Journal of Life Science 2010 Vol. 20. No. 8. 1186~1192 ©JLS / ISSN 1225-9918

Analysis of Quantitative Trait Loci (QTLs) for Seed Size and Fatty Acid Composition Using Recombinant Inbred Lines in Soybean

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Received July 1, 2010 / Accepted August 26, 2010

Soybean [*Glycine max*(L.) Merr.] is an important crop, accounting for 48% of the world market in oil crops. Improvements in economic traits, such as quality and oil constituents, arethe most important objectives in soybean breeding. The objective of this study was to identify quantitative trait loci (QTLs) that control seed size and fatty acid contents in soybean. 115 $F_{2:10}$ recombinant inbred lines (RIL) developed from a cross of 'Keunolkong' and 'Iksan10' were used. Narrow-sense heritability estimates based on a plot mean on 100 seed weight, saturated fatty acid (palmitic acid + stearic acid), and oleic, linoleic, and linolenic acid content were 0.72, 0.60, 0.83, 0.77 and 0.81, respectively. The 100 seeds weight was related to seven QTLs located on chromosomes 1, 3, 8, 9, 16 and 17. Two independent QTLs for saturated fatty acid content were identified on chromosomes 17 and 19. Five independent QTLs for oleic acid content wereidentified on chromosomes7, 11, 14, 16 and 19. Five QTLs for linoleic acid content were located on chromosomes 2, 11, 14, 16 and 19. Three QTLs for linolenic acid content were located on chromosomes 8, 10 and 19. Oleic, linoleic, and linolenic acid had one major common QTL on chromosome 19. Thus, linoleic and linolenic acid content were identified as common QTLs.

Key words : Soybean, 100 seeds weight, fatty acid, QTLs, SSR marker

Introduction

Soybean oil is an important source of vegetable oil for human food and nonfood applications and accounts for approximately 22% of the world's total edible oil production [5,18]. Soybean oil mainly consists of palmitic (C16:0), stearic (C18:0), oleic (C18:1), linoleic (C18:2), and linolenic (C18:3) acid [33]. Conventional soybean cultivars possesses oil with an average of 15.0% saturated fatty acid (palmitic and stearic acid) and 85% unsaturated fatty acid (oleic, linoleic and linloenic acid). The fatty acid composition of soybean oil completely determines its nutritional value [12], storage compatibility [25], industrial properties [21] and potential food applications [24,28]. Modification of fatty acid composition of soybean oil makes it more competitive in various segments of the food and industrial oil markets [9], and to make it more nutritional [12] has been an important objective of plant breeding and molecular genetics in recent years [29]. Altered fatty acid composition has been developed through traditional plant breeding [33] and application of chemical mutagens [6,10,31] that have extended the range of the five major fatty acid normally found in soybean oil unfortunate. Therefore, the manipulation of soybean oil quality by altering fatty acid composition is an important breeding objective in the world [27,33].

On the other hand, linkage established between nonfunctional or anonymous markers with QTL are fairly common, but they are subject to losing their association with desired phenotype through recombination. Molecular markers for causal mutations for quantitative traits harder to find than simply inherited traits because of the extensive analysis required for positional cloning or the availability of suitable candidate genes. However, these perfect molecular markers lack the ambiguity associated with QTL-type markers, and thus eliminate the problem of disassociation of the trait from linked anonymous locus. Marker-assisted selection (MAS) allows selection at the genotype level, or specifically the desired alleles, one time, without the need to track and stabilize phenotypes across several generations. Plants with the desired genotypes can be identified before pollination with MAS, allowing breeders to more efficiently cross and back-

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cross [1].

The primary objective of the present research was to improve the breeding efficiency of unsaturated fatty acid quality in soybean. This study was conducted to identify simple sequence repeats (SSR) markers associated with QTLs and marker-assisted selection (MAS) for oleic, linoleic, and linolenic acid contents in soybean.

Materials and Methods

Plant materials and field evaluation

The well-characterized soybean cultivars, 'Keunolkong' and 'Iksan10' were used as mapping parents. 'Keunolkong' is the pure-line derived from a local variety selected in Korea. It possesses early maturity, large seed size, high protein content, and low oil content. Iksan10 is the typical cultivar released from systemic breeding programs through the deliberate crossings KW552 × Pangsakong. This cultivar shows late maturity, small seed size, high protein content, and low oil contents.

We used genetic materials from the F_2-derived Recombinant inbreed line (RIL) population that were developed by single seed descent (SSD) from reciprocal crosses of 'Keunolkong'×'Iksan10'. This population, designated K/I, consisted of 115 F_{10} lines. The F_{10} seeds of each line were planted in a randomized complete block design, with two replications, at the NICS, RDA, Milyang, Korea, on 12 June 2001. Each entry was planted in a 1.5 m long paired-row plot with two seeds per hill. Spacing was 60 cm between rows and 10 cm between plants. Seed weight was determined by weighting 100 seeds per plot.

Measuring oil content and of fatty acids

The oil contents were determined by auto-soxhlet method with Buchi B-811 extracted system. 2 g of ground samples was extracted by hexane for 2 hr, pre-heated for ten minutes, and then dried 1 hour at 105°C. The moisture contents were analyzed by oven-dry method with 105°C for 2 hr, and then all protein contents were converted to dry matter base.

In order to determine the composition of soybean fatty acids, solvent extract oil was used. About 50 mg of oils was placed in a screw-capped vial, and 5 ml of methylation solution (H_2SO_4:MeOH:toluene=1 ml:20 ml:10 ml) was added. The sealed vial was heated on a water bath (100°C) for 60 min, and allowed to cool. After 5 ml of water and 5 ml of diethyl ether were added and shaken. The mixture was separated two layers and the upper layer (diethyl ether) was taken by Pasteur pipette. The diethyl ether layer was dried using anhydrous sodium sulfate for 5 min. Then the 1μl of diethyl ether solution was directly injected on to the GLC. A DS 6200 (DONAM Instruments Inc., Korea) gas chromatography with a flame ionization detector (FID) and 0.32 mm i.d. × 25 m HP-FFAP capillary column was used. The oven temperature was raised from 140°C (2 min holding) to 200°C at a constant rate of 8°C per min, and then held 10 minutes. The injector and detector port temperature were kept at 230 and 250°C, respectively. The carrier gas was nitrogen at a flow rate of 0.5 ml per min., and the split ratio at the injector port was 50:1.

DNA isolation and analysis:

Genomic DNA was isolated from fresh leaves following the procedure described by Keim et al. [15]. A total of 199 soybean SSR markers (http: //soybase.agron.iastate.edu/ssr.htm) were used to screen for polymorphisms between mapping parents. The primer pairs showing parental polymorphisms were used for SSR genotyping in RIL progenies. The PCR reaction was performed in a total volume of 10 μl containing 25 ng of template DNA, 0.15 M of each forward and reverse primers, 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°C for 2 min, followed by 40 cycles of PCR amplification using the following conditions; denaturation at 94°C for 25 sec, annealing at 47°C for 25 sec and extension at 68°C for 60 sec on a 96-Well GeneAmp PCR system 9700 (Applied Biosystems, USA).

Map construction and statistical analysis

Means of traits, correlation, and analysis of variance were determined by SAS program. Narrow-sense heritability was calculated on a per-plot basis, using estimates of the variance components [7]. Based on the segregation data subsets for SSRs and morphological markers, we constructed a linkage map with MapManager QT version 2.8 software [19]. Recombination fractions were converted to map distances by applying the Haldane map function [8].

The association between marker and QTL was tested according to the interval mapping methods of Whittaker et al. [32], using MapManager QT and single-factor ANOVA (SF-ANOVA). For each SSR and morphological marker, the

class means for seed weight, protein and oil concentration were compared for significance (p<0.05) using an *F*-test from the Type Ⅲ mean squares, as obtained from the General Linear Model (GLM) procedure of SAS.

If SF-ANOVA identified two or more linked markers associated with the seed weight, protein and oil content, multiple regression analysis was conducted by including all the significant markers on that linkage group in the model (SLG-Regr). All significant markers from the SLG-Regr analysis were then combined into a multiple-linkage group regression (MLG-Regr) at p<0.05 to determine the combination of independent markers those were explaining the greatest amount of phenotypic variation in a given trait. The probability level of 0.05 was selected to enhance our ability to detect QTLs associated with seed weight, protein and oil concentration. Finally, the coefficient of determination (R^2) obtained from MLG-Regr was used to provide an estimate of the percentage phenotypic variation explained by the markers.

Results and Discussion

100 seeds weight and oil contents

Variation of 100 seeds weight and oil content in the $F_{2:10}$ RIL population is presented in Table 1. 'Keounolkong' shows large seed weight and low oil content, while 'Iksan 10' is characterized with small seed weight and high oil content. There was significant difference (p<0.05) among the RIL for each traits in the population. There was transgressive segregation for seed weight and oil content with a few lines being significantly greater or lower than high and low parents. 100 seeds weight ranged from 10.65 to 22.60 g and oil content ranged 15.99 to 23.19%. Narrow-sense heritability of 100 seeds weight oil content was 0.72 and 0.57, respectively (Table 1).

Seed weight, protein and oil contents are three important traits in soybean determining seed quality. Smaller seed weight is performed in Asian markets for quality sprouts and natto, whereas large seed weight with high protein content in preferred for tofu and denjang (fermented soybean) production [17,26]. Chung et al. [4] have reported the heritability for protein and oil at 0.89 and 0.84, respectively. Panthee et al. [23] reported the heritability for seed size, protein and oil at 0.71, 0.66 and 0.54, respectively. The heritability observed in our population for indicated that selection response would be reasonable for achieving genetic gain.

Fatty acid contents

Variation of saturated fatty acid (palmitic acid + stearic acid), oleic, linoleic, and linolenic acid contents in the $F_{2:10}$ RIL population is presented in Table 1. 'Keounolkong' shows low saturated fatty acid, llinoleic, inolenic acid content, and high oleic acid contents. Transgressive segregation for unsaturated fatty acid was found a few lines being significantly greater or lower than high and low parents.

Saturated fatty acid content ranged from 15.99 to 23.19 and oleic acid content ranged from 19.42 to 42.24%, linoleic acid content ranged from 38.07 to 57.05%, and linolenic acid content ranged 5.46 to 9.39%. Narrow-sense heritability of saturated fatty acid, oleic, linoleic, and linolenic acid contents were 0.60, 0.83, 0.77 and 0.81, respectively (Table 1). There was a strongly negative correlation between oil and linolenic acid content (r=-0.351, p<0.001), oleic acid and linoleic acid content (r=-0.964, p<0.001), and oleic acid and linolenic acid contene (r=-700, p<0.001). On the other hand, linoleic acid content was strongly positively correlated with linolenic acid content (r=0.560, p<0.001) (Table 2). Kim et al. [13]

Table 1. Descriptive statistics for100 seeds weight, oil content, saturated fatty cid oleic acid, linoleic acid and linolenic acid contents in 117 RIL population of 'Keunolkong' × Iksan 10'

Traits	Parents		RIL population		$h^{2†}$
	Keunolkong (mean±SD)	Iksan 10 (mean±SD)	Range	Mean±SD	
100 seed weight	24.70±0.29	9.25±0.20	10.65-22.60	20.60±1.48	0.72
Oil content	17.32±0.37	20.91±0.02	15.99-23.19	19.06±1.24	0.57
Saturated fatty acid	13.72±0.40	15.01±0.12	12.59-16.09	14.64±0.62	0.60
Oleic acid	27.45±0.58	22.23±0.64	19.42-42.24	25.97±3.38	0.83
Linoleic acid	51.31±0.91	54.47±0.39	38.07-57.05	51.56±2.82	0.77
Linolenic acid	7.67±0.17	8.28±0.37	5.46-9.36	7.83±0.74	0.81

†Heritability on a per-plot basis.

Table 2. Correlation coefficients among 100 seeds weight, oil content, saturated fatty cid oleic acid, linoleic acid and linolenic acid contents in 117 RIL population of 'Keunolkong' × Iksan 10'

	100 seeds weight	Oil content	Saturated fatty acid	Oleic acid	Linoleic acid
Oil content	-0.068^{ns}				
Saturated fatty acid	-0.073^{ns}	0.050^{ns}			
Oleic acid	0.217*	-0.068^{ns}	-0.226*		
Linoleic acid	-0.184^{ns}	0.163^{ns}	0.031^{ns}	-0.964***	
Linolenic acid	-0.228*	-0.351***	0.072^{ns}	-0.700***	0.560***

*Significant at 0.05 level.
***Significant at 0.001 probability level.
ns, Not significant (p>0.05)

have reported the heritability for oleic, linoleic, and linolenic acid contents 0.85, 0.82 and 0.81, respectively. The heritability observed in our population for indicated that selection response would be rational for achieving genetic gain.

QTL analysis for seed traits

The SF-ANOVA analysis identified twenty five markers as potentially associated with 100 seeds weight content. MLG-Regr analysis showed that seven QTL markers on chromosome 1, 3, 8, 9, 17, 16 were significantly associated with 100 seeds weight (Table 3). Individual QTLs explained relatively phenotypic variation (2.91~113.23%) though they accounted for total phenotypic variations of 50.01% for 100 seeds weight. One major QTL, sct001 on chromosome 16, explained 13.23% of the phenotypic variation.

Seed weight per seed, is an important yield component of soybean and is generally positively correlated with seed yield [3]. Soybean cultivars with either very small or very large seed weights are used in the production of many specialty human foods. Seed weight is very easily affected by environmental conditions, and previous reports showed that polygenic influence results in a large numbers of QTLs [2,16,30]. Compared with the previous study, LG F (Ch. 13), I (Ch. 20) and K (Ch. 9) might be almost identical with QTLs previously reported [11,14,20,22].

MLG-Regr analysis showed that two QTL markers on chromosome 17 and 19 were significantly associated with saturated fatty acid content (Table 3). The satt154 on chromosome 17 explained 7.80% of the phenotypic variation, and satt523 on chromosome 19 explained 10.71% of the phenotypic variation (Table 3).

The SF-ANOVA analysis resulted in thirteen markers as potentially associated with oleic acid content. MLG-Regr analysis showed that four QTL markers, satt590 on chromosome 7, satt197 on chromosome 11, satt556 on chromosome 14, satt183 on chromosome 16 and sct010 on chromosome 19 were significantly associated with oleic acid content (Table 3). Individual QTLs explained relatively low phenotypic variation though they accounted for total phenotypic variations of 29.10% for oleic acid content.

The SF-ANOVA revealed that eight markers were detected as potentially associated with linoleic acid content. MLG-Regr analysis identified five QTLs on chromosome 2, 11, 14, 16 and 19 (Table 3). Five independent QTLs near the marker satt590 on chromosome 2, satt197 on chromosome 11, satt556 on chromosome 14, satt183 on chromosome 16, and sct010 on chromosome 19 were identified with accounting of 3.72, 7.82, 4.33, 5.98 and 7.55% of phenotypic variation, respectively. Moreover, their individual QTLs showed a relatively low phenotypic explanation though they accounted total phenotypic variation of 31.03% for linoleic acid content.

Based on the SF-ANOVA analysis in th RIL population, ten markers were showed significantly ($p<0.05$) associated with linolenic acid content. Three QTLs were identified on chromosome 8, 10 and 19. In the MLG-Regr analysis, those QTLs explained 28.00% of total phenotypic variation of the oil content. The QTL located near the marker satt238 on chromosome 19 was detected as major QTL contributing to $R2$=14.97 (Table 3).

Kim et al. [13] reported that unsaturated fatty acid contents, marker allele on LG C1 (Ch 4) increased the contents of oleic and linoleic acid, but LG L (Ch 19) was minor QTL marker. In our results, marker on chromosome 19 turned out to be a major QTL for oil and unsaturated fatty acid content. If colligated the result of this study, it is believed that the seed composition material as oil and fatty acid content were mainly controlled by environmental stresses and

Table 3. Marker distributions and QTLs associated with 100 seeds weight, oil content, saturated fatty acid oleic acid, linoleic acid and linolenic acid contents in 117 RIL population of 'Keunolkong' × Iksan 10'

Traits	Chromosome number	Markers	SF-ANOVA†		Alleic means		MLG-Regra	
			P	R^2 (%)	K/K‡	S/S‡	P	R^2 (%)
100 seed weight	1	satt147	0.0348	4.10	16.59	15.65	NA	8.25
	3	satt530	0.0123	5.76	16.86	15.71	0.0339	5.28
	3	satt521	0.0005	10.70	16.84	15.32	0.0016	10.21
	8	satt187	0.0007	10.00	16.83	15.63	NA	6.02
	9	satt417	0.0064	6.62	16.63	15.43	0.0028	2.91
	16	sct 001	0.0001	12.38	16.68	14.97	<0.0001	13.23
	17	satt372	0.0454	3.72	15.69	16.56	0.0347	4.11
Oil content	2	satt546	0.0070	6.67	19.39	18.75	NA[b]	6.10
	6	satt100	0.0156	5.59	19.37	18.77	0.0069	4.94
	19	satt418	0.0093	6.27	18.92	19.71	0.0202	7.47
Saturated fatty acid	17	satt154	0.0005	10.54	14.41	14.82	0.0007	7.80
	19	satt523	0.0003	12.27	14.52	15.07	<0.0001	10.71
Oleic acid	7	satt590	0.0312	4.27	26.67	25.25	NA	3.42
	11	satt197	0.0024	8.26	26.86	24.99	NA	7.82
	14	satt556	0.0158	5.27	26.85	25.30	0.0191	4.33
	16	satt183	0.0160	5.21	26.64	25.09	0.0160	5.98
	19	sct 010	0.0032	7.70	26.93	25.05	0.0011	7.55
Linoleic acid	2	satt537	0.0426	3.79	51.99	50.90	NA	5.73
	11	satt197	0.0019	8.66	50.82	52.41	NA	7.42
	14	satt556	0.0041	7.39	50.66	52.21	0.0051	5.80
	16	satt183	0.0343	4.04	51.07	52.21	NA	4.93
	19	sct 010	0.0037	7.48	50.78	52.33	0.0018	7.14
Linolenic acid	8	satt177	0.0250	4.69	7.95	7.63	0.0337	9.53
	10	satt173	0.0473	3.73	7.66	7.94	NA	3.50
	19	satt238	0.0032	7.71	7.67	8.12	0.0053	14.97

† SF-ANOVA: single-factor analysis of variance, MLG-Regr: multiple regression with all significant markers from the SLG-Regr model

‡ K/K: Keunolkong, I/I: Iksan 10.

they are seed size on genotypes. Finally, we suggest that both the identified QTLs and recently identified lines of germplasms in this report will promote breeders in accumulation favorable alleles for improvement in soybean quality.

Acknowledgement

This work was supported for two years by Pusan National University Research Grant.

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초록 : 콩 재조합자식계통을 이용한 콩 종자의 크기와 지방산 조성의 양적 형질 유전자좌 분석

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콩은 세계 유지작물시장에서 48%을 차지하는 중요한 작물이다. 콩 종실의 크기와 기름함량의 양적 및 질적 개선이 콩 육종에 있어서 가장 중요한 목적중의 하나이다. 이 연구의 목적은 종실의 크기와 지방산조성을 조절하는 양적 형질 유전자좌를 밝히는 것이다. 큰올콩과 익산10호의 교배로부터 F2:10 세대의 재조합자식계통 115계통을 이용하였다. 협의 유전력 검정에서는 백립중이 0.72, 포화지방산(팔미트산 + 스테아릭산)이 0.60, 올레익산이 0.83과 리놀레익산이 0.77 및 리놀렌산이 0.81을 나타내었다. 백립중과 연관된 양적형질유전자좌는 염색체 1번, 3번, 8번, 9번과 16번 및 17번에 7개로 나타났다. 포화지방산은 염색체 17번과 19번에 2개의 독립된 양적 형질 유전자좌가 연관되어 있었다. 올레익산 함량에 대해서는 다섯 개의 독립적인 양적 형질 유전자좌가 염색체 7번, 11번, 14번과 16번 및 19번에서 확인하였다. 리놀레익산 함량에 대한 5개의 양적 형질 유전자좌는 염색체 2번, 11번, 14번과 16번 및 19번에 있었다. 리놀렌산 함량은 3개의 양적형질유전자좌가 염색체 8번과 10번 및 19번에 관련되어 있었다. 그리고 올레익산과, 리놀레익산 및 리놀렌산에 공통적으로 확인되는 주요 양적 형질 유전자좌는 염색체 19번 이었다.