model. Baker *et al.* (1973) showed that the dominant variance of early-maturing traits was greater than the additive variance, and the genetic effects of the genes affecting early-maturing traits were primarily dominant. Godoy and Palomo (1999) reported that of 13 early maturity components, all traits, with the exception of days to first square, vertical flowering interval, boll maturation period and production rate index showed significant additive variance. Song *et al.* (2005) described that four early-maturing traits, namely growth period, date of first flower, boll period and first fruiting branch node exhibited primarily additive effects. In this study, we analyzed the genetic effects of early-maturing traits utilizing a molecular diagnostic and found more QTL displayed dominant or over-dominant effects in both populations. In Pop I, a total of 15 QTL displayed additive effects and 18 QTL displayed dominant or over-dominant effects; in Pop II, a total of 9 QTL displayed additive effects and 12 QTL displayed dominant or over-dominant effects (Table 3). Fan *et al.* (2006a) identified 10 QTL for early-maturing traits, including first fruiting branch node, bud period, flower and boll period, growth period and yield percentage before frost, of which four QTL displayed additive effects and six displayed dominant or over-dominant effects. This result is consistent with the present findings, suggesting that early-maturing traits may primarily be controlled by dominant and over-dominant effects. Of course, owing to the influence of limited markers and QTL analysis software, it is likely that some micro-effect QTL have yet to be detected, limiting our ability to fully explain the inheritance of quantitative traits at the molecular level. This necessitates that classical quantitative and molecular quantitative genetics should be used in tandem in the future to classify the inheritance of early-maturing traits more accurately.

Limited by QTL reliability, only a minority of QTL identified have been applied to marker-assisted selection in cotton at present (Guo *et al.* 2005, Wang *et al.* 2007), and the majority of QTL are still unavailable for breeding. This requires accumulating robust enough data to find common QTL, which have high reliability, can be detected through multiple generations, environments or populations. Sun *et al.* (2012) carried out QTL mapping for fiber quality traits across multiple generations and environments in upland cotton. They identified nine common QTL for fiber quality traits in F_2, $F_{2:3}$ and RILs simultaneously, of which two QTL for fiber strength were detected in all three generations and all four environments. Qin *et al.* (2009) also detected eight common QTL for four fiber quality traits across two populations in upland cotton. The above common QTL could be used in marker-assisted selection to improve fiber quality. In this study, at least four common QTL, *qBP-17* for bud period (BP), *qGP-17a/qGP-17b* (*qGP-17*) for growth period (GP), *qYPBF-17a/qYPBF-17b* (*qYPBF-17*) for yield percentage before frost (YPBF) and *qHFFBN-17* for height of first fruiting branch node (HFFBN), were detected in both populations. They should be reliable and could be utilized for marker-assisted selection to facilitate cotton early maturity. It was encouraging to note that the common QTL *qBP-17* had a LOD score not only > 3 but also exceeding permutation threshold, explaining 12.6% of the phenotypic variation (Table 3). This QTL should be considered preferentially in MAS. In addition, *qFFBN-9* (Pop I) for first fruiting branch node (FFBN), *qFBP-7* (Pop II) and *qFBP-17* (Pop I and Pop II) for flower and boll period (FBP) were localized in the same chromosomes of the genetic map constructed by Zhang *et al.* (2008, 2009). Due to the lack of bridge markers, these QTL may be confirmed as common in future studies through accumulating more information. It was also established in this study that despite the fact that few common QTL for several traits were detected, a strong genetic correlation existed among early-maturing traits (Table 2), notably, seedling period was significant or highly significant positively correlated with bud period, flower and boll period and growth period and significant or highly significant negative correlated with yield percentage before frost. This indicates that utilizing the markers linked closely to minor reliable QTL for individual traits for marker assisted selection can provide an effective approach toward simultaneous improvement of related traits.

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