African Journal of Biotechnology Vol. 8 (2), pp. 167-175, 19 January, 2009
Available online at http://www.academicjournals.org/AJB
ISSN 1684–5315 © 2009 Academic Journals

Full Length Research Paper

Bayesian mapping QTL for fruit and growth phenological traits in *Lablab purpureus* (L.) Sweet

Juan Yuan, Runqing Yang and Tianlong Wu*

School of Agriculture and Biology, Shanghai Jiaotong University, Shanghai 200240, P. R. China.

Accepted 17 December, 2008

In order to map the QTLs for the agronomic traits in *Lablab purpureus* (L.) Sweet, we designed an F_2 population derived from lablab accession ('Meidou2012' and 'Nanhui23') for construction of genetic linkage map and repeatedly measured three fruit traits (pod length, pod diameter and pod fresh thickness) and three growth phenological traits (flowering time, podding time and harvest maturity period) in F_2 population and F_3 lines from two planting years. Bayesian model selection was used to analyze main effect QTL, epistatic QTL and QTL by environment interactions (QEs) as well. 41 main effect QTLs (19 for fruit traits and 22 for growth phenological traits) were identified on 11 linkage groups with small phenotypic variances. Thirty nine pairs epistatic QTLs (19 for fruit traits and 20 for growth phenological traits) were also found which accounted for large proportions of phenotypic variations. And 11 QEs (8 for fruit traits and 3 for growth phenological traits) were detected only in F_3 lines. Six QTLs and one QEs were found to be pleiotropy. Pod length, pod diameter, pod fresh thickness, flowering time, podding time and harvest maturity period each had stable QTLs, which could be useful for breeding purposes and scientific reasoning.

Key words: Lablab, fruit traits, growth phenological traits, Bayesian model selection, interacting QTL, QEs.

INTRODUCTION

Lablab purpureus (L.) Sweet (2n = 22) is an ancient legume species distributed in the tropics and the subtropics of the world. It is believed to be a native of India, south-east Asia or Africa (Shivashankar et al., 1993). Lablab has many outstanding qualities: It can produce a large bulk of green materials with high protein concentration (Kay, 1979). Lablab provides food, fodder and soil protection during prolonged dry periods when many other plant species have become desiccated (Schaafthausen, 1963; Wood, 1983; Ibewiro et al., 2000). It is an important ley legume for animal fodder and green manure in mixed crop-livestock in tropical and subtropical Australia. Notably, in south and south-east Asia, lablab is currently used as a pulse crop, and the immature pods serve as a vegetable (Duke and Kretschmer, 1981). Moreover, both the grain and the immature pods of lablab are a lesser human food source in Africa (Smartt, 1985).

Lablab performs obvious difference among species in fruit and growth phenological traits. pod length, pod diameter and pod fresh thickness in lablab are main traits for marketing quality and yield of immature pods and growth phenological traits can influence yield. These traits are typically controlled by a multitude of genes, often collectively referred to as QTL. Genetic mapping of the QTLs for fruit traits and growth phenological traits have been reported in other leguminous crops. Blair et al. (2006) found 3 QTLs for pods per plant, 7 QTLs for days to flowering and 2 QTLs for days to maturity across the two locations in common bean. Zhang et al. (2004) identified 8 QTLs for days to flowering distributed over three linkage groups, 11 QTLs for days to maturity distributed on five linkage groups and 6 QTLs were detected for pods per node mapped on four groups in soybean. Using four different populations of soybean, Wang et al. (2004) identified four QTLs for days to maturity on linkage groups C2, L, M and O, respectively. The QTLs for fruit traits were also reported in other crop as in legume (Chaim et al., 2001; Ku et al., 2000).

Mapping QTL not only explains genetic architecture for these traits, but also is useful for marker-assisted selection (MAS) of them. For mapping quantitative trait loci,

---

*Corresponding author. E-mail: tianlongwu-26@163.com. Tel: +86-21-64789018. Fax: +86-21-58024666.

there are many statistical methods available, such as least square, maximum likelihood and Bayesian method. Bayesian model selection within the framework of Bayesian mapping has became powerful and efficient because of ability to quickly analyze the interacting QTL models with many effects in experimental crosses (Yi et al., 2005). In order to map the QTLs for the agronomic traits in lablab, we have designed an F_2 population derived from a lablab accession ('Meidou2012') and another accession ('Nanhui23') for construction of genetic linkage map and repeatedly measured six agronomic traits in F_2 population and F_3 lines from two planting years. The objective of this study is to simultaneously identify the main effect and epistatic QTLs for fruit traits and growth phenological traits in three generations and to evaluate the QTL by environment interactions in F_3 lines with Bayesian model selection.

MATERIALS AND METHODS

Plant material

The two annual accessions of lablab, 'Meidou2012' and 'Nanhui23' were chosen as parent to develop the F_2 population and F_3 lines. The parents are distinct from each other in fruit traits and growth phenological traits. The F_1 hybrids from the cross of the parent selfed to produce 136 F_2 individuals which selfed to obtain F_3 lines. The F_2 population and F_3 lines were used for QTL mapping.

Linkage map

With the F_2 population, the genetic linkage map was constructed, which included 131 loci (122 RAPD and 9 nine morphological loci) on the fourteen linkage groups covering 1302.4 cM of genome of lablab with the average marker distance of 9.9 cM (Figure 1).

Field evaluation and character examination

The two parental accessions, F_2 population and F_3 lines were grown at the experimental farm of Shanghai Jiaotong University, Shanghai, China. The F_2 population was planted in spring, 2006 and F_3 lines were in autumn, 2006 and spring, 2007, respectively. The temperature and photoperiod of the two planting years were obviously different. F_3 lines were arranged in a randomized complete block design with two replications per year. Each replication had six plants, and individual plants were spaced 60 cm apart in rows placed 100 cm apart. Measurements were taken on six traits including pod length (*PL*), pod diameter (*PD*), pod fresh thickness (*PFT*), flowering time (*FT*), podding time (*PT*) and harvest maturity period (*HMP*). All measurements were taken on F_2 and F_3 individuals and averaged within each F_3 lines. The average length and diameter of three pods on the first inflorescence were denoted as pod length (cm; pod apex to the pedicel attachment) and pod diameter (mm, at maximum width), respectively, at beginning of physiological maturity. The pod fresh thickness (mm, distance between two exocarps) was measured by the average fresh thickness of three pods on the first inflorescence when seeds in these pods arose. The flowering time was defined as the number of days from sowing to appearance of the first flower. The podding time represented the number of days from sowing to appearance of the first pod and the harvest maturity period represented the number of days from sowing to appearance of the first ripe pod.

Bayesian mapping QTL

In F_2 population, assume that there are *q* quantitative trait loci responsible for a trait of interest, the genetic mapping model with interacting QTL for single trait can be then constructed on the basis of the Cockerham's genetic model (Kao and Zeng, 2002), denoted by:

$$y_i = \mu + \sum_{j=1}^{q} (z_{ij} a_j + w_{ij} d_j) + \sum_{j=1}^{q-1} \sum_{k=j+1}^{q} [x_1(aa)_{jk} + x_2(ad)_{jk} + x_3(da)_{jk} + x_4(dd)_{jk}] + e_i \tag{1}$$

In F_3 lines, taking phenotype mean of F_3 line as phenotype values of corresponding F_2 individual, we used these F_2 individuals' genotyped makers with known genetic map to locate the QTL for agronomic traits and analyze the QEs. The genetic mapping model with epistatic QTL for single trait and QEs can be then constructed on the basis of the Cockerham's genetic model (Kao and Zeng, 2002), denoted by:

$$y_{ik} = \mu + \sum_{j=1}^{q} (z_{ij} a_j + w_{ij} d_j) + x_e e_k + \sum_{j=1}^{q} [x_{ae}(ae)_{jk} + x_{de}(ae)_{jk}] + + \sum_{j=1}^{q-1} \sum_{j'=j+1}^{q} [x_1(aa)_{jj'} + x_2(ad)_{jj'} + x_3(da)_{jj'} + x_4(dd)_{jj'}] + \varepsilon_i \tag{2}$$

where μ is the population mean; α_j and d_j for $j = 1, 2\ldots, q$ are the additive and dominant effects of the jth QTL, respectively; Variable z and w are the genotype indicators corresponding to the additive and dominant effects; *aa*, *ad*, *da* and *dd* are the epistatic effects between the two QTLs due to additive×additive, additive×dominant, dominant×additive, and dominant×dominant interactions, respectively. e_k is the kth environmental effect and x_e is related indicator variable; $x_{ae} = zx_e$, $x_{de} = wx_e$ and $x_i = zw$ for i=1, 2, 3, 4; and ε_i is the residual error.

The linkage map-wide interacting QTL for all traits on model (1) or (2) has been analyzed by adopting Bayesian model selection (Yi et al., 2005) implemented in the package R/qtlbim (www.qtlbim.org) released by Yandell et al. (2007). Because the homogenous and heterogenous genotype cannot be distinguished for RAPD markers, they were treated as missing and the multipoint method (Jiang and Zeng, 1997) has therefore been used to infer the probabilities of the three genotypes for each QTL. According to the results by the composite interval mapping, we set the expected number of main effect QTL at 3 and number of epistatic QTL at 4, so that upper bound of the number of QTL is $7 + 3\sqrt{7} = 15$. The initial values of other parameters are assigned to be defaults. For all analyses, the MCMC algorithm ran for 1.2×10^5 iterations after discarding the first 1000 iterations as burn-in. To reduce serial correlation in the stored samples, the chain was trimmed by keeping one observation in every 40 iterations, yielding 3000 samples for posterior analysis.

In posterior analysis, Bayes factors of main effects and epistasis per locus or pair of loci are individually calculated and compared with a BF threshold of 3, or 2ln(BF) = 2.1, to claim the presence of QTL (Kass and Raftery, 1995).

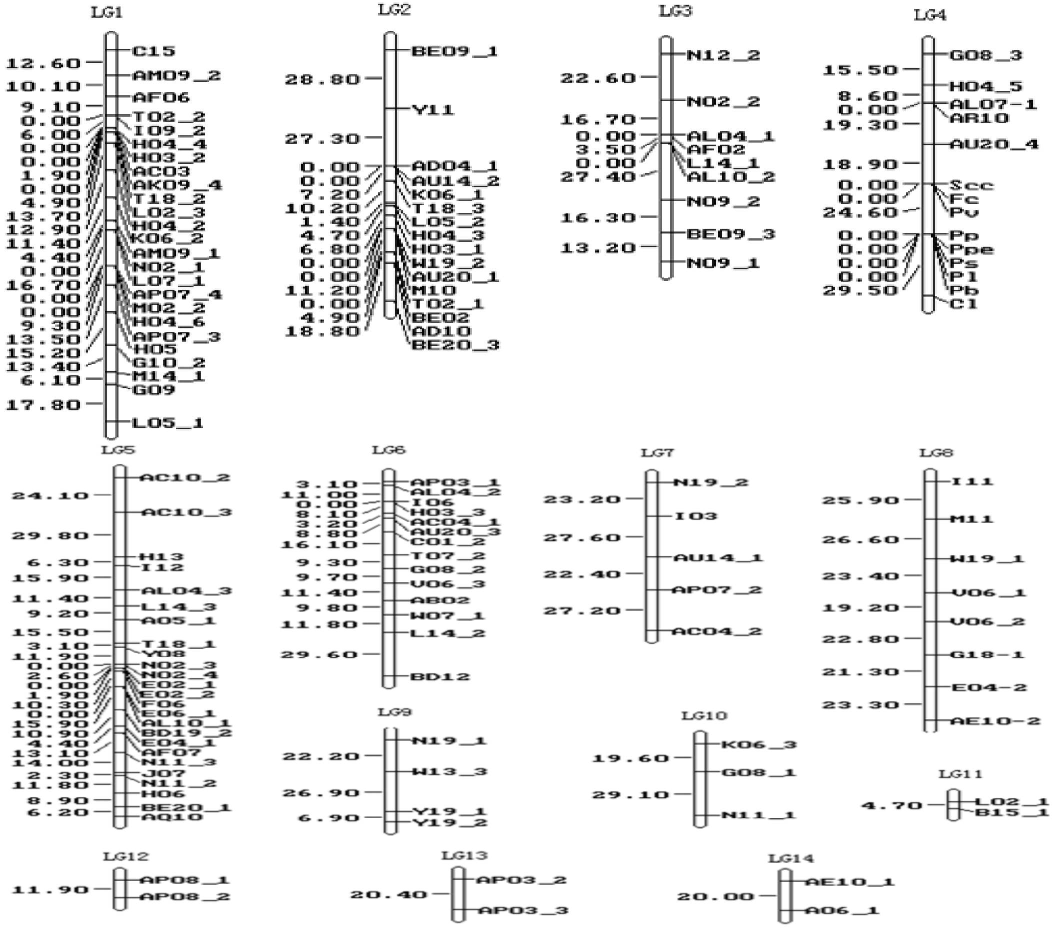

Figure 1. Genetic linkage map of lablab based on an F_2 population derived from a cross of 'Meidou2012' × 'Nanhui 23'. Linkage groups are ordered based on the number of loci and the genetic length. Numbers to the left of the vertical bars indicate the distances in cM, and locus names are listed to the right of the bars. RAPD loci are named after their respective primers followed by a series number indicating the fragment scored.

RESULTS

Phenotypic variation and trait correlations

Table 1 lists the mean phenotypic value, range of value, standard deviation, coefficient of variation, skewness and kurtosis for three fruit traits and three growth phenological traits in F_2 population and F_3 lines. For each quantitative trait, significant ($P<0.05$) differences were found between 'Meidou2012'and 'Nanhui23'. All values of quantitative traits in 'Nanhui23' were larger than those in 'Meidou2012' except pod length and pod diameter. The mean value of each trait was consistent with the standard deviation. All traits showed a broad (Kurtosis) distribution and low skewness values. Altogether, all the investigated traits were suitable for QTL mapping in F_2 population and F_3 lines.

The correlations between six agronomic traits in F2 population and F3 lines are calculated (Table 2). As expected, most of correlations are significant at 5.0% significant level, except for pod diameter and three growth phenological traits, pod fresh thickness and three growth phenological traits. The character and significance of these relationships were consistent in population and planting year without pod diameter and growth phenological traits, pod fresh thickness and three growth phenological traits. The positive correlation between flowering time and potting time was the highest.

Identification of QTLs and evaluation of QEs for each trait

The analyzed results including additive effects, dominance effects, epistatic effects, 2lnBF, HPD (the region of highest posterior density) and heritability (the proportion of phenotypic variance explained by QTL) in three generations and QEs in F_3 lines for detected QTLs, which are summarized in Tables 3, 4 and 5, respectively.

Table 1. Descriptive statistics of fruit traits and growth phenological traits in parents, F_2 population observed in 2006 (upper) and F_3 lines observed in 2006 (middle) and 2007 (lower).

Trait[a]	Parents		Population					
	Miedou2012	Nanhui23	Range	Mean	SD	CV	Kurtosis	Skewness
PL	10.8	5.9	6.0-11.2	8.7	1.01	11.6	-0.04	-0.06
	10.5	8.2	5.8-10.4	8.0	0.89	11.3	-0.04	0.44
	10.9	6.2	6.2-11.1	8.8	0.96	10.9	-0.29	0.19
PD	3.5	2.4	2.0-3.6	2.8	0.31	11.0	0.03	0.14
	3.7	2.7	2.3-4.8	3.3	0.40	12.3	1.10	0.34
	3.4	2.6	2.0-3.8	2.9	0.31	10.6	0.66	0.04
PFT	0.39	0.55	0.30-0.71	0.42	0.13	15.3	0.93	1.03
	0.38	0.51	0.35-0.68	0.48	0.06	12.1	0.80	0.48
	0.39	0.54	0.29-0.79	0.43	0.08	17.9	1.04	0.93
FT	46.2	58.6	42.0-72.0	57.9	5.20	9.0	0.75	-0.10
	46.8	58.9	36.5-77.8	48.9	7.86	16.1	1.29	1.16
	73.3	85.0	65.9-87.8	76.0	4.48	5.9	-0.52	0.02
PT	50.0	62.0	46.0-75.0	60.9	5.23	8.6	0.83	0.13
	51.0	62.5	40.0-80.0	52.4	7.76	14.8	1.50	1.33
	77.0	88.3	70.0-91.8	79.7	4.62	5.8	-0.61	0.03
HMP	73.5	85.0	68.0-97.0	81.3	5.09	6.3	0.46	0.31
	73.2	84.8	66.0-97.0	76.4	6.16	8.1	0.90	1.17
	99.1	110.5	92.9-111.4	101.7	3.53	3.5	-0.18	-0.14

[a] Trait abbreviations: pod length (PL), pod diameter (PD), pod fresh thickness (PFT), flowering time (FT), podding time (PT) and harvest maturity period (HMP).

Table 2. Phenotypic correlation coefficients between mean values of fruit traits and growth phenological traits in F_2 population in observed 2006 (upper) and F_3 lines observed in 2006 (middle) and 2007 (lower).

Trait[a]	*PL*	*PD*	*PFT*	*FT*	*PT*	*HMP*
PD	0.43** 0.38** 0.42**	1				
PFT	-0.26** -0.18* -0.06	0.24** -0.22* -0.25**	1			
FT	0.27** 0.12 0.26**	0.16 -0.13 0.10	-0.01 0.16 -0.14	1		
PT	0.23** 0.12 0.27**	0.11 -0.13 0.12	0.01 0.17 -0.17	0.96** 0.99** 0.99**	1	
HMP	0.19* 0.15 0.25**	0.16 -0.07 0.17	0.04 0.16 -0.06	0.91** 0.96** 0.83**	0. 90** 0.96** 0.83**	1

[a] Trait abbreviations: pod length (*PL*), pod diameter (*PD*), pod fresh thickness (*PFT*), flowering time (*FT*), podding time (*PT*) and harvest maturity period (*HMP*). * and ** Absolute values above 0.174 are significant at $P = 0.05$, and absolute values above 0.228 are significant at $P = 0.01$.

Table 3. Summary of statistics for main effect QTLs obtained with Bayesian model selection on fruit traits and growth phenological traits in the F_2 population and F_3 lines.

Trait[a]	generation	LG	HPD[b]	Additive[c]	Dominance	Heritability (%)[d]	2lnBF
PL	F_2	5	[88.5, 163.4]	-0.54	-0.14	4.7	4.79
PL	F_2	6	[60.7, 78.6]	0.34	0.00	8.3	6.52
PL	F_2	8	[27.9, 137.2]	0.00	-0.68	4.3	3.35
PL	F_3	1	[110.7, 122.0]	0.01	0.17	0.2	2.71
PL	F_3	4	[101.7,103.8]	0.35	0.06	6.4	6.03
PL	F_3	5	[92.1, 137.8]	-0.24	-0.31	4.0	7.34
PL	F_3	6	[0.0, 76.1]	0.18	-0.06	4.3	7.10
PL	F_3	7	[98.3, 100.4]	-0.16	-0.01	3.0	6.45
PL	F_3	9	[48.7 56.0]	0.10	0.00	2.4	2.17
PL	F_3	13	[0.0, 2.0]	-0.13	-0.02	2.7	3.39
PD	F_2	3	[13.4, 77.3]	0.19	-0.04	3.8	4.78
PD	F_2	4	[62.3,105.2]	0.10	-0.02	2.8	3.72
PD	F_2	5	[68.7, 228.5]	-0.18	-0.18	4.7	3.16
PD	F_3	4	[84.9, 105.9]	0.27	0.00	4.1	7.46
PD	F_3	10	[0.0, 6.5]	0.00	-0.18	2.1	3.90
PFT	F_2	5	[15.0, 229.5]	0.44	-0.13	7.2	2.48
PFT	F_3	3	[39.3, 63.9]	-0.17	-0.11	1.9	5.17
PFT	F_3	5	[34.7, 60.2]	0.07	0.00	1.1	6.02
PFT	F_3	9	[47.0, 56.0]	0.02	-0.28	6.3	8.95
FT	F_2	1	[123.4, 140.7]	-0.25	0.05	8.3	5.29
FT	F_2	2	[57.1, 91.5]	0.26	-0.10	5.1	5.93
FT	F_2	4	[64.4, 84.9]	0.00	-0.22	9.6	5.81
FT	F_2	5	[114.3, 122.9]	0.14	-1.28	5.5	2.70
FT	F_2	6	[34.2,131.9]	-0.16	0.25	4.6	2.86
FT	F_3	3	[42.8, 76.3]	0.01	0.79	0.9	2.83
FT	F_3	4	[62.3, 86.9]	0.01	-0.38	0.7	4.43
FT	F_3	6	[36.2, 80.7]	0.03	-0.09	0.4	6.36
PT	F_2	1	[123.4, 138.7]	-0.20	-0.14	7.0	4.89
PT	F_2	2	[60.2, 92.5]	0.36	-0.32	7.6	7.68
PT	F_2	3	[47.9, 68.2]	-0.08	-0.43	4.2	3.62
PT	F_2	4	[64.4, 84.9]	0.00	-0.91	6.4	5.22
PT	F_2	6	[60.7, 131.9]	-0.12	-0.17	4.9	3.68
PT	F_3	3	[42.8, 74.3]	0.01	0.68	0.6	2.92
PT	F_3	4	[62.3, 93.2]	0.00	-0.36	0.8	4.26
PT	F_3	6	[36.2, 80.7]	0.02	-0.08	0.3	5.48
HMP	F_2	1	[11.6, 145.8]	-0.28	-0.12	9.2	5.91
HMP	F_2	2	[55.1, 86.4]	0.30	0.02	9.2	5.33
HMP	F_2	4	[65.4, 86.9]	0.00	-0.67	4.1	3.90
HMP	F_2	6	[34.2, 131.9]	-0.16	-0.16	5.3	3.18
HMP	F_3	4	[62.3, 86.9]	0.00	-0.32	0.6	4.99
HMP	F_3	6	[36.2, 80.7]	0.01	0.00	0.2	6.35

[a] Trait abbreviations: pod length (*PL*), pod diameter (*PD*), pod fresh thickness (*PFT*), flowering time (*FT*), podding time (*PT*) and harvest maturity period (*HMP*). [b] HPD is the region of highest posterior density. [c] Additive positive value indicates the 'Meidou2012' genotype having a positive effect on the trait. [d] heritability is the proportion of phenotypic variance explained by main-effect QTL.

Pod length

Mapping analysis for pod length revealed 3 and 7 main effect QTLs distributed on eight linkage groups on the basis of data from 2006 in F_2 population and combined data from 2006 and 2007 in F_3 lines (Table 3). Each main effect QTL explained from 0.2 to 8.3% of the phenotypic variance. The additive effects of the QTLs ranged from -0.54 to 0.35. Four QTLs were negative additive, suggesting that alleles from 'Nanhui23' increased the pod length at four QTLs on linkage groups 5, 7 and 13.

Three pairs in F_2 population and ten pairs in F_3 lines performed epistatic interactions also were detected (Table 4). The effects of additive by additive interaction between QTLs were smaller, while the effects of dominant by dominant interaction between QTLs were larger. Seven each of effects of additive by dominant interactions and dominant by additive interactions were larger, suggesting that these interactions strongly impacted pod length. Eight interactions each explained more than 10.0% of the phenotypic variance. The result of QEs in F_3 lines was present in Table 5. Four QTLs on linkage groups 1, 4, 5 and 6 displayed significant interactions with years. The QEs explained a total of 2.59% of the phenotypic variance.

Pod diameter

Three main effects QTLs in F_2 population and two in F_3 lines were identified to be significant and each QTL accounted for between 2.1 and 4.7 % of the phenotypic

Table 4. Summary of statistics for espistatic effects obtained with Bayesian model selection on fruit traits and growth phenological traits in the F_2 population and F_3 lines.

Trait[a]	Generation	Position	Heritability[b] (%)	*aa*[c]	*dd*[d]	*ad*[e]	*da*[f]	2lnBF
PL	F_2	LG5[88.5, 163.4]×LG6[60.7, 78.6]	30.2	0.91	2.93	1.74	1.32	8.26
PL	F_2	LG5[88.5, 163.4]×LG8[27.9, 137.2]	27.4	0.54	2.67	2.34	1.09	7.69
PL	F_2	LG6[60.7, 78.6]×LG8 [27.9, 137.2]	19.6	0.65	8.08	0.87	1.26	8.12
PL	F_3	LG1[110.7, 122.0]×LG6[0.0, 76.1]	11.1	0.37	1.56	0.80	0.92	7.52
PL	F_3	LG1[110.7, 122.0]×LG9[48.7 56.0]	12.1	0.14	1.04	0.52	0.58	5.90
PL	F_3	LG4[101.7,103.8]×LG7[98.3, 100.4]	11.8	0.63	3.43	1.16	1.02	12.13
PL	F_3	LG5[92.1, 137.8]×LG6[0.0, 76.1]	13.5	0.83	4.08	2.85	1.92	12.72
PL	F_3	LG5[92.1, 137.8]×LG13[0.0, 2.0]	6.6	0.14	1.00	1.67	0.61	12.18
PL	F_3	LG6[0.0, 76.1]×LG7[98.3, 100.4]	13.3	0.32	0.76	0.17	0.67	11.02
PL	F_3	LG6[0.0, 76.1]×LG9[48.7 56.0]	6.6	0.09	1.24	0.40	0.31	8.97
PL	F_3	LG6[0.0, 76.1]×LG13[0.0, 2.0]	3.9	0.00	0.71	0.42	0.48	6.72
PL	F_3	LG7[98.3, 100.4]×LG13[0.0, 2.0]	3.2	0.21	0.52	0.00	0.11	5.61
PL	F_3	LG9[48.7 56.0]×LG13[0.0, 2.0]	3.7	0.00	0.61	-	-	6.69
PD	F_2	LG3[13.4, 77.3]×LG4[62.3,105.2]	18.5	0.38	1.88	0.73	0.47	7.69
PD	F_2	LG4[62.3,105.2]×LG5[68.7, 228.5]	12.8	0.66	1.99	1.16	1.25	8.15
PD	F_3	LG4[84.9, 105.9]×LG10[0.0, 6.5]	5.1	0.01	0.62	0.18	0.07	5.33
PFT	F_3	LG3[39.3, 63.9]×LG5[34.7, 60.2]	12.7	0.25	3.43	0.74	0.98	6.84
PFT	F_3	LG3[39.3, 63.9]×LG9[47.0, 56.0]	17.6	0.54	1.47	0.36	0.82	13.19
PFT	F_3	LG5[34.7, 60.2]×LG9[47.0, 56.0]	12.0	0.37	1.43	0.60	0.74	10.83
FT	F_2	LG1[123.4, 140.7]×LG2[57.1, 91.5]	32.1	0.31	2.44	1.38	0.94	8.96
FT	F_2	LG1[123.4, 140.7]×LG4[64.4, 84.9]	23.4	0.51	5.68	1.60	1.09	8.19
FT	F_2	LG2[57.1, 91.5]×LG4[64.4, 84.9]	22.3	0.35	4.20	0.98	0.48	9.74
FT	F_2	LG2[57.1, 91.5]×LG5[114.3, 122.9]	20.7	0.66	2.60	1.03	0.94	7.69
FT	F_3	LG3[42.8, 76.3]×LG6[36.2, 80.7]	3.8	0.34	0.96	0.35	0.64	6.66
FT	F_3	LG4[62.3, 86.9]×LG6[36.2, 80.7]	4.6	0.06	1.11	0.26	0.37	7.39
PT	F_2	LG1[123.4, 138.7]×LG2[60.2, 92.5]	29.9	0.25	2.28	0.85	1.62	9.37
PT	F_2	LG1[123.4, 138.7]×LG3[47.9, 68.2]	24.5	0.38	4.39	0.56	1.20	8.61
PT	F_2	LG1[123.4, 138.7]×LG4[64.4, 84.9]	35.8	0.15	5.34	2.09	0.97	9.06
PT	F_2	LG1[123.4, 138.7]×LG6[60.7, 131.9]	20.7	0.62	3.62	1.71	1.49	8.07
PT	F_2	LG2[60.2, 92.5]×LG3[47.9, 68.2]	13.4	0.09	2.01	0.56	1.21	8.53
PT	F_2	LG2[60.2, 92.5]×LG4[64.4, 84.9]	19.9	0.53	4.07	1.07	0.63	9.24
PT	F_2	LG3[47.9, 68.2]×LG4[64.4, 84.9]	32.1	0.31	3.22	1.72	0.79	8.26
PT	F_2	LG3[47.9, 68.2]×LG6[60.7, 131.9]	20.7	0.49	2.93	1.69	1.14	7.69
PT	F_3	LG4[62.3, 93.2]×LG6[36.2, 80.7]	9.0	0.11	1.11	0.43	0.29	7.56
HMP	F_2	LG1[11.6, 145.8]×LG2[55.1, 86.4]	31.2	0.25	1.53	1.18	1.19	8.14
HMP	F_2	LG1[11.6, 145.8]×LG4[65.4, 86.9]	21.1	0.44	3.99	1.59	1.41	9.43
HMP	F_2	LG1[11.6, 145.8]×LG6[34.2, 131.9]	19.1	0.50	4.64	1.49	1.57	8.65
HMP	F_2	LG2[55.1, 86.4]×LG6[34.2, 131.9]	25.2	0.65	4.69	1.79	1.10	8.26
HMP	F_2	LG4[65.4, 86.9]×LG6[34.2, 131.9]	26.6	0.99	4.04	1.47	1.46	7.63

[a] Trait abbreviations: pod length (*PL*), pod diameter (*PD*), pod fresh thickness (*PFT*), flowering time (*FT*), podding time (*PT*) and harvest maturity period (*HMP*).

[b] Heritability is the proportion of phenotypic variance explained by QTL epistatic effect [c] *aa* is the effect of additive by additive interaction between QTLs.

[d] *dd* is the effect of dominant by dominant interaction between QTLs.

[e] *ad* is the effect of additive by dominant interaction between QTLs.

[f] *da* is the effect of dominant by additive interaction between QTLs.

variance. The ‘Meidou2012’ alleles contributed to pod diameter at four QTLs except the QTL on linkage group 5. Among these identified QTLs, three pairs of epistatic interaction were detected in three generations, and had two significant effects on pod diameter with relative high *aa, dd, ad* and *da* in F_2 population. The two epistatic

Table 5. Summary of statistics for QEs obtained with Bayesion model selection on fruit traits and growth phenological traits in the F_3 lines.

Trait[a]	LG	Heritability[b] (%)	QEs[c]	(QTL) position	2lnBF
PL	1	0.85	0.11	117.5	2.79
PL	4	0.72	0.00	101.7	2.64
PL	5	0.24	-0.05	94.4	2.42
PL	6	0.78	-0.01	71.6	3.36
PD	4	0.14	0.02	99.5	3.12
PFT	5	2.05	0.18	58.1	3.19
PFT	8	0.38	0.08	149.8	2.65
PFT	9	0.08	0.00	56.0	2.83
FT	6	0.55	-0.06	42.3	3.80
PT	6	0.36	0.22	42.3	2.85
HMP	6	0.43	0.42	44.3	4.97

[a] Trait abbreviations: pod length (*PL*), pod diameter (*PD*), pod fresh thickness (*PFT*), flowering time (*FT*), podding time (*PT*) and harvest maturity period (*HMP*).
[b] Heritability is the proportion of phenotypic variance explained by QTL-environment interaction. [c] QEs is the QTL by environment interactions.

interaction in F_2 population explained more than 10.0% of the phenotypic variance, suggesting that these interactions strongly impacted pod diameter. One QEs interaction in F_3 lines was detected and accounted for 0.14% of the phenotypic variance.

Pod fresh thickness

In three generations, analysis of the data resulted in the detecting of 1 and 3 main effect QTLs for pod fresh thickness on linkage group 5, 3, 5 and 9, respectively (Table 3), which explained from 1.1 to 7.2% of the phenotypic variance. All QTLs were positive additive except one QTL on linkage group 3, suggesting that alleles from 'Meidou2012' increased the pod fresh thickness at three QTLs on linkage group 3 and 9. All of the dominant effects for the trait were either negative or zero, indicating that the 'Nanhui23' alleles perform dominant.

For pod fresh thickness, 3 pairs of epistatic interactions were only identified in F_3 lines (Table 4), which contributed to relative high proportion of the phenotypic variance (12.0-17.6%). The effects of *ad* and *da* on linkage groups 3 and 5 were higher, suggesting that the interaction between two QTLs on linkage groups 3 and 5 strongly impacted pod fresh thickness. Three QEs in F_3 lines were also detected on linkage groups 5, 8 and 9, which together accounted for 2.51% of the phenotypic variance.

Flowering time

The analysis resolved five main effect QTLs for flowering time with higher phenotypic variance (4.6-9.6%) in F_2 population and three QTLs with relatively low phenotypic variance (0.4-0.7%) in F_3 lines. The 'Meidou2012' alleles at five QTLs increased the trait, while the 'Nanhui23'alleles from remaining two QTLs on linkage groups 1 and 6 in F_2 population contributed to the trait. Four and two pairs of epistatic interactions for flowering time were found in three generations. Four pairs of epistatic interactions explained 20.7-32.1% of the phenotypic variance in F_2 population, while two pairs of epistatic interactions were detected with relative small phenotypic variance (3.8-4.6%) in F_3 lines. Among the six pairs, only three interactions in F_2 population strongly impacted flowering time with relative high epistasis of *ad* and *da*. One QEs interaction in F_3 lines was mapped on linkage group 6 which explained 0.55% of the phenotypic variance.

Podding time

Similarly, five and three main effects of QTLs were detected for podding time in three generations (Table 3). The proportion of phenotypic variance explained by a single QTL ranged from 4.2 to 7.6% in F_2 population and 0.3 to 0.8% in F_3 lines. The 'Meidou2012' alleles contributed to increased podding time at three QTLs while the 'Nanhui23'alleles at another three QTLs increased the trait. For the epistatic interactions between QTLs for podding time, eight pairs of epistatic interactions in F_2 population were found with relatively high phenotypic variance (13.4 -35.8%), *ad*, and *da*, implying that all the interactions, especially one on linkage groups 1 and 4, highly affected podding time; on the other hand, only one pair in F_3 lines was detected with relative low phenotypic variance, *ad* and *da*, indicating that the interaction might not significantly influence the podding time. In addition, a QE interaction in F_3 lines was found on linkage group 6, which accounted for 0.36% of the phenotypic variance.

Harvest maturity period

For harvest maturity period, four and two main effects of QTLs were found in three generations. These QTLs explained from 4.1 to 9.2% and 0.2 to 0.6% of the phenotypic variance, respectively, of which the two on linkage groups 1 and 2 both accounted for the highest phenotypic variance (9.2%). The phenotype values of harvest maturity period were increased by ‘Meidou2012’ alleles at two QTLs, however, the values increased by ‘Nanhui23’ at another two QTLs. As to epistatic interactions for the trait, five interactions only in F_2 population were detected with high *ad* and *da* values, and the phenotype variance of interactions ranged from 19.1 to 31.2%, showing that these interactions greatly influenced harvest maturity period. In addition, one QEs was mapped and explained 0.43% of the phenotypic variation.

The co-localization of agronomic traits

Some QTLs for same trait were identified in the same regions in three generations (Table 3). We detected nine QTLs (two for podding time on linkage group 3 and 4; both two for flowering time and harvest maturity period on linkage group 4 and 6; both one for pod length and harvest maturity period on linkage group 5 and one for pod diameter on linkage group 4), which in F_2 population explained the phenotypic variances for the same trait were higher than that in F_3 lines.

On the other hand, from data in F_2 population and combined data from two planting years in F_3 lines, some main effects of QTLs for different traits were detected in the same regions on linkage groups (Table 4). We found that one QTL within the HPD [47.0 56.0] on linkage group 9 was responsible for pod length and pod fresh thickness in F_3 lines, the two QTLs within the HPD [123.4 140.7] on linkage group 1 and the HPD [57.1 91.5] on linkage group 2 in F_2 population and one QTL within the HPD [42.8 76.3] on linkage group 3 in F_3 lines for flowering time and podding time, one QTL within the HPD [34.2 131.9] on linkage group 6 in F_2 population for flowering time and harvest maturity period, the one QTL within the HPD [62.3 86.9] on linkage group 4 in three generations for all of three growth phenological traits, showing the pleiotropy. Furthermore, the QEs for flowering time and podding time was discovered at the 42.3 cM on linkage group 6 and the effect for harvest maturity period was at the near position (44.3 cM) on the same linkage group.

DISCUSSION

Many QTLs mapping for fruit traits and growth phenological traits have been reported in other leguminous crops (Blair et al., 2006; Chaim et al., 2001; Ku et al., 2000), and the QEs for crops were reported less. Jiang et al. (2004) detected environment interactions for 18 of the main effect QTLs and 14 pairs of the epistatic interactions for rice. With associated data of four environments, QEs contributed less to fiber length in cotton when compared with additive and epistatic effects (Wang et al., 2006). Xing et al. (2002) used a mixed linear model approach to detect QEs, and thirteen QTLs with main effects showed QEs, no QEs was detected for the QTLs involved in epistatic interactions. However, aforementio-ned QTLs had been analyzed by using either least require or maximum likehood method. We had employed Beyesian model selection to dissect the genetic basis of six agronomic traits on the linkage map of lablab constructed by self (J. Yuan, Shanghai Jiaotong University, China, personal communication) in three generations and identified a total of 41 main effect QTLs (19 for fruit traits and 22 for growth phenological traits), 39 epistatic effects involving 19 for fruit traits and 20 for growth phenological traits and 11 QEs (8 for fruit traits and 3 for growth phenological traits) (Tables 3, 4 and 5).

The phenotypic variance of these main effect QTLs ranged from 0.2 to 9.2%. The significant QTLs explained larger than 5.0% on four QTLs for fruit traits and ten for growth phenological traits, which could underlie the genetics basis of fruit traits and growth phenological traits in lablab. Moreover, the phenotypic variances explained by epistasis for all traits were larger than those explained by main effect QTLs. Thus, the genetic architecture of these traits appeared to be complex. The situation also existed in other plant (Jiang et al., 2004). As to the QEs, the variances for fruit traits were less than those of main effect QTLs, while the variances explained by QEs for growth phenological traits were equal to those of main effect QTLs, suggesting that growth phenological traits are more sensitive to environmental changes.

Related traits tend to be co-localized within the genome. In many cases, the co-localization of the QTLs for related traits could be probably the result of pleiotropic effects of a single gene or be caused by the traits which are dependent on each other (Frary and Doganlar, 2003). Some recent studies on the molecular mechanism of pleiotropy have suggested that pleiotropy is largely due to consequence of a single molecular function of the gene product, rather than the involvement of the same gene product in several molecular processes (Kumar et al., 2007; He and Zhang, 2006). In this study, we have found six main effect QTLs on linkage group 1, 2, 3, 4, 6 and 9 and one QEs on linkage group 6 performed pleiotropy through separately analyzing six traits with Bayesian model selection, adequately showing the pleiotropy of gene exist in wide range. Nevertheless, it is necessary to develop Bayesian model selection for multiple traits for powerfully and precisely mapping the kind of QTLs.

The same QTLs detected across more than one environment can be thought as stable QTLs. In three generations, flowering time, podding time and harvest maturity period each had two stable QTLs while pod length, pod diameter and pod fresh thickness each had only one stable QTL, which could be useful for breeding purposes and scientific reasoning. In addition, these stable QTLs in F_2 population explained phenotypic variances for the same traits were higher than those in F_3 lines except for pod diameter trait, suggesting that fruit traits and growth phenological traits were subject to environmental impact.

To our knowledge this is the first time that QTLs for six agronomic traits including three fruit traits and three growth phenological traits have been mapped in lablab. Our study will increase the genetic markers' information associated with agronomic traits and aid the process of identifying causative genes in lablab. Beneficial genetic variance knowledge can be incorporated in breeding programs to enhance genetic improvement through molecular assisted selection in lablab.

ACKNOWLEDGEMENTS

We are grateful to Prof. Lihuang Zhu for his guidance during the experiment. We are also very thankful to Prof. Runqing Yang for his help in providing the mapping method and correcting the computing program.

REFERENCES

Blair MW, Iriarte G, Beebe S (2006). QTL analysis of yield traits in an advanced backcross population derived from a cultivated Andean×wild common bean (*Phaseolus vulgaris* L.) cross. Theor. Appl. Genet. 112: 1149-1163.

Chaim AB, Paran I, Grube RC, Jahn M, Vanwijk R, Peleman J (2001). QTL mapping of fruit-related traits in pepper (Capsicum annuum). Theor. Appl. Genet. 102: 1016-1028.

Duke JA, Kretschmer AE (1981). *Lablab purpureus* (L.) Sweet Handbook of legume of world economic importance. Plenum Press, New York and London, pp. 102-106.

Frary A, Doganlar M (2003). QTL analysis of morphological traits in eggplant and implications for conservation of gene function during evolution of solanaceous species. Thero. Appl. Genet. 107: 359-370.

He XL, Zhang JZ (2006). Toward a molecular understanding of pleiotropy. Genetics 173: 1885-1891.

Ibewiro B, Sanginga N, Vanlauwe B, Merckx R (2000). Evaluation of symbiotic dinitrogen inputs of herbaceous legumes into tropical cover-crop systems. Biol. Fertil. Soils 32: 234-242.

Jiang C, Zeng ZB (1997). Mapping quantitative trait loci with dominant and missing markers in various crosses from two inbred lines. Genetica, 101: 47-58.

Jiang GH, He YQ, Xu CG, Li XH, Zhang Q (2004). The genetic basis of stay-green in rice analyzed in a population of doubled haploid lines derived from an *indica by japonica* cross. Theor. Appl. Genet. 108: 688-698.

Kao CH, Zeng ZB (2002). Modeling Epistasis of Quantitative Trait Loci Using Cockerham's Model. Genet. 160: 1243-1261.

Kass RE, Raftery AE (1995). Bayes factors. J. Am. Stat. Assoc. 90: 773-795.

Kay DE (1979). Crop and product digest No 3 food legumes. London: Tropical Products Institute, p. 120.

Ku HM, Grandillo S, Tanksley SD (2000). fs8.1, a major QTL, sets the pattern of tomato carpel shape well before anthesis. Theor. Appl. Genet. 101: 873-878.

Kumar N, Kulwal PL, Balyan HS, Gupta PK (2007). QTL mapping for yield and yield contributing traits in two mapping populations of bread wheat. Mol. Breed. 19: 163-177.

Schaafthausen RV (1963). Dolichos lablab or Hyacinth bean: Itsuses for feed, food and soil improvement. Econ. Bot. 17: 146-153.

Shivashankar G, Kulkarni RS, Shashidhar HE, Mahishi DM (1993). Improvement of field bean. Veg. Crop 5: 277-286.

Smartt J (1985). Evolution of grain legumes Ⅱ Old and new world pulse of lesser economic importance. Exp. Agric. 21: 1-18.

Wang BH, Guo WZ, Zhu XF, Wu YT, Huang NT, Zhang TZ (2006). QTL mapping of fiber quality in an elite hybrid derived-RIL population of upland cotton. Euphytica 152: 367-378.

Wang D, Graef GL, Procopiuk AM, Diers BW (2004). Identification of putative QTL that underlie yield in interspecific soybean backcross populations. Theor. Appl. Genet. 108: 458-467.

Wood IM (1983). Lablab (*Lablab purpureus*) for grain and forage production in the Old Irrigation Area. Aust. J. Exp. Agric. Anim. Hush. 23: 162-171.

Xing YZ, Tan YF, Hua JP, Sun XL, Xu CG, Zhang Q (2002). Characterization of the main effects, epistatic effects and their environmental interactions of QTLs on the genetic basis of yield traits in rice. Theor. Appl. Genet. 1065: 248-257.

Yandell BS, Mehta T, Banerjee S, Shriner D, Venkataraman R, Moon JY, Neely WW, Wu H, Smith RV, Yi N (2007). R/qtlbim: QTL with Bayesian interval mapping in experimental crosses. Bioinformatics 23: 641-634.

Yi N, Yandell BS, Churchill GA, Allison DB, Eisen EJ, Pomp D (2005). Bayesian model selection for genome-wide epistatic quantitative trait loci analysis. Genetics 170: 1333-1344.

Zhang WK, Wang YJ, Luo GZ, Zhang JS, He CY, Wu XL Gai JY, Chen SY (2004). QTL mapping of ten agronomic traits on the soybean (*Glycine max* L. Merr.) genetic map and their association with ESTmarkers. Theor. Appl. Genet. 108: 1131-113.