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Full Length Research Paper

Quantitative trait loci (QTL) mapping for inflorescence length traits in *Lablab purpureus* (L.) sweet

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Lablab purpureus **(L.) sweet is an ancient legume species whose immature pods serve as a vegetable in south and south-east Asia. The objective of this study is to identify quantitative trait loci (QTLs) associated with quantitative traits such as inflorescence length, peduncle length from branch to axil, peduncle length from axil to lowermost flowering node, rachis length, node number of inflorescence, rachis internode length, node order of the first inflorescence and node order of lowest inflorescence, which are key characters affecting the output of vegetable cultivars of lablab. A molecular linkage map was constructed using a F_2 population derived from the cross (Meidou2012 × Nanhui 23). The map covers 1302.4 cm with 131 loci (122 RAPD and nine morphological markers) and consist 14 linkage groups. In the F_2 population and derived F_3 families, a total of 46 QTLs explained from 8.1 to 55.0% of phenotypic variance of the traits. Of them, 16 QTLs were detectable in the same linkage regions among different generation/season combinations, and 10 QTL clusters were mapped. It suggests that, genes which control inflorescence growth were pleiotropic or coincident involving more than one trait. Thus, these QTLs may be tagged for marker assisted selection to improve yield of lablab.**

Key words: Inflorescence length, lablab, linkage map, quantitative trait loci (QTLs), random amplification of polymorphic DNA (RAPD).

INTRODUCTION

Lablab purpureus (L.) sweet (2n = 22) commonly known as lablab, hyacinth bean, Egyptian and Indian bean is an ancient legume species. It has been believed to be a native of India, south-east Asia or Africa, although latest results only support Africa as its origin (Maass et al., 2005).

In China, lablab serves as vegetable and medicinal herb. In recent years, the market demand for immature pod of lablab gradually has exceeded the supply. It is needed to improve the output of immature pod whose increase, however, has been confined by shattering and pod dropping. Through years of observation, we found that shattering and pod dropping are significantly associated with inflorescence length (*IL*) trait and its related traits. On average, the percentage of shattering and pod dropping on a long inflorescence is about 5%, but attained 15 to 20% on a short one (Yuan et al., unpublished). Lablab's inflorescence is an axillary, many-flowered raceme, with a peduncle 4 to 23 cm long and a rachis 2 to 24 cm long (Shivashankar et al., 1993). The inflorescence consists of peduncle length from branch to axil *(PBA)*, peduncle length from axil to lowermost flowering node *(PALFN)* and rachis length *(RL)*. However,

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Abbreviations: ***IL,*** Inflorescence length; ***PBA,*** peduncle length from branch to axil; ***PALFN,*** peduncle length from axil to lowermost flowering node; ***RL,*** rachis length; ***NNI,*** node number of inflorescence; ***RIL,*** rachis internode length; **RAPD,** random amplification of polymorphic DNA; **QTLs,** quantitative trait loci; **PCR,** polymerase chain reaction; ***Ps,*** purple stem; ***Ppe,*** petiole; ***Pn,*** nervure; ***Pb,*** bract; ***Pf,*** flower; ***D,*** dasyphyllous; ***Dgl,*** dark green leaf; ***Dgp,*** pod; ***Bm,*** black mottle on the seed testa; **SDL,** segregation distorting loci; ***NFI,*** node order of the first inflorescence; ***NLI,*** node order of lowest inflorescence.

despite highly variable inflorescence lengths in lablab (Shivashankar et al., 1993; Pengelly and Maass, 2001), the number of flowers at the same florescence node remains the same (Yuan et al., unpublished). Thus, with the development of flowers and pods on the short inflorescence of lablab, the large density of flowers or small early pods per unit area may cause heavy shattering and pod dropping. Inflorescence length-related traits also affect the output of a lablab crop. For example, node number of inflorescence *(NNI)* is crucial for the rachis internode length *(RIL)*, which influences the density of flowers or small early pods per unit area. Besides, the positions of the first and lowest inflorescences would also affect pod number and prematurity of each plant, accordingly indirectly influencing the output of immature pod in lablab.

Lablab is a crop where the inflorescence length trait and its related traits vary observably (Pengelly and Maass, 2001). Genetic analysis of important agronomic traits in lablab is only incipient (Chikkadevaiah et al., 1979) and genetic studies on lablab inflorescence have been reported less, though the first lablab molecular linkage map has been constructed by Konduri et al. (2000). However, genes that control inflorescence length have been analyzed in other legume crops. For example, in pea (*Pisum sativum*), three genes have been identified to control the inflorescence length type (JIC 2007), of which *dt* changes the peduncle length from axil to lowermost flower, while Pr and Pre influence inflorescence length. In soybean (*Glycine max*), a positive correlation has been observed between inflorescence length and flower number and also between inflorescence length and pod number (You and Ga, 1995), suggesting that inflorescence length trait was controlled by multigenes. Furthermore, You and Ga (1995) suggested that, inflorescence length in soybean was a quantitative character affected by ecological surroundings, growth condition and other environmental factors and that short inflorescence was less influenced by above factors than the long inflorescence. However, there are few systematic studies available on the quantitative nature of inflorescence length traits in legume crops so far.

The purpose of this study is to: (1) Construct a linkage map with universal random amplification of polymorphic DNA (RAPD) markers based on an F_2 population derived from two lablab accessions that are distinct from each other in inflorescence length; (2) use the map for tagging quantitative trait loci (QTLs) controlled inflorescence length trait, its component and related traits in the F_2 population and F_3 families.

MATERIALS AND METHODS

Plant material and traits evaluation

The annual lablab accessions, 'Meidou2012' and 'Nanhui23', originated from Hunan province and Shanghai in China, respectively, and were used as parents and the F_2 populations and F_3 families derived from the cross between the parents. They are distinct from each other in inflorescence length trait, its component and related traits. The 136 F_2 mapping individuals were obtained by allowing the self-pollination of the F_1hybrid. The F_3 families were developed from each F_2 by bud self-pollination for QTL analysis.

The parents, F_2 populations and F_3 families were grown in the greenhouse of experimental farm of Shanghai Jiaotong University and the experiment took place under the same soil conditions. The parents and F_2 population were planted during rainy season from March to July 2006. Measurements were taken on eight quantitative inflorescence traits and other nine qualitative traits were recorded. These traits were also evaluated in the parents and F_3 families both during sunny season from August to November 2006 and rainy season from March to July 2007 under the same developmental stage as in the parents and F_2 population. The experiment with parents and F_{3s} were arranged in a randomized complete block design with two replications. Each replication had six plants spaced 60 cm apart in rows placed 100 cm apart. All traits including eight quantitative and nine morphological traits were recorded for each individual in the F_2 population and F_3 families (Table 1). Traits were assessed as the mean of three measurements when all flowers on the first three inflorescences measured were in full flower.

Nine morphological traits were stem, petiole, nervure, leaf, bract and pod pigmentation, dasyphyllous, and flower and seed testa color. These traits were assessed when the individuals were in flowering period according to Tariqul (2004).

DNA extraction and RAPD procedure

DNA was extracted from freeze-dried leaves following the improved method described by Fang and Huang (1999). DNA amplification was carried out in 10 μl volume of a uniform reaction mixture containing 40 to 60 ng of template DNA, polymerase chain reaction (PCR) mix 1×, 1.6 mM $MgCl_2$, 200 nM of each primer, 200 μM of each dNTPs and 1.25 U Taq polymerase (Invitrogen) according to the following procedure: Denaturation at 94°C for 3 min, followed by 45 cycles of 15 s at 94°C, 30 s at 37°C and 50 s at 72°C and finally, 6 min at 72°C. All PCR products were separated on 1% agarose gel in 1×TBE with a cooling system for 30 min at 260 V. After electrophoresis, gels were soaked in 1.0 μg/ml ethidium bromide water solution for 30 min for fragment vizualisation. The primer sequences of publicly available RAPD markers were provided by the Operon technologies Inc.

Linkage mapping

All RAPD markers used were dominant. The segregation ratio of RAPD and nine morphological markers was tested with χ^2-test ($P \leq 0.01$) for goodness of fit to 3:1 segregation ratio. Linkage mapping was performed by Mapmaker 3.0 (Lander et al., 1987; Lincoln et al., 1992) with Kosambi function. Linkage map was determined with a minimum LOD score of 4.0 and a maximum distance of 30.0 cM. The marker orders were assigned with the 'compare', 'try' and 'ripple' commands.

QTL detection

QTL mapping was determined with QTLcartographer2.5 by composite interval mapping. 1000 permutations were done in order to determine significance of a QTL at the critical significance level of 0.05. The LOD score peaks were used to estimate the most likely positions of QTLs on the linkage map. The additive effect and phenotypic variance of individual QTLs were estimated. The amount of phenotypic variance explained was determined using the coefficient of determination (R^2). QTL nomenclature followed that of Villalta et al. (2007).

Table 1. Quantitative traits measured for the each individual plant in F_2 the population and F_3 families developed from two *L. purpureus* accessions.

Trait	Abbreviation	Unit	Description
Inflorescence length	*IL*	cm	Length from branch to the uppermost flowering node on inflorescence. Consists of PBA, PALFN, and RL
Peduncle length from branch to axil	*PBA*	cm	Distance between branch and axil on inflorescence
Peduncle length from axil to lowermost flowering node	*PALFN*	cm	Distance between axil and lowermost flowering node on inflorescence.
Rachis length	*RL*	cm	Rachis length from lowermost to uppermost flowering node order on inflorescence.
Node number of inflorescence	*NNI*	number	Number of flowering nodes on inflorescence.
Rachis internode length	*RIL*	cm	Mean distance between inflorescence nodes; ratio of RL to (NNI-1).
Node order of the first inflorescence	*NFI*	node order	Node order on main stem, where first inflorescence flowered.
Node order of lowest inflorescence	*NLI*	node order	Node order on the main stem, where lowest inflorescence flowered.

RESULTS

Phenotypic variation and trait correlations

The phenotypes of nine morphological traits of two parents were distinctly different (data not shown). The phenotypes of F_1 plants had the same characteristics as ‘Nanhui23’, namely, purple stem (*Ps*), petiole (*Ppe*), nervure (*Pn*), bract (*Pb*) and flower (*Pf*), dasyphyllous (*D*), dark green leaf (*Dgl*) and pod (*Dgp*) and black mottle on the seed testa (*Bm*). F_2 segregation of these traits showed a good fit to expected ratios (data not shown), suggesting that a dominant gene controls each of them. Therefore, tentative dominant genes for these traits as follow: *Ps*, *Ppe*, *Pn*, *Pb*, *Pf*, *D*, *Dgl*, *Dgp*, *Bm*. These genes could be incorporated with molecular markers into the linkage map of lablab.

Phenotypic means and their standard deviations, range of variation, skewness and kurtosis for the inflorescence length trait, its component and related traits are presented in Table 2. For each of these traits, significant (P ≤ 0.05) differences were found between ‘Meidou2012’ and ‘Nanhui23’. Means for all traits in the three cross generation/season combinations were higher than those in parents except RL in F_3/autumn and *NNI* in F_2 population. All traits showed a broad (kurtosis) distribution and low skewness values. Altogether, all the investigated traits were suitable for QTL mapping in the three combinations. As expected, all correlations were significant at 5% level and consistent in planting year except for node order of the first inflorescence (*NFI)* and other six quantitative traits, node order of lowest inflore-scence (*NLI)* and other six quantitative traits in F_2/spring and F_3/autumn (data not shown). The positive correlation between IL and RL was the highest.

Construction of the linkage map

97 RAPD primers selected out of the 696 screened primers could generate clear, reliable and reproducible polymorphisms in the mapping population. They produced 180 stable and repeatable polymorphic RAPD fragments. Finally, 122 RAPD fragments and nine morphological markers were used to construct the linkage map. The map contained fourteen linkage groups and spanned 1302.4 cm with a mean marker interval of 9.9 cm (Figure 1). In the map, nine tentative genes were located on linkage group 4. *Bm*, *Pf* and *Pn* were co-located at one locus while *Ps*, *Ppe*, *Dgl*, *Pb* and *Dgp* were mapped together at the other locus. *D* was located at one end of the linkage group. Among the total linked loci, 63 RAPD showed segregation distortion. More than half of the distorted loci were clustered in some regions on the linkage map, especially on linkage groups 3 and 5. Moreover, all the marker loci on the linkage groups from 8 to 14 were distorted (Figure1).

QTL mapping for inflorescence length trait and its component traits

QTLs found at the same location on linkage groups in two or three generation/season combi-

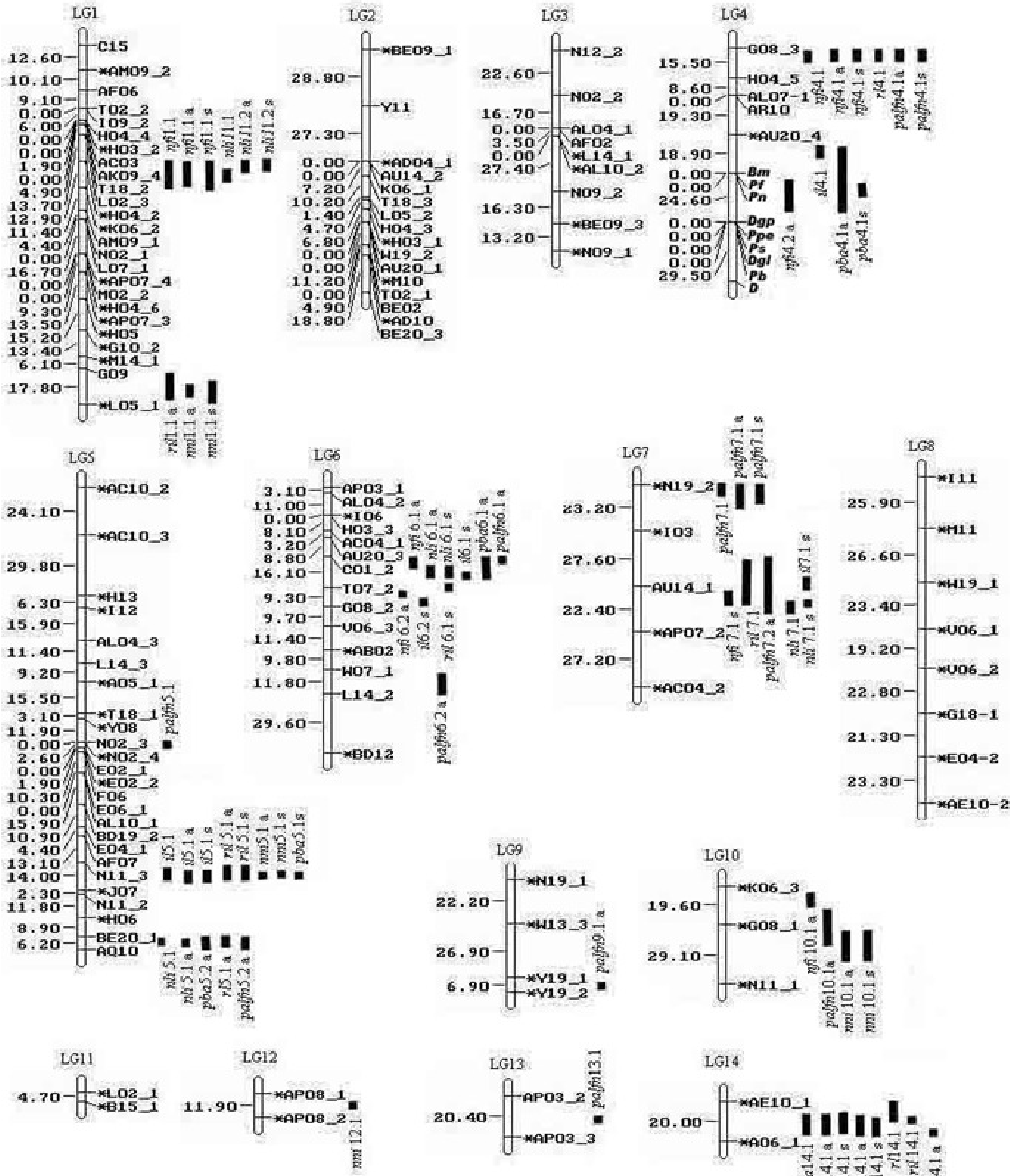

Figure 1. The linkage map and locations of QTLs associated with inflorescence length traits, its component and related traits in *L. purpureus*. Linkage groups are ordered based on the number of loci and the genetic length. Numbers to the left of the vertical bars indicate the distances in cM and locus 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. Loci showing segregation distortions are indicated with an asterix (*).QTLs are presented as bars to the right of the linkage groups with the length of the bar representing the interval of the markers. QTLs are designated by name on the right of the bars.

Table 2. Descriptive statistics for inflorescence length trait, its component traits and related traits in the parents, F_2, F_3/autumn and F_3/spring progenies.

Trait[a]	Generations	Mean(cm)	Range(cm)	SD	Skewness	Kurtosis	Meidou2012	Nanhui23	MP value [b]
IL	F2	26.4	2.4-60.2	11.4	0.1	-0.0	8.0	35.7	21.9
	F3 autumn	28.5	1.4-52.5	14.4	-0.6	-1.0	4.4	49.1	26.7
	F3 spring	23.5	3.0-39.5	10.4	-0.7	-0.9	8.6	32.7	20.7
PBA	F2	10.3	0.0-21.3	4.5	-0.2	-0.2	4.2	16.0	10.1
	F3 autumn	9.0	0.2-31.5	4.7	0.3	1.1	1.8	13.2	7.5
	F3 spring	8.0	0.7-13.3	3.5	-0.5	-1.0	3.7	10.0	6.9
PALFN	F2	7.3	0.8-14.0	2.9	-0.1	-0.4	2.4	8.4	5.4
	F3 autumn	6.5	0.4-12.7	3.1	-0.4	-0.8	1.2	8.3	4.7
	F3 spring	6.0	0.9-9.3	2.4	-0.8	-0.7	2.8	8.9	5.9
RL	F2	8.8	0.6-32.2	5.7	0.9	1.1	1.4	11.3	6.3
	F3 autumn	13.0	0.8-30.6	7.9	-0.2	-1.1	1.3	27.5	14.4
	F3 spring	9.6	0.9-19.1	4.8	-0.5	-0.9	2.1	13.8	8.0
NNI	F2	6.5	3.0-13.7	1.8	0.9	1.1	5.3	7.8	6.6
	F3 autumn	9.7	2.8-16.3	3.7	-0.3	-1.3	4.0	15.0	9.5
	F3 spring	7.4	0.4-10.8	2.1	-0.8	0.1	5.0	9.7	7.4
RIL	F2	1.5	0.3-3.9	0.7	0.2	-0.3	0.3	1.4	0.8
	F3 autumn	1.3	0.3-2.8	0.5	-0.5	-0.5	0.4	2.0	1.2
	F3 spring	1.3	0.4-1.9	0.5	-0.7	-1.1	0.5	1.6	1.1
NFI	F2	7.4	3.0-14.0	2.2	0.4	0.0	5.7	8.7	7.2
	F3 autumn	6.5	3.3-13.7	2.0	1.0	1.0	5.0	6.3	5.7
	F3 spring	5.0	3.6-6.7	0.6	0.1	-0.3	4.3	5.3	4.8
NLI	F2	5.8	2.0-14.0	1.9	0.9	1.0	5.3	5.0	5.2
	F3 autumn	5.3	3.0-10.5	1.7	0.9	1.0	4.3	4.0	4.2
	F3 spring	4.4	2.7-6.0	0.7	-0.2	-0.4	3.0	4.3	3.7

[a] Trait abbreviations; inflorescence length (*IL*); peduncle length from branch to axillae (*PBA*); peduncle length from axil to lowermost flowering node (*PALFN*); rachis length (*RL*); node number of inflorescence (*NNI*); rachis internode length (*RIL*); node order of the first inflorescence (*NFI*) ; node order of lowest inflorescence (*NLI*). [b] MP value is the mid-parent mean.

nations were considered asingle QTL and a total of 46 significant QTLs were mapped for eight traits in three combinations as presented in Figure 1.

Mapping analysis for inflorescence length trait and its component traits revealed 24 QTLs distributed on eight linkage groups in three combinations (Table 3). Eleven QTLs were found for *PALFN*, five each for *IL* and *PBA* and three for *RL*. The proportion of phenotypic variance explained by a single QTL ranged from 9.6 to 48.7% in which 22 QTLs each explained >10% of phenotypic variance. The most significant QTLs were *il*4.1 in F_2 population, *pba*4.1, *palfn*7.1 and *rl*5.1 in F_3/autumn that explained 48.7, 38.4, 23.6 and 25.3% of phenotypic variance, respectively.

All detected QTLs for *IL* had positive additive effects of the allele from the parent 'Meidou2012'. Meanwhile, some QTLs for each component trait of inflorescence length trait were associated with the 'Meidou2012' allele, while the remaining QTLs were associated with the 'Nanhui23' allele, that is, the QTLs on linkage group 4 and 5 increased the length of *PBA*, while the QTLs on linkage group 6 and 14 reduced the trait. As expected, there were overlaps between the QTLs for *IL* and *PBA* on linkage group 4 and 5, between *PALFN* and *RL* on linkage group 4 and among the QTLs for *PBA*, *PALFN* and *RL* on linkage group 5 and 14 (Figure 1). These co-located QTLs for inflorescence length trait and its component traits exhibited the same directions of additive effects.

QTL mapping for inflorescence length-related traits

For inflorescence length-related traits, 22 QTLs were identified on eight linkage groups, including four QTLs for *NI*, five for *RIL,* seven for *NFI* and six for *NLI* in three combinations. The QTLs for these traits explained from 8.2 to 55% of phenotypic variance, including 17 QTLs explained >10% of phenotypic variance. The QTL, *nni*10.1 demonstrated the most significant effect in the study, explaining 55% of phenotypic variance (Table 3).

The estimation of the additive effect of lablab alleles showed that, they increased *NFI* at 6 loci, *RIL* and *NLI* at 4 loci, respectively, *NNI* at 2 loci and reduced the corresponding trait at the remaining QTLs. In addition, there were overlaps between these traits. It was notable

Table 3. Location of QTLs for inflorescence length trait, its component traits and related traits in the F_2 and F_3 progenies developed from two *L. purpureus* accessions.

Trait[a]	QTL[b]	Generation	LG[c]	Nearest marker	LOD	R^2 (%)	Additive[d]
IL	*il*4.1	F_2	4	AU20-4-Scc	3.83	48.7	0.53
	il5.1	F_2	5	N11-3-J07	2.87	13.8	7.84
		F_3/A	5	N11-3-J07	3.44	13.0	4.35
		F_3/S	5	N11-3-J07	3.38	15.6	4.25
	*il*6.1	F_3/S	6	C01-2-T07-2	2.52	12.7	0.47
	*il*6.2	F_3/S	6	T07-2-G08-2	2.67	16.6	1.53
	*il*7.1	F_3/S	7	AU14-1-AP07-2	2.52	13.2	2.86
PBA	*pba*4.1	F_3/A	4	AU20-4-Pp	4.84	38.4	1.45
		F_3/S	4	Pv-Pp	2.61	21.1	1.38
	*pba*5.1	F_3/S	5	N11-3-J07	2.83	10.8	4.79
	*pba*5.2	F_3/A	5	BE20-1-AQ10	3.44	18.2	6.54
	*pba*6.1	F_3/A	6	C01-2-T07-2	3.07	15.9	-1.36
	*pba*14.1	F_2	14	AE10-1-A06-1	2.92	18.0	-2.46
		F_3/A	14	AE10-1-A06-1	3.84	26.5	-2.29
		F_3/S	14	AE10-1-A06-1	2.85	26.6	-2.68
PALFN	*palfn*4.1	F_3/A	4	G08-3-H04-5	4.84	10.7	5.02
		F_3/S	4	G08-3-H04-5	2.60	9. 6	1.38
	*palfn*5.1	F_2	5	N02-4-E02-1	2.93	10.1	0.06
	*palfn*5.2	F_3/A	5	BE20-1-AQ10	3.44	15.7	7.41
	*palfn*6.1	F_3/A	6	C01-2-T07-2	2.56	11.2	0.35
	*palfn*6.2	F_3/A	6	W07-1-L14-2	3.48	19.2	-0.05
	*palfn*7.1	F_2	7	N19-2-I03	2.74	12.4	5.0
		F_3/A	7	N19-2-I03	4.28	23.6	8.84
		F_3/S	7	N19-2-I03	3.23	13.4	4.74
	*palfn*7.2	F_3/A	7	I03-AP07-2	3.72	20.7	1.64
	*palfn*9.1	F_3/A	9	Y19-1-Y19-2	2.63	21.3	3.69
	*palfn*10.1	F_3/A	10	K06-3-N11-1	2.77	13.4	0.78
	*palfn*13.1	F_2	13	AP03-2-AP03-3	2.53	14.6	6.10
	*palfn*14.1	F_3/A	14	AE10-1-A06-1	3.03	18.6	-4.28
		F_3/S	14	AE10-1-A06-1	2.76	12.7	-2.04
RL	*rl*4.1	F_2	4	G08-3-H04-5	2.68	9.7	3.36
	*rl*5.1	F_3/A	5	BE20-1-AQ10	3.95	25.3	12.28
	*rl*14.1	F_2	14	AE10-1-A06-1	2.88	18.6	-3.77
NNI	*nni*1.1	F_3/A	1	G09-L05-1	2.60	24.8	7.63
		F_3/S	1	G09-L05-1	3.20	19.7	5.66
	*nni*5.1	F_3/A	5	N11-3-J07	2.88	11.8	6.54
		F_3/S	5	N11-3-J07	2.60	11.7	3.85
	*nni*10.1	F_3/A	10	G08-1-N11-1	4.16	55.0	-2.25
		F_3/S	10	G08-1-N11-1	3.48	31.8	-1.19
	*nni*12.1	F_2	12	AP08-1-AP08-2	2.57	18.0	-2.94
RIL	*ril*1.1	F_3/A	1	G09-L05-1	4.13	17.2	7.58
	*ril*5.1	F_3/A	5	N11-3-J07	3.74	16.8	7.71
		F_3/S	5	N11-3-J07	3.20	15.3	4.42
	*ril*6.1	F_3/S	6	C01-2-T07-2	2.70	11.1	1.05
	*ril*7.1	F_2	7	I03-AP07-2	3.10	12.4	2.78
	*ril*14.1	F_2	14	AE10-1-A06-1	2.51	15. 2	-3.08
NFI	*nfi*1.1	F_2	1	H04-2-K06-2	5.94	20.6	6.58
		F_3/A	1	H04-2-K06-2	3.86	12.1	5.93
		F_3/S	1	H04-2-K06-2	5.43	19.2	5.73
	*nfi*4.1	F_2	4	G08-3-H04-5	3.75	13.23	4.43

Table 3. Contd.

		F_3/A	4	G08-3-H04-5	2.61	8.2	3.96
		F_3/S	4	Pv-Pp	3.51	13.3	3.69
	*nfi*4.2	F_3/A	4	G08-3-H04-5	2.62	9.1	4.88
	*nfi*6.1	F_3/A	6	C01-2-T07-2	2.64	8.4	-0.64
	*nfi*6.2	F_3/A	6	T07-2-G08-2	2.62	8.1	6.92
	*nfi*7.1	F_3/S	7	AU14-1-AP07-2	2.68	16.6	0.74
	*nfi*10.1	F_3/A	10	K06-3-G08-1	2.77	18.9	5.12
NLI	*nli*1.1	F_2	1	K06-2-AM09-1	2.56	8.1	3.85
	nli1.2	F3/A	1	H04-2-K06-2	2.73	9.4	5.09
		F3/S	1	H04-2-K06-2	2.73	9.12	3.95
	nli5.1	F2	5	BE20-1-AQ10	2.74	15.7	6.64
		F3/A	5	BE20-1-AQ10	3.16	24. 5	9.91
	nli6.1	F3/A	6	C01-2-T07-2	2.66	15.4	1.06
		F3/S	6	C01-2-T07-2	2.81	14.2	-0.86
	nli7.1	F2	7	AU14-1-AP07-2	2.72	16.0	5.32
		F3/S	7	AU14-1-AP07-2	2.53	15.8	2.78
	nli14.1	F3/A	14	AE10-1-A06-1	2.76	16.0	-1.44

The note of Table 3 has been omitted,I add them as follow:
"a Trait abbreviations: inflorescence length (IL), peduncle length from branch to axillae (PBA), peduncle length from axil to lowermost flowering node (PALFN), Rachis length (RL), node number of inflorescence (NNI), rachis internode length (RIL), node order of the first inflorescence (NFI) and node order of lowest inflorescence (NLI).
b QTLs are named by an abbreviation of the traits, where trait designation is followed by two digits which represent the linkage group number and a QTL number.
c LG is abbreviate of the linkage group.
d The positive value of the additive effect means that the alleles increase the phenotypic value came from parent 'Meidou2012'. The negative value means the opposite."

that, the QTLs *nni*1.1 and *nni*5.1 overlapped in locations with *ril*1.1 and *ril*5.1. There were also overlaps between *NFI* and *NLI* on linkage group 1 and 6, among *RIL*, *NFI* and *NLI* on linkage group 7 (Table 3; Figure 1). These co-located QTLs for inflorescence length-related traits were all in the same direction of additive effects.

DISCUSSION

The linkage map

In this study, nine morphological markers were mapped at three loci of linkage group 4; *Bm*, *Pf* and *Pn* were co-located at one locus and *Ps*, *Ppe*, *Dgl*, *Pb* and *Dgp* at another locus. These markers which are associated with each other may be controlled or affected by a single gene (Kumar et al., 2007). This was not shown in other population of lablab, but in cowpea (*Vigna unguiculata*). In the study of cowpea (Fery, 1980), flower color and seed coat color were also significantly associated, indicating that the genes controlling flower and seed coat color are operating similarly in these two legume crops. Different from lablab, in azuki bean (*Vigna angularis*), however, seed coat color is controlled by a single dominant gene and is highly correlated with stem pigmentation, but not with pod pigmentation (Jin and Chen, 1996; Kaga et al., 1996).

The first molecular linkage map of lablab comprised seventeen linkage groups and covered 1610 cm (Konduri et al., 2000), while the current map consisted of fourteen linkage groups with coverage of 1302.4 cm though the haploid chromosome number of lablab is only eleven. This phenomenon suggests that, a substantial proportion of the lablab genome has not been determined by markers (Konduri et al., 2000), the phenomenon may have been caused by too few markers and relatively small populations in the two studies.

Segregation distortion

Marker deviation from the expected Mendelian segregation ratio is a common phenomenon present in almost all species studied so far (Konduri et al., 2000). Segregation distortion may be due to gametophytic competition or sporophytic selection (O'Donoughue et al., 1992) and the degree of distortion would be affected by sex and parental interactions (Liu et al., 1996). Our study revealed 63 loci deviated from 3:1 ratio and clustering of deviating loci. The clustering of deviating loci on specific linkage groups has been reported in many crops, such as maize (Yan and Tang, 2003; Zhang and Zhao, 2007). In this study, over half of the deviating loci were clustered in several linkage regions especially on linkage groups 3 and 5. A previous study (Vogl and Xu, 2000) have identified that, these distortions are caused either by differential representation of segregation distorting loci (SDL) genotype in gametes before fertilization or by viability differences of SDL genotypes after fertilization but before genotype scoring. In both cases, the observable phenotype is a distortion of marker locus genotype in the chromosomal region close to the SDL (Vogl and Xu, 2000).

Correlations among inflorescence length trait and its related traits

In general, related traits have significant correlations (Frary and Doganlar, 2003). As expected, *IL* showed significant positive correlations to its component traits. Significant correlations were also found between *PBA* and *PALFN*, *PBA* and *RL*, *PALFN* and *RL*. The strongest correlation was found between *IL* and *RL*, suggesting that *RL* may be the most important component of *IL*.

Number of QTLs and stable QTLs

The first linkage map of lablab has been constructed (Konduri et al., 2000), however, the QTL mapping for inflorescence length traits in lablab have not been reported. In the current study, a range of QTL was found for inflorescence length trait, its component and related traits in more than one generation/season combinations. The number of detected QTLs per trait ranged from three to eleven, which is certain that those traits are governed by many loci.

The same QTLs detected in more than one generation/season combinations can be thought as stable QTLs. The stable QTLs were detected in other crops (Lin and Chen, 2007). In the current study, *NFI* had two stable QTLs while *IL*, *PBA* and *PALFN* each had only one in three combinations. When the QTLs detected in two combinations were considered, the number of stable QTLs was 11 including four QTLs for *NLI*, three for *NNI*, two QTLs for *PALFN* and one QTL for *PBA* and *RIL*. The stable QTLs for inflorescence length trait, its component and related traits may reflect the heritability of those traits.

Co-localization of QTLs

Related quantitative traits also tend to be co-localized within the genome. In many cases, the observed co-localization of QTLs for related quantitative traits could be the result of pleiotropic effects of a single gene or be caused by traits, which are dependent on each other (Frary and Doganlar, 2003). In the current study, over half of detected QTLs were co-located and clustered in ten specific regions on linkage groups, of which a particular case is the QTLs for *IL*, *PBA*, *PALFN*, *RIL*, *NFI* and *NLI* on the linkage group 6 that gathered in a region between C01-2 and T07-2. It seems that, the pleiotropic effects of some major single genes exist and affect the inflorescence size-parameters in lablab. The co-locations of QTLs for different traits were found in other crops (Blair et al., 2006).

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