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Identification of Quantitative Trait Loci Associated with Leaf Length, Width and Length/width Ratio in Two Recombinant Inbred Lines of Soybean (*Glycine max* L.)

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The increasing apparent photosynthetic rate per leaf area may improve seed yield in soybean. Leaf area, length and width are related to the photosynthetic capability of the plant. In this study, two populations derived from the cross of Keunolkong, Shinpaldalkong and Iksan10 were evaluated with simple sequence repeat (SSR) markers to identify length, width and length/width ratio of leaf. Leaf length/width ratio were significantly negative correlation with leaf width in K/S and K/I populations. In the K/S population, two minor QTLs for leaf length (LL) were found on LG D1b+W and L. Two QTLs on LG J and L were related to LL in K/I population. Two and three minor QTLs were identified in leaf width with total phenotypic variation of 13% and 18.04 in K/S and K/I populations, respectively. The leaf length/width ratio, two QTLs on LG I and L, and three QTLs on LG C1, E and L were related to K/S and K/I populations, respectively. Thus it is assumed that the leaf traits are very much dependent on the genotype used and different breeding approach should be considered for the selection of favorite leaf traits in soybean breeding programs.

Key words – QTLs, SSR marker, leaf length, leaf width, leaf length/width ratio, soybean

The soybean (*Glycine max* (L.) Merr.) is one of the worlds major grain crops. Grain or pod numbers per unit area are the main yield component in most annual crops [3,13]. In soybean, yield is often related to the seed filling period, i.e. a long filling period may translate into higher seed yields [4]. Extending the effective seed filling period required the maintenance of an active photosynthetic canopy; therefore, the length of filling period in partly related to green leaf area duration [12]. Selection for high specific leaf weight in soybean may increase apparent photosynthetic rate per unit leaf area, which in turn may improve seed yield [16]. Thomson *et al.* [19] observed that increasing apparent photosynthetic rate per unit leaf area may improve seed yields in soybean, and selection for high specific leaf weight may increase leaf area.

On the other hand, genotypic differences in specific leaf weight [11,17] and leaf area [7,20] have been demonstrated in soybean. Leaf area, length, and width are related to the photosynthetic capability of the plant. The traits affect the amount of light penetrating the canopy, the amount of light capture and the CO_2 fixation and it is known that they are controlled by several genes linked to those which control height and yield [14]. Mansur *et al.* [15] identified two QTLs for leaf size on linkage group (LG) 2 and 16 on the genetic map of a Minsoy×Noir 1 population in soybean. Keim *et al.* [9] also reported that leaf length was located on LG H using on F_2 population derived from a cross between *Glycine max* and *G. soja*. They also identified three markers related to leaf width on LG A, H, and unknown LG. In another study, Mansur *et al.* [14] identified three markers on LG U5, U6, and U14 for leaf length and three markers on LG U2a, U10a, and U11 for leaf width.

The primary object for the present research was improved the breeding efficiency of leaf traits in soybean. Several experiments were conducted: 1) to determine QTLs associated leaf length, width and length/width ratio in the soybean genome, and 2) to compare QTLs position across two RILs populations.

Material and methods

Plant materials and field evaluation

Three well-characterized soybean cultivars, Keunolkong, Shinpaldalkong and Iksan10 were used as mapping parents. Keunolkong is the pure line derived from a local variety selected in Korea. It possesses susceptibility to early maturity, short stem length, and large seed size. Mean while, Shinpaldalkong and Iksan10 are the typical cultivars released

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from systemic breeding programs through the deliberate crossings, Will×(Elf×SS74185) and KW552×Pangsakong, respectively. Shinpaldalkong showed the lateral maturity, long stem length, and medium seed size while Iksan10 showed the lateral maturity, long stem length, and small seed size.

Two RIL populations were collected from the crosses of Keunolkong against Shinpaldalkong and Iksan10. The cross Keunolkong×Shinpaldalkong generated 117 F_{10} RILs that were derived from individual F_2 plants by single seed descent (SSD) methods. This was referred to as the K/S population. The cross Keunolkong×Iksan10 RIL population, consisting of 115 F_{10} lines and also derived from SSD methods was designated as the K/I population. The F_{10} seeds of each line were planted in a randomized complete block design with two replications at Yeongnam Agr. Res. Inst., NICS, RDA in 2001. Each entry was planted in a 1.5 m long paired-row plot. Two seeds per hill were planted, with a spacing of 60 cm between row and 10 cm between plants. The seeds were planted on June 12, 2001.

The following traits were evaluated: flowering date as leaf length (LL), leaf width (LW) in cm (measured on only 10 plants per replication). In addition to these traits, leaf length/width ratio (LR) were calculated. The leaf measurements were made on a fully expanded trifoliate leaf four nodes from the top of the plant. The data were taken when all the cultivars were at approximately flowering (R1 and R2) [5].

DNA isolation and PCR analysis

Genomic DNA was isolated from the fresh leaves following the procedure described by Keim *et al.* [10]. Quality and intactness of DNA were checked using an agarose-gel electrophoresis and DNA was diluted to a working concentration with TE buffer (pH 8.0) and stored at -20℃ until use. A total of 199 soybean simple sequence repeat (SSR) markers [2] were used to screen polymorphisms between mapping parents. The primer pairs showing parental polymorphisms were used for SSR genotyping in each RIL progeny. The PCR reaction was performed in a total volume of 10 $\mu\ell$ containing 25 ng of template DNA, 0.15 M of each forward and reverse primer, 200 M of each dNTP, 2 mM $MgCl_2$, 0.1% Triton X-100, 1×reaction buffer (10 mM Tris-HCl pH 8.5, 100 mM KCl) and 0.5 U of *Taq* DNA polymerase (BioBasic Taq Polymerase, Applied Bio Basic, Canada). Template DNA was initially denaturated at 94℃ for 2 min, followed by 40 cycles for PCR amplification using the following conditions; denaturation at 94℃ for 25 sec, annealing at 47℃ for 25 sec and extension at 68℃ for 60 sec on a 96-Well GeneAmp PCR system 9700 (Applied Biosystem, Forster city, CA, USA). The segregation patterns for each SSR marker in the population were determined by electrophoresis on polyacrylamide or agarose gels. Following electrophoresis, the gel was stained with the silver sequencing kit (Promega, Madison, WI, USA) or ethidiun bromide and scored for map construction.

Map construction and statistical analysis

Based on the segregation data of SSR markers and morphological traits, linkage map was constructed using the MapManager QT (version 2.8) [13]. Recombination fractions were converted to map distances by applying the Haldane map function [6]. Where possible, linkage groups were named according to the designations of the consensus USDA map [2].

The locations of QTLs were evaluated by using the MapManager QT software [13]. Single-factor ANOVA of the quantitative traits after classifying plants according to marker types were also performed. For each of the SSR markers and morphological traits, the marker class means of leaf traits were compared for significance ($P < 0.05$) using an *F*-test from the TypeIII mean squares obtained from the GLM Procedure SAS program (Statistical Analysis System, Cary, NC).

If single-factor ANOVA identified two or more linked markers associated with a leaf length, width and length/width ratio, a multiple regression analysis was conducted by including all the significant markers on the a linkage group (SLG-Regr). Forward and stepwise selection procedures were applied in the regression analysis. The significant markers that were retained in the SLG-Regr analysis were assumed to identify unique QTLs on that linkage group. All significant markers from the SLG-Regr analysis were combined in a multiple linkage group regression group (MLG-Regr) to determine the combination of independent markers that explains the greatest amount of phenotypic variation in a given trait. This probability level was selected to enhance our ability to detect QTLs associated with leaf traits. The coefficient of determination (R^2) form MLG-Regr was used to provide an estimate of the percent of phenotypic variation explained by the markers.

Results

Genetic map

The detailed descriptions of the genetic maps were previously provided in Kang [8]. In the K/S population, a total of 110 markers consisting of 108 SSR and two morphological markers (hilum and pubescence color) were incorporated into 19 linkage groups. The nineteen linkage groups of the K/S population map covered a total distance of 1890 cM with an average distance of 17.2 cM. The linkage map of the K/I population consisted of 20 linkage groups defined by 99 SSR and two morphological markers (flower and hilum color), spanning 1590 cM. On an average, this map presented the density of one marker every 15.9 cM. In this report, the only present linkage groups where the tentative QTLs associated with leaf length, width and length/width were identified (Fig. 1 and Fig. 2)

Phenotypic evaluation and correlations of leaf traits

Variation of leaf length, width, and length/width ratio of two RILs are presented in Table 1. The leaf type of Keounolkong is a round type, while it is ellipse type in Shinpaldalkong and Iksan10. The ranges of values in two RILs were exceeds those of the parental value for each of the traits. And the K/S population showed more wide variation compare to K/I population in all traits. This results, probably, can explain the strong correlation between seed size and leaflet type [16,19].

To study correlations between characters, correlation coefficient was evaluated (Table 2). As shown in Table 2, the same direction of leaf type was observed between K/S and K/I populations. And the ratio of length/width ratio showed a negative correlations with width while low positive correlations were observed in length of leaf. Thus it is proposed that the leaf type was mainly affected by the width rather than length in two RIL populations.

Distribution of QTLs associated with leaf length

Based on the single-factor ANOVA in K/S population, six markers were detected as potentially linked to leaf length (LL) (Table 3). Individually, these markers accounted from 3.74% to 9.55% of the phenotypic variation. The only one marker allele of Shinpaldalkong on linkage group (LG) L increased the LL while the others were controlled by the Keunolkong alleles. In the SLG-Regr model, the marker of satt157 on LG D1b+W was identified to be associated with LL (Table 3). When all the markers were subjected to MLG-Regr, the marker of satt157 on LG D1b+W and satt243 on LG O accounting 5.59% and 5.8% of relatively low phenotypic variation was confirmed to control all the other markers associated with LL.

Table 2. Correlation coefficients among the leaflet traits in K/S and K/I populations

Traits		Leaf length	Leaf width
Leaf width	K/S	0.588**	
	K/I	0.808**	
Leaf length/width ratio	K/S	0.254**	-0.613**
	K/I	0.338**	-0.277**

**: significant at 1% level.

In the K/I population, a total of fifteen markers on LGs D2, G, J, K, L and N were found to be associated with LL, as shown in Table 4. The percentages of phenotype variation explained by each marker were ranged from 3.6% to 11.32%. The alleles of Keunolkong were contributed to increase LL at the detected markers. When the markers on each linkage group were subjected to MLG-Regr analysis, two independent QTLs on the marker of satt431 on LG J and satt523 on LG L were identified with accounting total phenotypic variation of 24.62%. And the QTLs located on the marker of satt523 on LG L was detected as a major QTL controlling LL with a relatively high phenotypic explanation of 17.44%.

Distribution of QTLs associated with leaf width

Based on the single-factor ANOVA in K/S population, seven markers were detected as potentially linked to leaf width (LW) (Table 3). Individually, these markers accounted for 3.58% to 9.57% of variations for LW, and 3.72% to

Table 1. Variation of leaf length, width and length/width ratio in K/S and K/I populations

Trait*	Parents			K/S population		K/I population	
	Keunolkong	Shinpaldalkong	Iksan10	Mean±SD	Range	Mean±SD	Range
LL	10.74	9.55	7.93	9.93±0.86	7.88~12.96	9.25±1.02	6.71~10.74
LW	7.52	5.77	4.76	6.56±0.69	4.33~9.71	6.19±0.66	4.64~8.00
LR	1.43	1.66	1.67	1.52±0.13	1.07~2.08	1.50±0.10	1.31~1.83

*LL, LW and LR represents the leaf length, width and length/width ratio, respectively.

Table 3. Locations, significance levels and percent of phenotypic variance (R^2) of QTLs associated with leaf length, width and length/width ratio in K/S population.

Markers	LG	SF-ANOVA		Alleic means		SLG-Regra		MLG-Regr	
		P^a	R^2 (%)	K/K[c]	S/S[c]	P^a	R^2 (%)	P^a	R^2 (%)
Leaf length (LL)									
satt236	A1	0.014	5.18	10.11	9.72	NA[b]	-	-	-
satt197	B1	0.021	5.11	10.07	9.68	NA	-	-	-
satt216	D1b+W	0.038	3.74	10.07	9.74	-	-	-	-
satt157	D1b+W	0.005	8.63	10.11	9.66	0.005	8.52	0.039	5.59
satt324	F	0.001	9.55	10.15	9.60	NA	-	-	-
sct 010	L	0.001	9.55	9.63	10.18	NA	-	0.040	5.80
Total									11.38
Leaf width (LW)									
satt063	B2	0.035	3.83	6.43	6.70	NA	-	-	-
satt216	D1b+W	0.003	7.56	6.73	6.35	NA	-	0.004	8.03
satt151	E	0.004	7.35	6.79	6.41	NA	-	0.020	4.97
satt324	F	0.040	3.72	6.67	6.40	NA	-	-	-
satt166	L	0.040	3.72	6.70	6.43	-	-	-	-
satt229	L	0.001	8.95	6.72	6.34	0.001	10.33	-	-
satt592	O	0.010	5.88	6.71	6.37	NA	-	-	-
Total									13.00
Leaf length/width ratio (LR)									
satt236	A1	0.033	3.95	1.55	1.49	NA	-	-	-
satt063	B2	0.025	4.28	1.55	1.49	NA	-	-	-
satt157	D1b+W	0.033	4.97	1.54	1.48	-	-	-	-
satt189	D1b+W	0.024	4.4	1.56	1.5	-	-	-	-
satt141	D1b+W	0.049	3.37	1.55	1.5	0.010	7.41	-	-
satt212	E	0.008	5.97	1.49	1.56	0.008	6.06	-	-
satt151	E	0.034	3.97	1.49	1.54	-	-	-	-
satt146	F	0.012	5.94	1.49	1.56	NA	-	-	-
satt472	G	0.002	8.34	1.49	1.57	NA	-	-	-
satt571	I	0.127	5.32	1.55	1.49	NA	-	0.013	6.55
satt132	J	0.045	3.54	1.54	1.49	0.045	3.54	-	-
satt215	J	0.025	4.31	1.55	1.49	-	-	-	-
sct 010	L	<0.001	11.05	1.47	1.56	<0.001	11.55	<0.001	17.31
satt166	L	0.001	8.89	1.48	1.56	-	-	-	-
satt229	L	0.011	5.63	1.5	1.56	-	-	-	-
satt373	L	0.040	3.77	1.79	1.55	-	-	-	-
satt592	O	0.003	7.54	1.49	1.56	-	-	-	-
satt243	O	0.005	7.13	1.48	1.55	0.005	7.63	-	-
Total									23.87

[a]SF-ANOVA: single factor analysis of variance
SLG-Regr: multiple regression with markers on each linkage group
MLG-Regr: multiple regression with all significant markers from the SLG-Regr model
[b]NA: Not applicable. Not linked to other markers
[c]K/K: Keunolkong, S/S: Shinpaldalkong

8.95% of variations for LW. The only one marker allele of Shinpaldalkong on LG B2 increased the LW while the others were controlled by the Keunolkong alleles (Table 3). When all the markers were subjected to MLG-Regr, the marker of satt216 on LG D1b+W and satt151 on LG E accounting 8.03% and 4.97% of relatively low phenotypic variation was confirmed to control all the other markers associated with LW.

In the K/I population, the initial single-factor ANOVA analysis detected seven markers for LW (Table 4). When

Table 4. Locations, significance levels and percent of phenotypic variance (R^2) of QTLs associated with leaf length, width and length/width ratio in K/I population.

Markers	LG	SF-ANOVA		Alleic means		SLG-Regra		MLG-Regr	
		P^a	R^2 (%)	K/K[c]	I/I[c]	P^a	R^2 (%)	P^a	R^2 (%)
Leaf length (LL)									
sat022	D2	0.048	3.64	9.46	9.06	NA[b]	-	-	-
satt501	G	0.017	5.28	9.53	9.06	NA	-	-	-
satt596	J	0.020	5.30	9.43	9.00	0.007	6.85	-	-
sct 001	J	<0.001	10.10	9.48	8.79	-	-	-	-
satt431	J	0.034	4.08	9.40	8.97	0.004	8.6	0.008	7.18
satt417	K	0.032	4.09	9.44	9.03	NA	-	-	-
satt495	L	0.011	5.74	9.42	8.91	-	-	-	-
satt238	L	0.012	5.50	9.41	8.89	-	-	-	-
satt523	L	<0.001	11.32	9.37	8.50	0.018	6.45	<0.001	17.44
satt278	L	0.001	9.56	9.39	8.53	-	-	-	-
satt418	L	0.004	7.52	9.36	8.64	-	-	-	-
satt398	L	0.002	8.38	9.4	8.57	-	-	-	-
satt497	L	0.002	8.76	9.39	8.55	-	-	-	-
satt313	L	0.044	3.60	9.33	8.85	-	-	-	-
satt530	N	0.026	4.53	9.54	9.11	NA	-	-	-
Total									24.62
Leaf width (LW)									
satt050	A1	0.023	4.63	6.32	6.03	-	-	-	-
satt236	A1	0.037	3.87	6.34	6.08	0.027	4.4	-	-
satt180	C1	0.012	5.68	6.37	6.06	NA	-	0.027	4.37
satt501	G	0.033	4.20	6.35	6.09	NA	-	-	-
satt406	J	0.033	4.05	6.32	6.06	-	-	-	-
sct001	J	0.003	7.37	6.32	5.94	<0.001	9.87	0.008	7.03
satt417	K	0.040	3.80	6.32	6.07	NA	-	-	-
satt495	L	0.016	5.21	6.29	5.97	0.037	4.98	-	-
satt523	L	0.017	5.38	6.25	5.87	-	-	-	-
satt278	L	0.019	5.16	6.26	5.86	-	-	-	-
satt418	L	0.023	4.70	6.24	5.87	-	-	-	-
satt398	L	0.021	4.85	6.25	5.84	-	-	-	-
satt497	L	0.029	4.42	6.25	5.86	-	-	-	-
satt022	N	0.013	5.36	6.34	6.04	NA	-	0.008	6.64
Total									18.04
Leaf length/width ratio (LR)									
satt177	A2	0.013	5.63	1.52	1.47	NA	-	-	-
satt180	C1	0.049	3.54	1.47	1.51	NA	-	0.025	5.35
satt460	C2	0.002	8.31	1.46	1.52	0.014	5.88	-	-
satt100	C2	0.019	5.30	1.47	1.52	-	-	-	-
satt483	E	0.042	3.73	1.52	1.48	0.003	7.60	-	-
satt369	E	0.011	5.71	1.47	1.52	0.017	5.23	0.043	4.22
satt523	L	0.023	4.84	1.50	1.45	NA	-	0.025	5.65
Total									15.22

[a]SF- ANOVA, SLG-Regr, MLG-Regr and [b]NA are the same as in Table 3.
[c]K/K: Keunolkong, I/I: Iksan10

the MGL-Regr analysis was adapted, three QTLs for LW was detected. And their phenotypic variation explained by each QTLs were very low as less than 7% of variation. More interest thing is there are no common markers between K/S and K/I populations related to LW.

Distribution of QTLs associated with leaf length/width ratio

The single-factor ANOVA analysis identified eighteen markers as potentially associated with length/width ratio (LR) in K/S population (Table 3). Individual markers accounted from 3.37% to 11.05% of the phenotype variation. The MLG-Regr analysis identified only two QTLs associated with LR. And the QTLs located on the marker of sct010 on LG L was detected as a major QTL controlling LR with a relatively high phenotypic explanation of 17.33%.

In the K/I population, the initial single-factor ANOVA analysis detected seven markers as potentially linked to the LR. And three putative QTLs associated with LR were detected by MLG-Regr analysis and explained total phenotypic variation of 15.22% (Table 4).

Discussion

For leaf size (length and width), Keunolkong showed the largest leaf size and followed by Shinpaldalkong and Iksan10 (Table 1). The range at the given traits in K/I population showed narrow variation compare to that of K/S population. Based on the relationship between seed size and leaf size, the phenotypic characteristics obtained in this study were the same as the result of Chung *et al.* [1] where large-seed strains had large leaf length and width.

As shown in Table 2, correlations between leaf traits provided additional insights into the leaf traits. The higher negative correlations between leaf width and length/width ratio were seen in this study. The length of leaf showed high positive correlations with width of leaf and the same direction of length/width was observed from K/S and K/I populations. Wiebold and Kenworthy [21] reported that single leaf expansion and total leaf area expansion rates were negatively correlated to specific leaf weight and leaf area. Several researchers [1,14,15] also identified a significant higher positive correlation between leaf length and leaf width.

Fig. 1 and Fig. 2 presents the genetic maps and locations of the each QTLs associated with leaf traits in two popu-

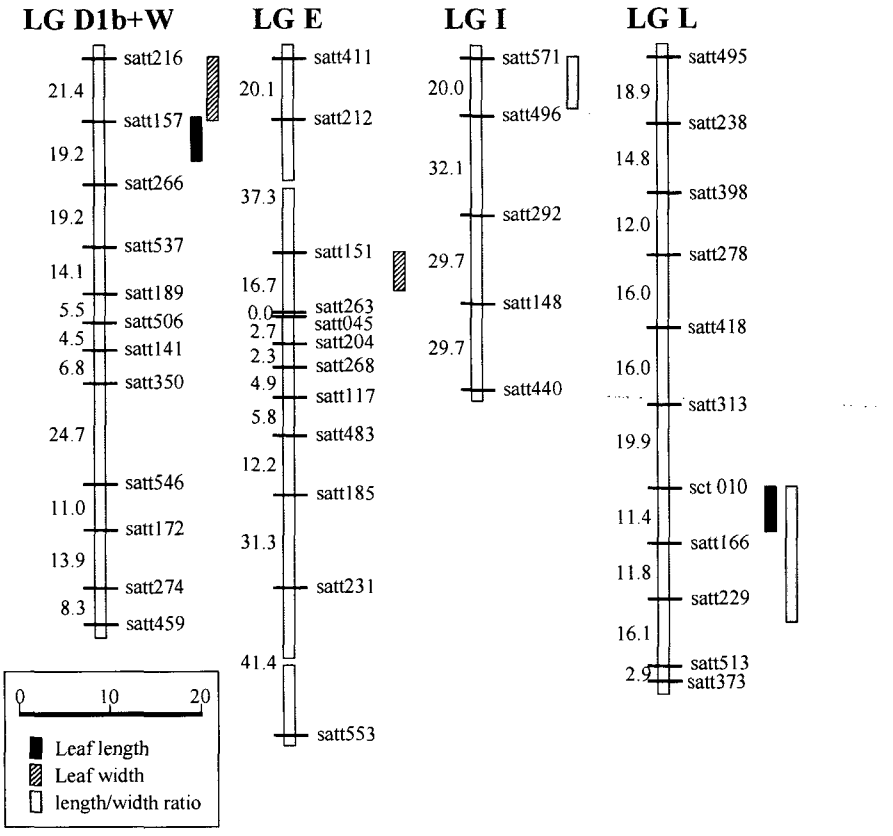

Fig. 1. The distribution of QTLs associated with leaf lenth, width and length/width ratio in K/S population. QTLs significance at the 5% level was presented with vertical bars. Details for each QTLs are given in Table 3. The vertical bars indicate the range where R^2 values of a QTL is significant at 5% level.

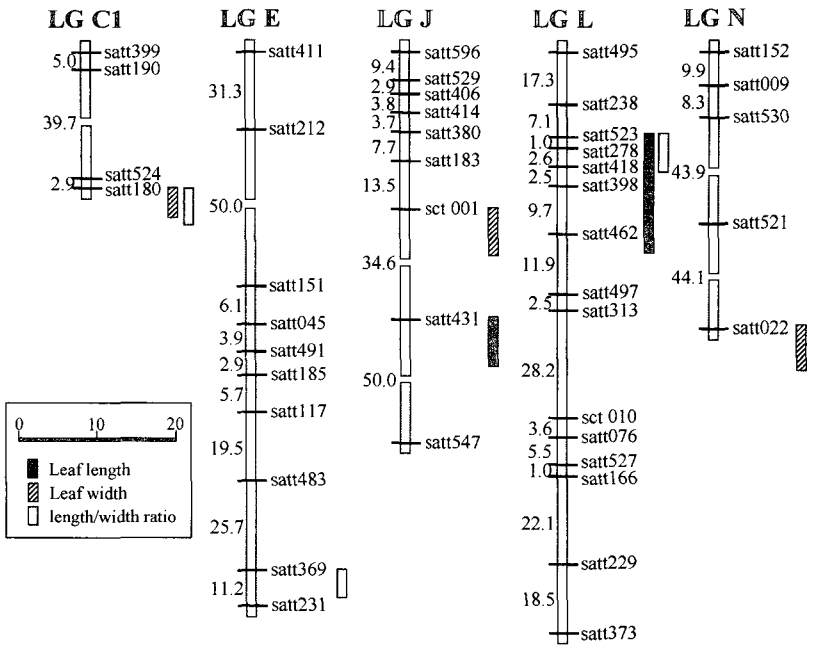

Fig. 2. The distribution of QTLs associated with leaf lenth, width and length/width ratio in K/I population. QTLs significance at the 5% level was presented with vertical bars. Details for each QTLs are given in Table 4. The vertical bars indicate the range where R^2 values of a QTL is significant at 5% level.

lations of K/S and K/I crosses. In this study, the two populations of K/S and K/I showed a quite different results of QTLs related to LL, LW and LR. In K/S population, these were no close relationships among the markers and only sct010 marker was common between LL and LR. And then, in the K/I population, most of markers were not common but showed the coincidence of QTLs of satt523 on LG L between LL and LR. In the previous study, Keim *et al.* [9] used F_2 population derived from a cross between *G. max* and *G. soja* for the QTLs related to leaf length and width. They found one QTL on LG H associated with leaf length and three markers on LG A, H, and unknown LG related to leaf width. Mansur *et al.* [15] identified two QTLs for leaf size in soybean on LG 2 and 16 on the genetic map. Mansur *et al.* [14] also detected three QTLs for leaf length on LG G, N and L, three QTLs for leaf width on LG E, H and unknown linkage group 14, and two QTLs for leaf size on LG H and unknown linkage group 11.

In this study, because of the lack of common markers used in mapping and different materials used. It was difficult to compare the position of QTLs directly associated with leaf traits between this study and previous studies. These complicated and uncommon characteristic of leaf types may explained as following two topics. That is first the leaf type was mainly dependent on a genotype as far as concerned the major QTLs. Second, the environmental factors could not help in leaf type where only the same direction of leaf size can be obtained.

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초록 : 두 집단의 재조합 근친교잡 계통 (RIL) 콩에서 엽장과 엽폭 및 장폭비와 관련된 양적형질 유전자좌 분석

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엽면적과 엽장 및 엽폭은 식물의 광합성 효율과 관련이 있다. 단위 엽면적당 광합성율을 증가는 콩에서 종실수량을 증가시킨다. 따라서 본 연구는 큰올콩과 신팔달콩 및 익산10호를 각각 교배하여 얻은 두 집단이 잎의 엽장과 엽폭 및 장폭비를 확인할 수 있는 SSR 마커를 선발하기 위하여 실시하였다. 잎의 장폭비는 두 집단에서 엽폭과 유의적인 부의 상관을 보였다. 엽장은 큰올콩/신팔달콩 조합에서 연관군 D1b+W와 L에서 두개의 작은 양적형질 유전자좌 (QTL)를 탐색하였으며, 큰올콩/익산10호 조합에서는 연관군 J와 L에서 두개의 양적형질 유전자좌가 관련하였다. 엽폭은 큰올콩/신팔달콩 조합에서 2개, 큰올콩/익산10호 조합에서 3개의 양적형질 유전자좌가 관련하였으며 이들은 각각 전체 형질 변이의 13% 및 18.04%를 설명할 수 있었다. 장폭비는 큰올콩/신팔달콩 조합에서 연관군 I와 L에서 2개, 큰올콩/익산10호 조합에서 연관군 C1과 E 및 L에서 3개의 양적형질 유전자좌가 관련하였다.