

RESEARCH ARTICLE

Quantitative trait loci mapping and genetic dissection for lint percentage in upland cotton (*Gossypium hirsutum*)

MIN WANG¹, CHENGQI LI² and QINGLIAN WANG^{2*}

¹Beijing Key Laboratory of Plant Resources Research and Development, Beijing Technology and Business University, Beijing 100048, People's Republic of China

²Henan Institute of Science and Technology, Xinxiang 453003, Henan, People's Republic of China

Abstract

Lint percentage is an important character of cotton yield components and it is also correlated with cotton fibre development. In this study, we used a high lint percentage variety, Baimian1, and a low lint percentage, TM-1 genetic standard for *Gossypium hirsutum*, as parents to construct a mapping populations in upland cotton (*G. hirsutum*). A quantitative trait locus/loci (QTL) analysis of lint percentage was performed by using two mapping procedures; composite interval mapping (CIM), inclusive composite interval mapping (ICIM) and the F_{2:3} populations in 2 years. Six main-effect QTL (M-QTL) for lint percentage (four significant and two suggestive) were detected in both years by CIM, and were located on chr. 3, chr. 19, chr. 26 and chr. 5/chr. 19. Of the six QTL, marker intervals and favourable gene sources of the significant M-QTL, *qLP-3*(2010) and *qLP-3*(2011) were consistent. These QTL were also detected by ICIM, and therefore, should preferentially be used for marker-assisted selection (MAS) of lint percentage. Another M-QTL, *qLP-19*(2010), was detected by two mapping procedures, and it could also be a candidate for MAS. We detected the interaction between two M-QTL and environment, and 11 epistatic QTL (E-QTL) and their interaction with environment by using ICIM. The study also found two EST-SSRs, NAU1187 and NAU1255, linked to M-QTL for lint percentage that could be candidate markers affecting cotton fibre development.

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Introduction

Lint percentage is one of the important cotton yield components and has high heritability in upland cotton (*G. hirsutum*). Lint percentage correlates with seed cotton yield, lint yield and other yield components at different strengths. In the last 40 years, improvement of fibre yield of American commercial cotton is closely related to an increase in lint percentage (Pan 1998). Zhang *et al.* (2003a) conducted genetic analysis of cotton varieties derived from different historic periods of cotton area in Yangtze river basin, China. Results suggested that yield components contributed differently to cotton yield in different periods and screening cotton with high lint percentage and big boll is still an effective way for yield breeding. Li *et al.* (2009b) performed correlation and path coefficient analyses on cotton yield characters of upland cotton varieties with different lint percentage. Results suggested that bolls per plant had largest contribution to

cotton yield followed by lint percentage. Contribution from boll weight was the least. Thus, an increase in lint percentage has great effect on improving cotton yield.

Cotton fibre is a single cell fibre, which develops from epidermal cells of the outer integuments of the ovule. Fibre development process can be divided into four stages: fibre initiation, fibre elongation, secondary wall thickening and maturation (Basra and Malik 1984; Graves and Stewart 1988). Cotton fibre development is a highly programmed and regulated process. In every stage of fibre development, there are many genes participating in the regulation of fibre cell development. The process of cotton fibre development is also the formation process of yield and quality. The strength of the ovular epidermic cell differentiation and fibre cell formation directly determines the fibre number per seed, and affects lint percentage, lint index and yield (Xu *et al.* 1995). Li *et al.* (2009a) performed correlation and grey relational analyses on fibre elongation density and fibre characters in cotton with different lint percentage. The correlation result suggested that fibre elongation density at either 0 dpa (days postanthesis) or 1 dpa had high positive correlation with lint

*For correspondence. E-mail: cottonmol@aliyun.com.

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percentage and lint index. The grey relational analysis was essentially consistent with the correlation analysis.

In recent years, based on molecular markers, the application and improvement of CIM, multiple interval mapping (MIM) and other mapping procedures have greatly promoted the genetic dissection of quantitative traits. Genetic dissection of QTL can help reveal the genetic mechanism of target character formation. Meanwhile, using the marker that is tightly linked to the target character QTL for character-tracking/ selection can decrease breeding population scale and selective blindness (Gupta *et al.* 1999; Fedak 1999). At present, QTL mapping for cotton lint percentage has been widely reported (Ulloa and Meredith 2000; Yin *et al.* 2002; Wu *et al.* 2003; Zhang *et al.* 2005; Saha *et al.* 2006; Abdurakhmonov *et al.* 2007; Shen *et al.* 2007; Wan *et al.* 2007; Li *et al.* 2008; Qin *et al.* 2008; Wu *et al.* 2009; An *et al.* 2010; Liu *et al.* 2011; Yu *et al.* 2013). More than 50 QTL for lint percentage were detected. However, these studies mainly used single mapping programme or single environment for assessing lint percentage. As a result, the reliability and stability of the identified QTL was low, which limited the MAS for effective application of lint percentage. Simultaneously, lint percentage epistasis and its interaction with environment were rarely obtained, and thus it was difficult to fully dissect genetic basis of lint percentage.

In this study, the upland cotton varieties, Baimian1 with high lint percentage and TM-1 with low lint percentage, were crossed for producing mapping populations. We performed QTL analysis for lint percentage by using two mapping procedures and phenotyping F_{2:3} populations in 2 years. The objectives of this study were to obtain reliable and stable main-effect QTL (M-QTL) for the target character, to explore the genetic basis of lint percentage considering various genetic effects, and to evaluate the correlation between lint percentage and fibre development.

Materials and methods

Parents and mapping population

Baimian1 was obtained from the Henan Institute of Science and Technology (HIST). This variety has some excellent properties such as high lint percentage, high yield, good quality, and disease and insect resistance (Wang 2004). TM-1 is a genetic standard for *G. hirsutum* derived from successive inbreeding of the commercial variety Deltapine 14, and it exhibits a low lint percentage and yield (Kohel *et al.* 1970). In the summer of 2008, Baimian1 was crossed with TM-1 to obtain F₁ seeds in the cotton breeding experimental fields of HIST. In the winter of 2008, F₁ individuals were self-pollinated and F₂ seeds were harvested in Hainan Province of China. In 2009, F₂ individuals were self-pollinated and F_{2:3} family line seeds were harvested. Then, F_{2:3} family line seeds were divided into two and were respectively planted along with their parents in the cotton breeding experimental fields of HIST in 2010 and 2011. The experiment was

laid out in a randomized complete block design with two replications and 15 plants in each row (0.8-m wide and 5-m long). All activities were performed as per the normal management practice.

Molecular marker trial

Genomic DNA was isolated from the two parents and F₂ individuals by using CTAB method with some modifications (Paterson *et al.* 1993). Parent polymorphism screening was conducted by using a total of 4083 pairs of SSR primers, which included BNL, CER, CGR, CIR, CM, COT, DPL, DC, GH, HAU, JESPR, MUCS, MUSB, MUSS, MGHES, NAU, SHIN, STV and TMB series. These primers were mainly selected from the published cotton interspecific and intraspecific genetic maps and the reported molecular markers linked with QTL for important traits of cotton (Zhang *et al.* 2003b; Nguyen *et al.* 2004; Mei *et al.* 2004; Lacape *et al.* 2005; Guo *et al.* 2007; Qin *et al.* 2008; Li *et al.* 2008; Jiang *et al.* 2009). Primer sequences were downloaded from cotton marker database (CMD, <http://www.cottonmarker.org>), and synthesized by Nanjing Jinsirui Biology Engineering, Nanjing, China. The polymorphic primers screened from parents were used to further analyse the genotype of F₂ individuals. Polymerase chain reaction (PCR) amplification and examination were conducted according to Zhang *et al.* (2002).

Phenotype data collection and analyses

To reduce environmental errors, average value of 10 plants per F_{2:3} family line of two replicates was surveyed as the final phenotypic value for corresponding F₂ individual. After cotton harvest, seed cotton yield and lint yield of parents and F_{2:3} populations were measured. Lint percentage was calculated by dividing lint yield by seed cotton yield. Statistical analyses of phenotype data were performed by using SPSS 17.0 (SPSS, Chicago, USA).

QTL mapping

Jionmap 3.0 was used to construct the genetic linkage map (Van Ooijen and Voorrips 2001). The lowest log-of-odds (LOD) value was 3.0, and the largest genetic distance was 50 cM. The M-QTL was detected by using the CIM program of WinQTLCart 2.5 (Wang *et al.* 2005). The QTL with a LOD value between 2.0 and 3.0 was defined as a suggestive QTL (Lander and Kruglyak 1995). The LOD significant threshold value was estimated by permutation tests 1000 times, and the QTL with a LOD value of more than the LOD threshold value was defined as a significant QTL (Churchill and Doerge 1994). By using MET program of the ICIM method of IciMapping program ver. 3.2 (Wang *et al.* 2012), we also detected M-QTL, QTL × environment interaction, epistatic QTL (E-QTL) and E-QTL × environment interaction. As for the analysis of M-QTL and QTL × environment interaction, the probability in stepwise regression was set

at 0.01 and the scanning step was 1 cM. A threshold LOD score of 2.5 was used to decide a significant QTL. As for the analysis of E-QTL and E-QTL \times environment interaction, the probability in stepwise regression was set at 0.0001 and the scanning step was 5 cM. A threshold LOD score of 5.0 was used to decide a significant QTL. QTL was nominated according to McCouch *et al.* (1997). The letter 'q' indicates QTL, and the abbreviation of character name and the chromosome or linkage group are followed in turn.

Results

Performance of lint percentage for parents and $F_{2:3}$ population

Performance of lint percentage for parents and $F_{2:3}$ population is listed in table 1. In two years, differences in lint percentage among the parents were highly significant, which indicated a good basis for exploring QTL. Lint percentage in both years of $F_{2:3}$ populations exhibited transgressive segregation, and the mean values approached mid-parent values. Lint percentage of $F_{2:3}$ populations in two years showed continuous distribution (figure 1), which confirmed normal distribution characteristics of a quantitative character.

Molecular marker screening and genetic map construction

Parent polymorphism screening was conducted using 4083 pairs of SSR primers, and at last 165 polymorphic markers including 16 distorted segregation loci were identified.

Table 1. Performance of lint percentage for parents and $F_{2:3}$ in two years.

Year	Parent		$F_{2:3}$		
	Baimian 1(P ₁)	TM-1(P ₂)	Range	Mean	SD
2010	40.05**	30.71	26.53–41.15	35.51	2.337
2011	42.16**	31.28	29.57–43.18	37.55	2.074

**Indicates significant difference between the two parents at 0.01 level.

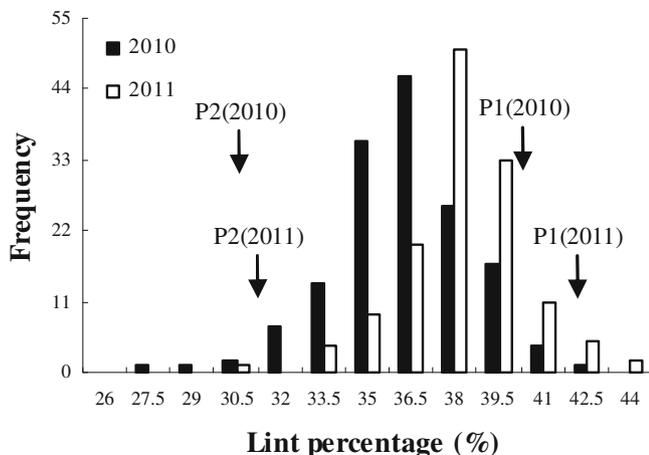


Figure 1. Distribution of lint percentage for $F_{2:3}$ in two years.

Genetic mapping was performed using all the polymorphic loci. A total of 144 makers were distributed in 37 linkage groups with a total length of 1273 cm, which covered 25.5% of the cotton genome. Average distance between markers was 8.84 cm. Eighteen linkage groups corresponded with 16 chromosomes, whereas for 19 linkage groups, corresponding chromosomes could not be associated. Owing to the objectives of this study, only linkage groups with the located QTL are shown in figure 2.

M-QTL and M-QTL \times environment interaction for lint percentage

Six M-QTL (four significant and two suggestive) for lint percentage were detected in two years by CIM. Three M-QTL were detected in 2010 and three others in 2011 (table 2; figure 2). In 2010, two significant QTL, *qLP-3*(2010) and *qLP-26*(2010), were located in marker intervals of DPL0095–NAU3839 on chr. 3 and of MGHES44–DPL0742 on chr. 26, respectively. They explained 29.6% and 11.6% of the phenotypic variation, and the favourable genes were both from Baimian1. One suggestive QTL, *qLP-19*(2010), was located in marker interval of NAU1187–NAU1255 on chr. 19, and explained 5.5% of the phenotypic variation. The favourable gene was from TM-1. In 2011, two significant QTL, *qLP-3*(2011) and *qLP-5/19*(2011), together with one suggestive QTL, *qLP-19*(2011), were detected. They were located on chr. 3, chr. 19 and chr. 5/chr. 19, respectively and explained from 8.6 to 28.2% of the phenotypic variation. All the favourable genes were from Baimian1. Noticeably, *qLP-3*(2011) was also detected in the same marker interval on chr. 3 in 2010.

Two significant lint percentages of M-QTL were detected by ICIM (table 3; figure 2), and their phenotypic variation explained by the additive effect was 16.70% and 0.83%, respectively. On the other hand, their phenotypic variation explained by the dominant effect was 10.70% and 40.00%, respectively. Simultaneously, these two QTL were also detected by CIM, and the marker intervals (DPL0095–NAU3839 and NAU1187–NAU1255) and favourable gene sources were in agreement with the CIM results. By ICIM, the interaction between two M-QTL and environment was also detected. Phenotypic variation explained by the additive \times environment interaction was 1.25% and 0.70%, respectively. Phenotypic variation explained by the dominant \times environment interaction was 1.62% and 13.39%, respectively.

E-QTL and E-QTL \times environment interaction for lint percentage

A total of 11 pairs of E-QTL and E-QTL \times environment interactions were detected (table 4). For E-QTL, genetic variance caused by the additive \times additive epistasis ranging from 0.028 to 0.718, caused by the additive \times dominant epistasis ranging from 0.042 to 1.929, caused by the dominant \times additive epistasis ranging from 0.032 to 3.164, and caused

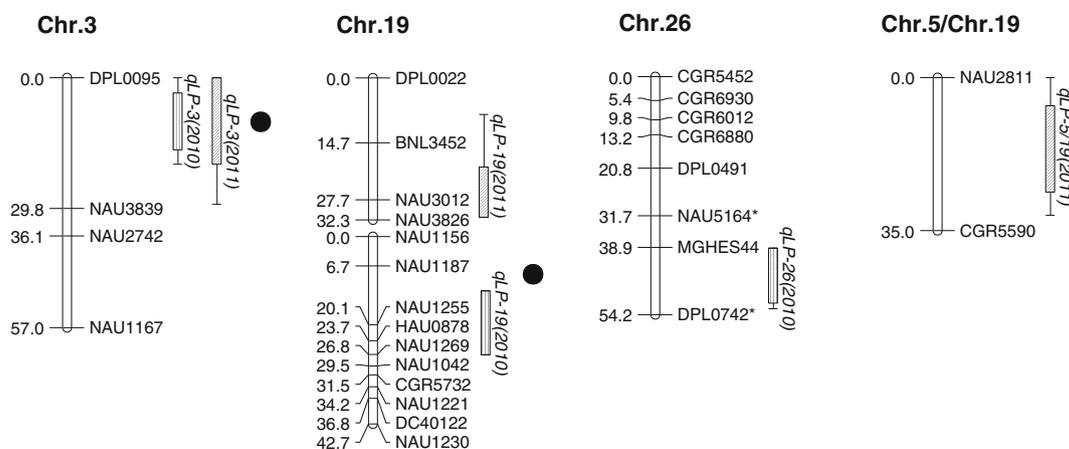


Figure 2. Location of lint percentage M-QTL in two years. Bars and whiskers indicate 1-LOD and 2-LOD QTL likelihood intervals by using CIM, respectively. ● Indicates location of M-QTL by using ICIM. *Means distorted segregation marker/locus.

Table 2. M-QTL for lint percentage detected by CIM in two years.

M-QTL	Chr.	Position (cM)	Flanking marker	LOD	Permutation threshold	A	D	R ² (%)	Direction
<i>qLP-3(2010)</i>	3	9.9	DPL0095–NAU3839	5.29*	2.37	1.49	1.51	29.6	Baimian1
<i>qLP-19(2010)</i>	19	18.1	NAU1187–NAU1255	2.13	2.37	−0.18	−1.09	5.5	TM-1
<i>qLP-26(2010)</i>	26	44.9	MGHES44–DPL0742	2.40*	2.37	1.15	0.96	11.6	Baimian1
<i>qLP-3(2011)</i>	3	8.2	DPL0095–NAU3839	2.76*	2.45	0.74	1.18	13.2	Baimian1
<i>qLP-5/19(2011)</i>	5/9	17	NAU2811–CGR5590	3.35*	2.45	0.94	−1.81	28.2	Baimian1
<i>qLP-19(2011)</i>	19	26.8	BNL3452–NAU3012	2.01	2.45	0.80	0.94	8.6	Baimian1

*LOD score is higher than the threshold calculated by permutation test. A, additive effect; D, dominant effect; R²(%), phenotypic variation explained; Direction means the parent provide favourable gene of lint percentage.

Table 3. M-QTL and M-QTL × environment interaction for lint percentage detected by ICIM.

Chr.	Position (cM)	Flanking marker	LOD (A)	LOD (AE)	R ² (A)	R ² (D)	R ² (AE)	R ² (DE)
3	4	DPL0095–NAU3839	3.74	1.45	16.70	10.70	1.25	1.62
19	7	NAU1187–NAU1255	2.66	0.70	0.83	40.00	0.70	13.39

Phenotypic variation explained by A, additive effect; D, dominant effect; AE, additive × environment interaction; DE, dominant × environment interaction.

by the dominant × dominant epistasis ranging from 0.008 to 1.757.

For the E-QTL × environment interaction, genetic variance caused by the interaction between additive × additive epistasis and environment ranging from 0.000 to 0.071, caused by the interaction between additive × dominant epistasis and environment ranging from 0.000 to 0.204, caused by the interaction between dominant × additive epistasis and environment ranging from 0.001 to 0.274, and caused by the interaction between dominant × dominant epistasis and environment ranging from 0.000 to 0.535. The above results suggested that genetic variance was more influenced by gene epistasis and less influenced by the interaction between epistasis and environment.

Discussion

Common QTL for potential breeding application

At present, only a minority of identified QTL in cotton have been successfully used for MAS (Guo *et al.* 2005; Wang *et al.* 2007), and the majority of QTL have not been applied in the breeding practice. It is required to explore the common QTL, which can always be detected in different generations, populations and environments (years or locations). These common QTL have high stability and can be used for MAS of target characters. Sun *et al.* (2012) located the QTL for cotton fibre quality characters, and reported that two QTL for fibre quality could be expressed in three generations and four environments in a stable way. These common QTL could be

Table 4. E-QTL and E-QTL × environment interaction for lint percentage detected by ICIM.

Chr.	Loci (i)		Loci (j)		V(AA)	V(AD)	V(DA)	V(DD)	V(AAE)	V(ADE)	V(DAE)	V(DDE)
	Flanking markers	Chr.	Flanking markers	Chr.								
20	GH428-CGR6484	15	NAU6584-NAU2741	15	0.209	0.820	0.307	1.380	0.010	0.131	0.016	0.095
12/26	CGR6012-CGR6880	18	NAU4105-DPL0864	18	0.365	0.042	1.297	0.019	0.023	0.118	0.129	0.000
19	NAU1187-NAU1255	5/19	NAU2811-CGR5590	5/19	0.310	1.929	0.032	0.625	0.004	0.000	0.274	0.001
19	NAU1187-NAU1255	11/21	CGR5578-NAU1366	11/21	0.361	1.670	0.790	0.051	0.035	0.005	0.001	0.535
3	DPL0095-NAU3839	23	NAU3052-TMB0382	23	0.718	0.379	0.601	1.189	0.007	0.204	0.027	0.000
14	SHIN1339-NAU4024	23	DPL0884-BNL3031	23	0.492	0.123	1.316	1.757	0.059	0.061	0.019	0.057
14	CGR5534-NAU5104	22	NAU2026-CGR6410	22	0.028	1.027	0.541	1.195	0.001	0.071	0.060	0.047
14	CGR5534-NAU5104	23	DPL0884-BNL3031	23	0.179	0.493	1.654	0.008	0.010	0.002	0.092	0.038
22	NAU5046-DPL0489	9	DPL0218-CGR6806	9	0.182	1.216	0.302	1.184	0.000	0.198	0.016	0.003
5/19	NAU2811-CGR5590	18	NAU4105-DPL0864	18	0.436	0.124	1.494	0.276	0.001	0.001	0.012	0.003
9	DPL0218-CGR6806	LG2	MUCS400-MGHES70	LG2	0.255	0.568	3.164	0.047	0.071	0.147	0.099	0.002

Genetic variance caused by the AA, additive × additive epistasis; AD, additive × dominant epistasis; DD, dominant × dominant epistasis; AAE the interaction between additive × additive epistasis and environment; ADE, the interaction between additive × dominant epistasis and environment; DAE, the interaction between dominant × additive epistasis and environment; DDE, the interaction between dominant × dominant epistasis and environment, respectively.

used for MAS of cotton fibre quality. For cotton lint percentage, Shen *et al.* (2007) reported one QTL *qLP-D6-1* could be identified and mapped in the same interval in four environments, but showed minor genetic effects. Liu *et al.* (2011) found 14 QTL for lint percentage observed in at least two environments in both or either one of the populations, RIL and IF₂. In this study, six M-QTL for lint percentage were detected in two years by CIM, and they were located on chr. 3, chr. 19, chr. 26 and chr. 5/chr. 19. Of these, the significant M-QTL, *qLP-3(2010)* and *qLP-3(2011)* were detected in both years, and the marker intervals and their favourable gene sources were consistent. These common QTL can be used for MAS of lint percentage. In addition, compared to previous studies, the obtained QTL for lint percentage in this study, *qLP-3(2010)/qLP-3(2011)* and *qLP-26(2010)*, were located on the same chromosomes derived from the mapping population constructed by Shen *et al.* (2007), Wu *et al.* (2009) and An *et al.* (2010). Due to lack of common markers, it has not yet been proved whether they belong to common QTL. Here, it has to be emphasized that lint index would give the breeder a far better assurance of superiority than the percentage could ever afford in some cases (Kearney 1912). Therefore, the QTL research on lint index should also be strengthened in future studies.

Necessity of detecting QTL using different mapping procedures

In recent years, along with the establishment and improvement of QTL location method and software, more and more QTL mapping procedures have been employed. Accurately located QTL can be used for MAS and map-based cloning; however, false positive QTL can mislead the application of location information. The QTL which can be simultaneously detected by different mapping procedures have high reliability (Su *et al.* 2010). Detection of QTL by some mapping procedures in rice, wheat and soybean have been reported (Liu *et al.* 2012; Ren *et al.* 2012; Xing *et al.* 2012). In cotton, Jia *et al.* (2011) located five M-QTL for boll weight and lint percentage with stable expression in several environments by two mapping procedures, CIM and MCIM. It provided an important reference for using molecular markers to breed cotton variety with high boll weight and lint percentage. Li *et al.* (2012) identified M-QTL, each one for node of first fruiting branch and its height by two mapping procedures. They suggested that these two QTL could be used for MAS of early maturity in cotton. This study detected six QTL for lint percentage by CIM and two QTL for lint percentage by ICIM. Although the M-QTL were rarely detected by ICIM, these two QTL were simultaneously detected by CIM. Marker intervals and their favourable gene sources were consistent with the CIM results. Therefore, they have high reliability and can be used for MAS of lint percentage. Particularly, the QTL located on chr. 3 was also detected by CIM. Therefore, this QTL can preferentially be considered for MAS of lint percentage.

Genetic basis of lint percentage

It has been proved that the genes regulating cotton yield characters exhibit additive–dominant effect (Godoy and Palomo 1999), interactive effect of additive–dominant and environment (Han and Liu 2002), epistasis effect and interactive effect of epistasis and environment (Li *et al.* 2000). In the field of modern genetics, the genetic theory of major gene together with polygene intends to study gene at individual level, and it also proved that genes regulating cotton yield exhibited additive, dominant and epistasis effects (Li *et al.* 2009b). Based on the molecular marker technology, QTL analysis will entirely and comprehensively analyse the quantitative characteristics. There are more studies on M-QTL for cotton lint percentage and very few studies on epistasis, whereas the studies on the interaction between QTL and environment are rarely reported. An *et al.* (2010) analysed the interactive effects of two-locus epistasis for lint percentage by using fibre and fuzz mutants. Results suggested that two marker loci significantly correlated with lint percentage, BNL1231-193 on chr. 11 and BNL3482-138 on chr. 26, exhibited epistatic interaction which explained 38.8% of the phenotypic variation. Zhang *et al.* (2009) detected two E-QTL for lint percentage located between marker interval NAU2173–NAU2272 on chr. 14 and marker interval TMG10–CM067 on chr. 25, and between marker interval TMG10–CM067 on chr. 25 and marker interval TMB0377–NAU1004 on LG10, respectively. They explained 4.9% and 14.68% of the phenotypic variation, respectively. In this study, the two M-QTL for lint percentage explained 27.40% (16.70% + 10.70%) and 40.83% (0.83% + 40.00%) of the phenotypic variation, respectively, and their interactive effects with environment explained 2.87% (1.25% + 1.62%) and 14.09% (0.70% + 13.39%) of the phenotypic variation, respectively. In addition, we also detected 11 epistatic QTL and their interaction with environment. Genetic variance induced by epistasis was more than that induced by the interaction between epistasis and environment. Results of our study provided important information for genuinely analysing genetic basis of lint percentage. Certainly, limited by molecular marker number and QTL analysis software, some micro-effect QTL have not been detected yet, and the genetic rule of quantitative characters has not been totally explained yet at the molecular level. Therefore, it is required to combine the classic quantitative genetics with modern molecular quantitative genetics, and continuously and genuinely illuminate genetic rules of quantitative characters in future studies.

Candidate markers influencing fibre development

Previous studies have suggested that there was a certain correlation between lint percentage and cotton fibre initiation and development (Xu *et al.* 1995; Li *et al.* 2009a). Abdurakhmonov *et al.* (2007) identified 17 SSR markers significantly correlated with lint percentage. Three EST-SSRs,

MGHES-31, MGHES-46 and MGHES-16, exhibited the similarities of nucleotide sequence with 6–10 dpa fibre EST sequences of *G. hirsutum* and *G. arboreum* nucleotide sequence. Consequently, they deduced that these EST-SSRs might be the ‘candidate’ loci contributing to cotton fibre development. In this study, two reliable M-QTL for lint percentage were detected between DPL0095–NAU3839 and NAU1187–NAU1255. In the four markers, DPL0095 was the genomic SSR, and all the other three markers were EST-SSRs. The marker NAU3839 was from *G. raimondii* at the stage of –3 to 3-dpa tissue floral. In CMD, sequence homology display of NAU3839 was a hypothetical protein, MtrDRAFT_AC146567g1v1. We compared this protein with NCBI by using BLASTp, and found that this protein function was not definite. Whether it associates with cotton fibre development needs to be further studied. Both NAU1187 and NAU1255 were from *G. arboreum*, 7–10 dpa fibre cDNA library (GenBank accession numbers BG444230 and BF271636). In CMD, their marker source sequence homology descriptions were E6-2 and E6-4, respectively. E6 was one of the earliest superior expression gene extracted from cotton fibre (John and Crow 1992). Therefore, we believe that NAU1187 and NAU1255 could be the candidate markers influencing fibre development, and they could provide functional genomics information in understanding cotton fibre development.

Acknowledgements

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