

Quantitative trait loci of seed traits for soybean in multiple environments

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ABSTRACT. Seed length and seed width are an important factor to the soybean yield. So the quantitative trait loci (QTL) location for seed length and seed width could assist the breeding of soybean. In this study, the QTL underlying seed length and seed width were studied. A recombinant inbred line population of soybeans derived from a cross between the American semi-draft cultivars Charleston and Dongnong 594 were used in 7 environments. The quantitative trait loci underlying seed length, seed width, and seed length/seed width were analyzed by the method of composite interval mapping. Then, the epistatic effects and the QTL-environment (QE) interaction effects were also analyzed. Some valuable QTL sites found had great

effect to the seed trait. Results showed that 7 QTLs underlying seed length were identified mainly on linkage groups D1a, C2, B1, A1, G, and A2. For the seed width, 7 QTLs were identified on linkage groups D1a and O. Two QTLs of seed length/seed width were identified on linkage groups D1b and C2. No QE interaction was found for QTLs of seed length and seed width in 7 environments. QTLs of seed length/seed width on linkage groups A1 and I had a QE interaction in 7 environments. Seven pairs of QTLs were identified that affected additive x additive epistatic effect of seed length, seed width, and seed length/seed width, which occurred among 8 linkage groups. These results supply a good foundation for molecular assistant breeding for soybean seed trait.

Key words: Soybean; Seed length; Seed width; Quantitative trait locus; Quantitative trait locus-environment interaction

INTRODUCTION

Soybean seed traits directly impart the composition of yield. Identifying the quantitative trait loci (QTLs) underlying seed traits is very useful for marker-assisted breeding. Seed size, seed weight, pods per plant, and number of seeds per plant are the main factors that determine soybean yield (Jin et al., 2010; Yesudas et al., 2013). By modifying genetic linkage maps, some QTLs of seed traits were identified, such as pod number, seed size, seed hardness, and seed weight (Keim et al., 1990; Lu et al., 1997; Tasma et al., 2001; Zhang et al., 2010). Significant progress has been made in understanding the regulation of seed formation through molecular and genetic studies of rice (Kitagawa et al., 2010). Now, more QTLs underlying seed traits have been identified in rice and maize than in other crops; especially in rice, a huge number of QTLs and genes of seed length and seed width were found (McKenzie and Rutger, 1983; Song et al., 2007). In addition, several functional genes involved in grain length and weight in rice were identified (Heang and Sassa, 2012; Ishimaru et al., 2013). Especially for maize, some seed trait genes were identified based on meta-analysis of yield-related QTLs from public resources (Wang et al., 2013).

Many studies showed that seed width was controlled by multiple genes. Nineteen QTLs underlying seed length and 14 QTLs underlying seed width were identified using 3 sets of recombinant lines: Minsoy x Archer, Minsoy x Noirl, and Noirl x Archer (Salas et al., 2006). Genetic analysis of the soybean seed trait revealed that seed length and seed width of the hybrid F_1 of a reciprocal cross were significantly different, suggesting the existence of a maternal inheritable effect. The seed length trait was jointly controlled by a pair of additive, dominant major genes and additive, dominant, and epistatic genes; seed width was controlled by multiple genes.

Five main effect QTL were found in three population [F(2:3), F(2:4) and F(2:5)], had higher heritability, greater than 20%, which population derived from the direct and reciprocal crosses of Lishuizhongzihuang with Nannong 493-1 (Xu et al., 2011). By the empirical Bayes algorithm, a 307-bp allele of QTL linked to satt453 was found via 257 soybean cultivars obtained by stratified random sampling from six geographic ecotypes in China (Niu et

al., 2013). The Harosoy and Clark cultivars were used as donator parents to construct two primary backcross introgression line, Hongfeng 11 was used as recurrent parent, and QTLs for large pods and seeds and related traits were located. Thirty-seven related QTLs were identified for 13 pod and seed traits, which were distributed on 18 linkage groups in 2 sets of introgression line groups. QTLs for seed length were identified on chromosomes F, J, and M, respectively. A seed width QTL was identified on chromosome C1 (Li et al., 2008). The Jindou 23 x Huibuzhi line was used to construct 474 family lines of F_{13} recombinant inbred line groups to use as a mapping population in soybean. A genetic map with 231 simple sequence repeat markers was constructed. Seed length, seed width, seed thickness, length/width, length/thickness, and width/thickness were studied in soybean. The analysis showed that 7 QTLs for seed length were located on chromosomes D1a, D2, and J_2, and 3 QTLs for seed width were located on chromosomes B1 and O (Liang et al., 2008).

In this study, QTLs underlying seed length, seed width, and seed length/seed width were identified for the first time in 7 different environments from 2006 to 2010. Some stable QTLs underlying seed length and seed width were found, and the QTL-environment (QE) interactions were also analyzed. Our results are very useful for gene mining and molecular breeding in soybean, which has a complex genetic background.

MATERIAL AND METHODS

Experimental materials

The F_{2-14} generations of a recombinant inbred line population including 147 lines derived from a cross between the American semi-draft cultivars Charleston and China variety Dongnong 594 were used from 2006 to 2010. The recombinant inbred lines were grown together with the parents at Harbin (45°43'N, 126°45'E, fine-mesic chernozem soil) and Hongxinglong (46°43'N, 131°34'E, fine-mesic chernozem soil) during 2006-2010. Seeds were planted in rows that were 5 m long and spaced 0.65 m apart and with a space of 5 cm between plants. Two replicates were used with a randomized complete block design from 2006 to 2007, and 3 replicates were used with a randomized complete block design from 2008 to 2010. Five plants of each line were randomly selected in each row as seed and pod trait donors that were later used to analyze and record the data from the usual methods for soybean (Sun et al., 2012).

Statistics and analysis

The length and width of 10 pods were measured per plant, and the average value was used as the phenotypic value of each line. A genetic map was constructed by our lab; this genetic map had 20 linkage groups. The total length of the genetic map was 1913.5 cM, the average distance between markers was 11.89 cM, and the length of each linkage group ranged from 0.4 to 309.5 cM (Sun et al., 2012). QTL testing for seed length, seed width, and seed length/seed width was performed using composite interval method (CIM) of QTLCart 2.5 software. The permutation test method was used to estimate the logarithm of odds (LOD) significant threshold value, and samples were repeated 1000 times. The QTLNetwork_v2.1 software was used to analyze QTL epistatic effects and QE interaction effects.

RESULTS

Phenotypic variation of 2 parents

From Table 1, it could be seen that the phenotypes of the 2 parents varied by the change in different locations from 2006 to 2010. The phenotype value of seed length/seed width of Dongnong 594 was greater than that of Charleston. The mid-parent value of seed length and seed width was the smallest in 2008.

Table 1. Performance of seed length, seed width and seed length/seed width of parents in different locations in different years.

Year	Parent	Seed length (mm)		Seed width (mm)		Seed length/seed width	
		Mean	Mid-parent value	Mean	Mid-parent value	Mean	Mid-parent value
2006 (A)	Charleston	7.440	7.29	6.880	6.62	1.081	1.102
	Dongnong 594	7.140		6.360		1.123	
2007 (A)	Charleston	7.240	7.53	6.580	6.60	1.100	1.140
	Dongnong 594	7.820		6.620		1.181	
2008 (A)	Charleston	6.433	6.752	5.580	5.252	1.153	1.294
	Dongnong 594	7.070		4.923		1.436	
2009 (A)	Charleston	7.247	7.204	6.567	6.308	1.104	1.144
	Dongnong 594	7.160		6.050		1.183	
2009 (B)	Charleston	7.147	6.876	6.433	6.020	1.111	1.144
	Dongnong 594	6.605		5.608		1.178	
2010 (A)	Charleston	7.940	7.816	7.153	6.76	1.110	1.159
	Dongnong 594	7.693		6.367		1.208	
2010 (B)	Charleston	7.567	7.574	6.573	6.241	1.151	1.217
	Dongnong 594	7.582		5.909		1.283	

Phenotypic variance of the recombinant inbred line groups

The phenotype data of seed length, seed width, and seed length/seed width showed a normal distribution in the recombinant inbred line. However, the average values of these 3 traits were similar to the parents. Therefore, these 3 traits were quantitative traits that were dominated by multiple genes. In some years, the standard deviation and kurtosis of seed length/seed width was greater, indicating that different environmental conditions had a huge effect on the phenotype of seed length/seed width. The skewness of seed length, seed width, and seed length/seed width was relatively small; individual traits had partial parental separation. From the phenotypic data of frequency distribution, each trait showed an approximately normal continuous distribution, which was suitable for QTL analysis (Table 2, Figure 1).

QTL mapping

QTL testing of seed length, seed width, and seed length/seed width was performed using the CIM method in the QTLCart 2.5 software. The LOD significant threshold values of traits were estimated by a permutation test using samples that were repeated 1000 times.

The data of seed length, seed width, and seed length/seed width were analyzed during 2006 to 2010. Seven QTLs underlying seed length were identified on linkage groups

D1a, C2, B1, A1, G, and A2. The contribution rates ranged from 0 to 0.16%, the additive effect was -0.23 to 0.20, and the LOD values ranged from 3 to 6.03 (Table 3, Figure 2). Six QTLs underlying seed width were identified on linkage groups D1a and O. The contribution rates ranged from 0 to 0.19%, the variation that was explained by the trait was 0.76%, and the LOD values ranged from 3.13 to 5.98. Two QTLs underlying seed length/seed width were identified on linkage group D1a in 2006 (A) and 2009 (B). The contribution rates ranged from 0.08 to 0.11%, the variation that was explained by the trait was 0.19%, the LOD values ranged from 3.11 to 3.38, and additive effects were relatively small and from the female parent.

Table 2. Performance of seed length, seed width and seed length/seed width of recombinant inbred line group in different locations in different years.

Year	Trait	Max. (%)	Min. (%)	Mean (%)	SD	Kurtosis	Skewness
2006 (A)	Seed length	8.29	6.565	7.182	0.30	1.160	0.60
	Seed width	7.12	6.01	6.563	0.23	-0.020	-0.16
	Seed length/seed width	1.22	1.033	1.09	9.45	5.370	1.67
2007 (A)	Seed length	8.47	7.313	6.51	0.34	1.420	0.81
	Seed width	7.26	6.12	6.585	0.23	0.210	0.51
	Seed length/seed width	1.209	1.048	1.11	0.03	-0.030	0.43
2008 (A)	Seed length	9.02	5.528	6.829	0.44	4.450	1.25
	Seed width	6.38	4.367	5.686	0.27	3.320	-0.73
	Seed length/seed width	1.531	1.035	1.201	0.06	7.150	1.93
2009 (A)	Seed length	7.86	6.04	7.138	0.28	1.170	-0.56
	Seed width	6.88	5.24	6.311	0.26	1.410	-0.58
	Seed length/seed width	1.222	1.077	1.131	0.03	-0.280	0.17
2009 (B)	Seed length	7.997	6.008	6.896	0.33	1.880	0.42
	Seed width	6.607	5.095	5.978	0.25	1.410	-0.51
	Seed length/seed width	1.265	1.08	1.154	3.55	-0.280	0.08
2010 (A)	Seed length	8.9	5.73	7.608	0.42	3.560	-0.86
	Seed width	7.267	4.88	6.582	0.36	3.280	-0.98
	Seed length/seed width	1.341	1.078	1.156	0.04	2.260	0.74
2010 (B)	Seed length	8.238	5.94	7.284	0.37	0.997	-0.32
	Seed width	6.781	5.04	6.024	0.33	-0.100	-0.03
	Seed length/seed width	1.42	1.102	1.211	0.06	0.590	0.65

Analysis of QTL epistatic effects and QE interaction effects

Analysis of QE interaction effects

Seed length/seed width QTLs had QE interaction effects. Two QTLs had environment interaction effects. These QTLs were located on linkage group A1 and I had additive effects values of 0.0155 and 0.0071, respectively, which reached the 0.01 significance level (Table 4). The contribution rates of the additive effect were 6.25 and 3.04%, the environment interaction contribution rates were 1.56 and 0.96%, and the total contribution rates of the environmental effects were significantly smaller than the total contribution rates of the additive effects. The GM1-A1-17 QE interaction effects reached a significant level ($P < 0.05$) in 2006 (A) and a significant level ($P < 0.01$) in 2010 (B). The GM14-I-1 QTL did not have a significant QE interaction effect from 2006 to 2010 (Table 4). No QE interaction was found for the seed width and seed length characteristics.

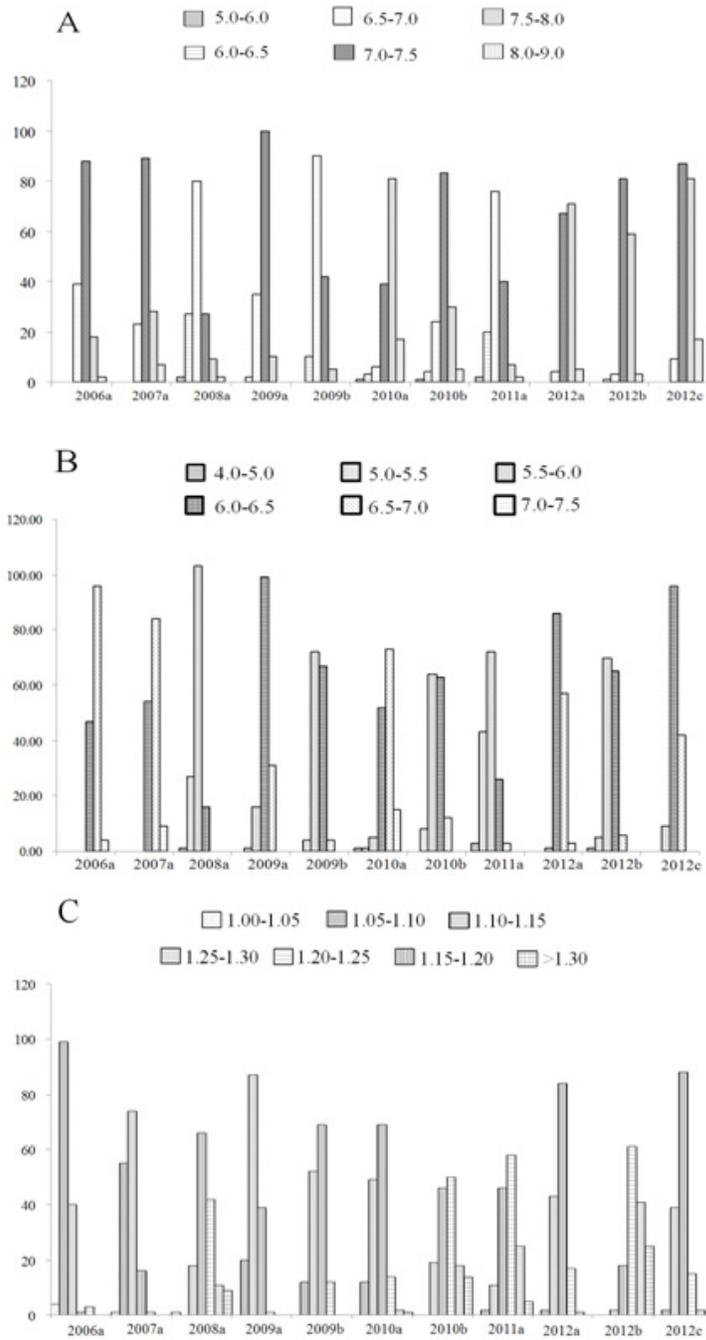


Figure 1. Frequency distribution of seed length, seed width, seed length/seed width of recombinant inbred line from 2006 to 2010. **A.** seed length, **B.** seed width, **C.** seed length/seed width.

Table 3. Quantitative trait loci of seed length, seed width, seed length/seed width and related trait in population.

Trait	Year	QTLs	Marker interval	Site	Confidence interval	LOD	Contribution rate	Additive effect
seed length	2006 (A)	GM7-D1a	satt383-satt267	224.4	224.0-228.9	3.00	0.08	0.13
	2007 (A)	GM6-C2	satt334-satt460	109.6	98.9-115.6	5.71	0.16	-0.18
	2008 (A)	GM3-B1	satt197-satt229	61.7	59.0-66.0	3.46	0.10	-0.23
	2009 (A)	GM1-A1	satt242-satt270	191.6	184.9-196.9	6.03	0.16	-0.13
		GM6-C2	sat_092-satt202	128	123.7-132.1	3.18	0.00	0.08
	2009 (B)	GM7-D1a	satt226-satt175	56.4	52.9-62.3	3.90	0.12	0.13
		GM12-G	satt505-sat_094	13.7	2.7-16.7	4.13	0.11	-0.12
	2010 (A)	GM1-A1	satt242-satt270	191.6	174.8-196.2	3.64	0.07	-0.14
		GM2-A2	sat_036-satt468	2.1	0.1-6.7	5.83	0.15	0.17
		GM2-A2	sat_036-satt468	6.5	0.1-20.8	3.06	0.09	0.12
seed width	2006 (A)	GM7-D1a	satt383-satt515	231.1	224.0-232.9	4.31	0.12	0.12
	2008 (A)	GM7-D1a	sat_124-satt220	126.3	120.5-133.0	3.13	0.09	-0.10
	2009 (A)	GM7-D1a	sat_106-satt267	220.8	211.9-228.9	4.45	0.12	0.12
		GM20-O	satt173-satt581	29.4	23.7-31.0	5.96	0.00	0.20
	2009 (B)	GM20-O	satt173-satt581	29.4	25.8-31.0	4.13	0.13	0.12
	2010 (A)	GM20-O	satt173-satt581	29.4	24.3-31.0	4.03	0.11	0.14
	2010 (B)	GM20-O	satt173-satt581	29.4	24.1-31.0	5.98	0.19	0.15
seed length/seed width	2006 (A)	GM8-D1b	satt459-sat_135	39.3	28.3-52.8	3.38	0.11	0.01
	2009 (B)	GM6-C2	satt460-satt202	127.7	123.3-133.4	3.11	0.08	0.02

A and B, indicate that the experimental base of Heilongjiang Land Reclamation Research and Breeding Center and Hongxinglong agricultural experimental field, respectively.

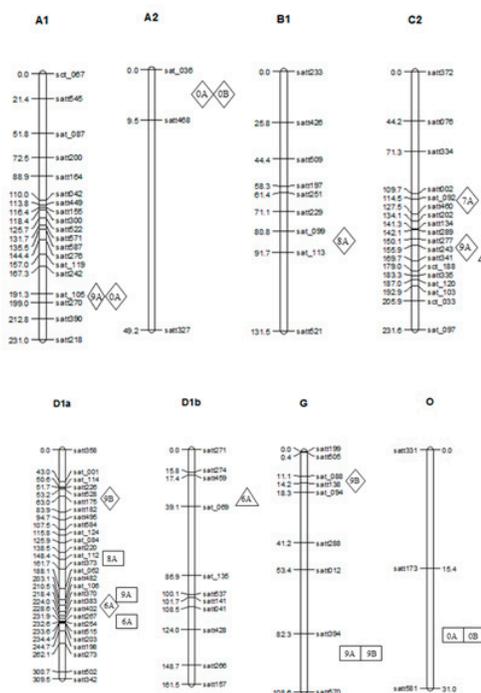


Figure 2. Loci distribution of seed length, seed width, and seed length/seed width of recombinant inbred line on linkage group. Diamond = seed length; rectangle = seed width; triangle = seed length/seed width; 6, 7, 8, 9, and 0 indicate the years for 2006, 2007, 2008, 2009, and 2010, respectively. A and B indicate the experimental base of Heilongjiang Land Reclamation Research and Breeding Center and Hongxinglong agricultural experimental field, respectively.

Table 4. Quantitative trait loci-environment effect analysis of seed length /seed width in population.

QTL	Marker interval	Site	Confidence interval	Contribution rate $h^2(a)$	Contribution rate $h^2(ae)$	A	AE1	AE2	AE3	AE4	AE5	AE6	AE7
GM1-A1-17	Satt270-Satt390	207.0	203.0-211.0	6.25	1.56	0.0155**	-0.0105*	-0.0011	0.0013	-0.0014	-0.004	0.003	0.0128**
GM14-1-1	Satt009-Satt530	1.0	0.0-7.9	3.04	0.96	-0.0071**	0.0013	0.0018	-0.0016	-0.0001	0.0016	-0.0015	-0.0013

*Significance level at 0.05; **Significance level at 0.01.

Epistatic interaction effects of QTLs

Seven pairs of QTLs that had additive x additive epistatic interaction effects were identified in 8 linkage groups (Figure 3, Table 5). One pair of seed length QTLs with additive x additive epistatic interaction effects occurred on the non-linkage interaction points GM15-J-3 and GM19-N-2. The additive effect value was 0.0537, and it was significant at the 0.01 level. The additive x additive contribution rate was 1.77%, the additive x additive environment contribution rate was 0.53%, and the additive contribution rate was significantly greater than that of the additive environment contribution rate.

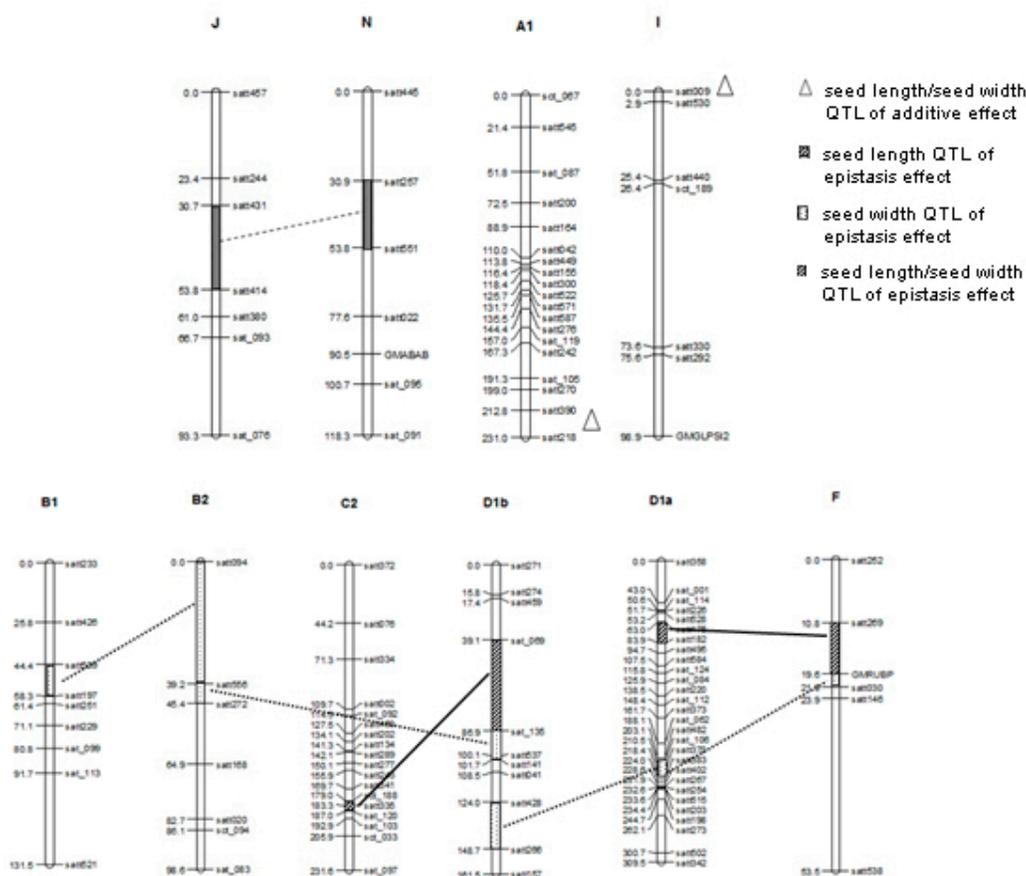


Figure 3. Distribution of the additive effect Quantitative trait loci (QTL) and epistatical effect QTL on linkage group.

Table 5. Analysis of additive x additive epistatic effect of seed length and seed width in population.

QTL_j	Seed length			Seed width			Seed length/seed width		
	GM15-J-3	GM3-B1-3	GM4-B2-2	GM7-D1a-19	GM7-D1a-19	GM6-C2-13	GM7-D1a-6		
marker interval_j	Satt431-satt414	Satt509-satt197	Satt556-satt272	Satt383-satt402	Satt383-satt402	Scl_188-satt335	Satt175-satt182		
site_j	31.7	111.2	43.2	224.0	224.0	182.0	63.0		
confidence interval_j	30.7-41.7	96.2-153.5	39.2-45.2	222.4-228.0	222.4-228.0	180.0-184.3	59.2-66.0		
QTL_j	GM19-N-2	GM4-B2-1	GM8-D1b-5	GM11-F-4	GM8-D1b-9	GM8-D1b-4	GM11-F-2		
marker interval_j	Satt257-satt551	Satt094-satt556	Sat_135-satt537	Satt030-satt146	Satt428-satt266	Sat_069-sat_135	Satt269-GMRUBP		
site_j	30.9	20	86.9	21.9	134	77.1	11.8		
confidence interval_j	27.0-36.9	12.0-28.0	78.1-92.9	19.6-22.9	124.0-144.0	67.1-91.9	5.0-16.8		
contribution rate h ² (aa)	1.77	5.89	2.20	1.35	3.21	2.50	2.03		
contribution rate h ² (aae)	0.53	0.56	0.68	1.15	0.52	3.47	1.92		
AA	-0.0537**	0.2023**	-0.0653**	-0.0198*	0.0544**	0.0106**	-0.0074**		
AAE1	0.0012	-0.0254	0.0144	0.0029	0.0005	-0.0103*	0.0044		
AAE2	0.0003	-0.0137	0.0141	-0.0018	0.0002	-0.0035	0.0025		
AAE3	-0.0003	-0.0167	0.0052	0.0269	-0.0004	-0.0151**	-0.0127**		
AAE4	-0.0003	-0.0178	-0.0028	0.0005	-0.0005	0.0020	0.0026		
AAE5	0.0002	0.0071	-0.0013	0.0074	-0.0070	0.0037	0.0021		
AAE6	-0.0010	0.0428	-0.0142	-0.0155	-0.0001	0.0019	0.0021		
AAE7	0.0000	0.0237	-0.0151	-0.0207	0.0010	0.0208**	-0.0010		

QTL = Quantitative trait loci *Significance level at 0.05; **Significance level at 0.01.

Four pairs of seed width QTLs with additive x additive epistatic interaction effects were identified. Two pairs occurred on the same QTL (GM7-D1a-19) between 2 other QTL sites, namely, GM8-D1b-9 and GM11-F-4. The additive effects were 0.0198 and 0.0544, respectively. Another 2 pairs of QTLs (GM3-B1-3 to GM4-B2-1 and GM4-B2-2 to GM8-D1b-5) had additive effects on the paternal parent. The recombinant types showed greater effects than the parental types. The additive x additive contribution rates ranged from 1.35 to 5.89%, the additive x additive environmental contribution rates ranged from 0.52 to 1.15%, and the additive x additive total contribution rate (12.65%) was significantly greater than that of the additive x additive environment contribution rate (2.91%).

Two pairs of seed length/seed width QTLs with additive x additive epistatic effects occurred between the non-linkage interaction loci. The additive effects were 0.0106 and 0.0074, and they were significant at the 0.01 level. One pair of QTLs with additive effects was from the female parent, and the effects of the parent types were greater than those of the recombinant types. Another pair of additive effects was from the male parent, and the effects of the recombinant types were greater than those of the parental types. The contribution rates of additive x additive effects ranged from 2.03 to 2.50%. The environmental contribution rates of the additive x additive effects ranged from 1.92 to 3.47%. The additive x additive environmental contribution rates of GM6-C2-13 and GM8-D1b-4 were greater than those of the additive x additive contribution rates. The additive x additive environmental contribution rate (5.39%) of seed length/seed width was greater than that of the additive x additive contribution rate (4.53%). The 7 different ecological conditions had little impact on seed length and seed width, and they had great influences on seed length/seed width during 2006 to 2010. The environment interaction effects on GM6-C2-13 and GM8-D1b-4 were significant at the 0.05 level in 2006 (A) and the 0.01 level in 2008 (A) and 2010 (B). The environment interaction effects on GM7-D1b-6 and GM11-F-2 were significant at the 0.01 level in 2008 (A).

DISCUSSION

Seed length and seed width had larger changes in the different ecological conditions with different genetic backgrounds; however, the trends of the change in seed length/seed width were consistent. Two QTLs were identified on linkage group D1b and C2, and they interacted with other linkage groups for seed length/seed width, which was not inconsistent with the results of QTL underlying seed length and seed width, respectively. Further studies were needed for traits and QTL analysis. However, there were several QTLs that were related to pod wall thickness and seed nitrogen accumulation. These would add confidence to the locus underlying seed length/seed width (Panthee et al., 2005; Guo et al., 2011).

The findings of this study demonstrate that certain QTL pairs display strong epistatic effects. To our knowledge, epistatic QTLs underlying seed width, seed length, and seed length/seed width of soybean have not been reported. In this study, 7 pairs of epistatic loci for seed length, seed width, and seed length/seed width were found; these loci occurred in the 8 linkage groups. They did not cover entire linkage groups in soybean. The additive effect contribution rates of the seed length and seed width were greater than those of additive environmental effects. The additive effect values were significant or very significant, and additive effects were significant. This result was similar that of a previous study, which reported that QTLs with significant additive and epistatic effects existed (Li et al., 2008).

Genes controlling yield traits depended on the specific environment. Yield traits and environment interaction were important factors that affected soybean yield. Therefore, QTLs that were identified in different environments were quite different (Paterson et al., 1991; Li et al., 2003). In this study, we analyzed the seed length and seed width of the groups in 7 different environmental conditions over the span of 5 years. The QE interaction had not been identified in each of the years. For seed length/seed width, the QE interactions were identified in the different environmental conditions. The additive x additive environmental contribution rates of GM6-C2-13 and GM8-D1b-4 were greater than those of the additive x additive contribution rates. The additive x additive total environmental contribution rate (5.39%) of seed length/seed width was greater than that of the additive x additive total contribution rate (4.53%) in soybean. The 7 different ecological conditions had less impact on seed length and seed width, then the ecological conditions had a great effect on seed length/seed width during 2006-2010. GM6-C2-13 and GM8-D1b-4 and the environment interaction effect reached a significant level in 2006 (A), and they reached a very significant level in 2008 (A) and 2010 (B). GM7-D1b-6, GM11-F-2, and the environment interaction effect reached a very significant level in 2008 (A). These results showed that 2 QTLs were greatly influenced by the environment and were not suitable for use in molecular-assisted breeding.

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