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Impact of epistasis and QTL × environment interaction on the accumulation of seed mass of soybean (*Glycine max* L. Merr.)

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Summary

The accumulation of seed mass in soybean is affected by both genotype and environment. The aim of the present study was to measure additive, epistatic and quantitative trait locus (QTL) × environment (QE) interaction effects of QTLs on the development of 100-seed weight in a population of 143 F_5 derived recombinant inbred lines (RILs) developed from the cross between the soybean cultivars 'Charleston' and 'Dong Nong 594'. Broad-sense heritability of 100-seed weight from 30 days (30D) to 80D stages was 0·58, 0·52, 0·62, 0·60, 0·66 and 0·57, respectively. A total of 17 QTLs with conditional additive (*a*) effect and/or conditional additive × environment interaction (*ae*) effect at specific stages were identified in ten linkage groups by conditional mapping. Of them, only 4 QTLs had significant *a* effect or *ae* effect at different stages of seed development. Among QTLs with significant *a* effect, five acted positively and six acted negatively on seed development. A total of 35 epistatic pairwise QTLs of 100-seed weight were identified by conditional mapping at different developmental stages. Five pairs of QTL showed the additive × additive epistatic (*aa*) effect and 16 QTLs showed the *aa* × environment interaction (*aae*) effect at the different developmental stages. QTLs with *aa* effect as well with their environmental interaction effect appeared to vary at different developmental stages. Overall, the results indicated that 100-seed weight in soybean is under developmental, genetic and environmental control.

1. Introduction

Seed weight, measured as mass per 100 seeds, is an important yield component of soybean and is normally positively correlated with seed yield (Burris *et al.*, 1973; Smith & Camper, 1975; Burton *et al.*, 1987). Seed weight is polygenically controlled and can range from 6 to 55 g per 100 seeds (Maughan *et al.*, 1996). It has been critical for the production of many oriental specialty food items, including tofu, natto, sprout and miso (Mian *et al.*, 1996). For example, soybean seed used for sprouts should possess small seed weight, whereas soybean seed used for tofu should have large seed weight. The demand for these products in the international market was steadily increasing at a rate of 3–5% every year (Griffis & Wiedermann, 1990). Thus, the seed weight of soybean was increasingly emphasized by breeders.

A variety of quantitative trait loci (QTLs) associated with soybean seed weight were identified in the past decade (Mansur *et al.*, 1996; Mian *et al.*, 1996; Hoeck *et al.*, 2003; Zhang *et al.*, 2004*a*; Panthee *et al.*, 2005), and soybean breeders have made progress in breeding programmes based on these QTLs. However, the genetic basis that underlies seed formation and development remains unclear, since the trait is controlled by multiple genes at different growth stages. Zhu (1995) proposed a conditional statistical method for calculating the dynamics of the causal genetic effects and variance components in developmental quantitative traits. Using this method,

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Atchley & Zhu (1997) analysed conditional epigenetic variability in mice, and Yan *et al.* (1998) detected QTLs with the developmental behaviour of plant height in rice. More recently, the association of developmental behaviour of quantitative traits, including morphological and seed quality traits, with molecular markers in soybean was reported (Sun *et al.*, 2006; Li *et al.*, 2007).

Soybean seed weight is a complex trait that is influenced by sets of genes during plant development. The genetic architecture of the complex trait consists of not only the actions of genes in a single locus, but also the inter-locus interactions. More and more evidence indicated that the complexity of the genetic architecture could be largely attributed to epistasis effect, which plays a significant role in heterosis, inbreeding depression, adaptation, reproductive isolation and speciation (Yang & Zhu, 2005). Evolution studies have elucidated that assembly and maintenance of favourable epistatic combinations adapted to a specific environment are a major mechanism of adaptation in various plant species (Allard, 1996). As was taken as an obvious example, the reproductive isolation between species arises through the accumulation of complementary genes that have no effect within a taxon, but which have a deleterious phenotypic effect when combined with genes from other taxa (Lynch, 1991; Orr, 1995; Hutter, 1997). Li *et al.* (1997) analysed inter-gene pool populations derived from crosses between *indica* and *japonica* cultivars of rice (*Oryza sativa* L.) using markers throughout the genome; the results showed that the performance of grain yield components is conditioned by high levels of digenic epistatic interactions in addition to the main effects of individual loci. Kulwal *et al.* (2005) analysed the grain protein content in hexaploid wheat using two different populations, and the results showed that a sizable proportion of the genetic variation was respectively due to interaction effects (28·59 and 54·03 %) and QTL main effects (7·24 and 7·22 %). William & Paul (2002) analysed the control of seed yield and other agronomic traits in the common bean using recombinant inbred lines (RILs) and revealed that both the main effect and epistatic QTL effect affected these traits. These results (Li *et al.*, 1997; William & Paul, 2002; Kulwal *et al.*, 2005) suggested that genetic variation is controlled by genes (QTLs) interactions to a certain extent.

QTL × environment (QE) interaction is another important component affecting quantitative traits. QE interaction reduces the association between phenotypic and genotypic values, and leads to variable levels of the significance of QTL effects across environments (Hayes *et al.*, 1993; Romagosa *et al.*, 1996). Paterson *et al.* (1991) analysed three traits in F_2 population of a tomato cross and found that only 4 of 29 QTLs were detected in all three environments. Lu *et al.* (1996) analysed six important agronomic traits in rice using a set of double haploid (DH) lines and reported that only 7 of 22 QTLs were significant in all three environments. Zhuang *et al.* (1997) analysed yield components and plant height in rice using F_2 lines and found that only 17 of the total 44 QTLs were detected in more than one environment. Yan *et al.* (1998) and Cao *et al.* (2001) reported that obviously QE interaction influences the development of plant height in rice. In soybean, QTLs for plant height and lodging were less consistent across environments, but were more consistent for maturity, indicating that QE interaction is trait-dependent (Lee *et al.*, 1996). These studies suggested that individual QTLs are sensitive to changes of the environment and that QE interaction plays an important role in affecting quantitative traits.

The impact of epistatic effect and QE interaction effect on plant height development of rice has been analysed by Cao *et al.* (2001). However, little information was available on soybean developmental behaviour. Sets of genes are expressed selectively at different growth stages of seed development and are influenced by both genotype and environment; hence, we found it necessary to investigate the epistatic effects as well the QE interaction effect during seed development of soybean by combining the statistical procedures for analysing conditional genetic effects (Zhu, 1995) and the QTL mapping method based on mixed model approaches (Wang *et al.*, 1999; Zhu, 1999). The temporal gene expressions including additive (*a*) effect, additive × additive epistatic (*aa*) effect and their QE interaction effect on seed weight are also discussed in the present study.

2. Materials and methods

(i) *Plant materials and field trials*

The mapping population, consisting of 143 F_5 derived RILs, was advanced by single-seed descent from crosses between 'Charleston' (provided by Dr R. L. Nelson, NSRL, University of Illinois, Champaign, Urbana, IL, USA) and 'Dong Nong 594' (developed by Northeast Agriculture University, Harbin, China). The RILs were extracted at F_5 generation, advanced without selection for seed size and maturity, and used for this study at $F_{5:9}$, $F_{5:10}$ and $F_{5:11}$.

The RILs and their parents were grown in a randomized complete block design with three replications at Harbin, China (45°N, fine-mesic chernozen soil) in 2004, 2005 and 2006. Rows were 3 m long with a space of 6 cm between two plants, and two-row plots were used. The field location was different each year, soil types differed slightly, planting dates differed by 2 days, the herbicides acetochlor and chlorimuron-ethyl were applied in different years, and

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soybean was rotated with corn. Furthermore, mean temperature and rainfall varied each year (23·1 °C, 477·6 mm in 2004; 24·9 °C, 569·1 mm in 2005; and 27·4 °C, 544·8 mm in 2005). Therefore, the environments in the 3 years were quite diverse.

Each plot for a single genotype provided 20 plants as seed donors per time point and there were three replications of the two row plots. Pods were picked from five to seven nodes of the main stem every 10 days from 30 days after flowering until maturity. The 30 day (30D) sample represented the R2 stage and the 80D sample represented the R8 stage of growth with intervening stages with about 10D intervals. Seeds were dried for 30 min in an oven at 105 °C and continuously dried at 50–70 °C until the seed weight was stable.

(ii) *Construction of the genetic linkage map*

In a previous study (data not shown), one genetic linkage map including 164 SSR markers and 35 RAPD markers was constructed using 143 F_5 derived RILs from the cross between 'Charleston' and 'Dong Nong 594'. The order of most markers is consistent with Cregan's map (Cregan *et al*., 1999). This genetic linkage map covered 3067·28 cM and the average distance between markers was 15·65 cM with the longest distance being 48·8 cM and the shortest distance being 0·5 cM. The average number of markers on each linkage group was 9·7 with an average length of 153·36 cM.

(iii) *Statistical analysis*

Wang *et al*. (1999) developed a program (QTLMapper version 1.0) to analyse QTLs with *a* and *aa* effects, as well as their environmental interaction effects on the RIL population at the harvesting stage. The phenotypic value of the *k*th RIL line in environment *h* can be partitioned by the following mixed linear model (Zhu, 1999):

$$\begin{aligned} y_{hk} = {} & \mu + a_i x_{A_{ik}} + a_j x_{A_{jk}} + aa_{ij} x_{AA_{ijk}} \\ & + u_{E_{hk}} e_{E_h} + u_{A_i E_{hk}} e_{A_i E_h} + u_{A_j E_{hk}} e_{A_j E_h} \\ & + u_{AA_{ij} E_{hk}} e_{AA_{ij} E_h} + \sum_{f(h)} u_{Mfk(h)} e_{M_{f(h)}} \\ & + \sum_{l(h)} u_{MM_{lk(h)}} e_{MM_{l(h)}} + \varepsilon_{hk}. \end{aligned} \tag{1}$$

The meaning of each parameter is as described in Wang *et al*. (1999) and Luo *et al*. (2001): y_{hk} is the phenotypic value of a quantitative trait measured on the *k*th RIL in environment *h*; μ is the population mean; a_i and a_j are *a* effects (fixed effects) of the two putative QTLs Q_i and Q_j, respectively; aa_{ij} is the *aa* effect (fixed effect) between Q_i and Q_j; $x_{A_{ik}}$, $x_{A_{jk}}$ and $x_{AA_{ijk}}$ are coefficients of QTL effect derived according to the observed genotypes of the markers M_{i-}, M_{i+} and M_{j-}, M_{j+} flanking the QTLs; e_{E_h} is the random effect of environment *h* with the coefficient $u_{E_{hk}}$; $e_{A_i E_h}$ and $e_{A_j E_h}$ are the random *ae* effects with coefficients $u_{A_i E_{hk}}$ and $u_{A_j E_{hk}}$ for Q_i and Q_j, respectively; $e_{AA_{ij} E_h}$ is the random *aa* × environment interaction (*aae*) effect with the coefficient $u_{AA_{ij} E_{hk}}$; $e_{M_{f(h)}}$ is the effect of marker *f* nested within the *h*th environment with coefficient $u_{M_{fk(h)}}$; $e_{MM_{l(h)}}$ is the effect of marker × marker interaction nested within the *h*th environment with coefficient $u_{MM_{lk(h)}}$; and ε_{hk} is the residual effect. The marker factors $e_{M_{f(h)}}$ and $e_{MM_{l(h)}}$ in the model are used to absorb *a* and *aa* effects of background QTLs (additional segregating QTLs other than the loci examined).

Conditional QTL analysis was conducted with the phenotypic value at time *t*, given the phenotypic behaviour at time $(t-1)$, using QTLMapper version 1.0 (Wang *et al*., 1999). Like that in eqn (1), the conditional value $y_{hk(t/(t-1))}$ can be partitioned as

$$\begin{aligned} y_{hk(t/(t-1))} = {} & \mu_{(t/(t-1))} + a_{i(t/(t-1))} x_{A_{ik}} + a_{j(t/(t-1))} x_{A_{jk}} \\ & + aa_{ij(t/(t-1))} x_{AA_{ijk}} + u_{E_{hk}} e_{E_{h(t/(t-1))}} \\ & + u_{A_i E_{hk}} e_{A_i E_{h(t/(t-1))}} + u_{A_j E_{hk}} e_{A_j E_{h(t/(t-1))}} \\ & + u_{AA_{ij} E_{hk}} e_{AA_{ij} E_{h(t/(t-1))}} + \sum_{f(h)} u_{M_{fk(h)}} e_{M_{f(h)(t/(t-1))}} \\ & + \sum_{l(h)} u_{MM_{lk(h)}} e_{MM_{l(h)(t/(t-1))}} + \varepsilon_{hk(t/(t-1))} \end{aligned} \tag{2}$$

with all the parameters defined as conditional effects. The QTLs detected by conditional mapping will reflect the net expression of genes during the time period from time $(t-1)$ to time *t*, independent of the genetic effects before time $(t-1)$.

The conditional phenotypic value $y_{hk(t/(t-1))}$ of 100-seed weight behaviour was obtained by the mixed model approaches for the conditional genetics of developmental quantitative traits (Zhu, 1995). The environment effect or replication effect is assumed to be random. However, the three environments/replications are not a random sample, due to year, field, population and other conditions. So the likelihood-ratio threshold was chosen as $\alpha = 0{\cdot}01$ for claiming putative QTLs, the genetic effects of which were further tested by a *t*-test with the jack-knifing resampling procedure. QTL was presented when genetic main effects (*a* and *aa* effects) or QE interaction effects (*ae* and *aae* effects) were significantly different from zero ($P \leqslant 0{\cdot}01$).

Broad-sense heritability of 100-seed weight was computed as $h^2 = h_g^2 / ((h_g^2 + h_e^2)/n)$, where h_g^2 and h_e^2 are the estimates of genetic and residual variance, respectively, derived from the expected mean squares of the variance and *n* is the number of replications (Blum *et al*., 2001).

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Table 1. *Statistical analysis of mean 100-seed weights (grams) at different days after pollination (D) for the parental cultivars and the F_5 derived RIL population. The means represent pods gathered from 5–7 nodes of each of 12 plants per genotype and from two plots per year. The experiment was conducted over 3 years, all in different fields at Harbin, China*

		100-seed weight (g)							
		Parents				RIL population			
Developmental stage (days)	Year	Charleston (mean ± S.D.) (g)	Dong Nong 594 (mean ± S.D.) (g)	Range	Mean ± S.D.	CV (%)	Skew	Kurt	Broad-sense heritability
30D	2004	0·42 ± 0·09	1·43 ± 0·27	0·20–2·82	1·17 ± 0·45	36·46	1·00	0·99	0·58
	2005	0·70 ± 0·24	0·81 ± 0·58	0·15–3·50	1·26 ± 0·74	56·68	0·72	−0·01	
	2006	0·41 ± 0·16	1·60 ± 0·75	0·38–6·20	2·19 ± 1·26	57·46	0·82	0·05	
40D	2004	2·19 ± 0·72	2·53 ± 0·72	2·60–3·59	3·05 ± 1·07	35·08	0·75	0·61	0·52
	2005	2·50 ± 0·86	3·83 ± 0·92	1·71–10·02	4·89 ± 1·47	30·07	0·33	0·34	
	2006	3·36 ± 1·01	6·41 ± 1·93	1·58–13·10	6·40 ± 2·66	41·56	0·33	−0·44	
50D	2004	3·69 ± 1·12	6·01 ± 2·01	3·13–12·74	6·50 ± 1·72	26·51	0·72	0·94	0·62
	2005	6·97 ± 2·51	10·91 ± 2·13	5·26–15·97	9·98 ± 2·27	22·91	0·10	−0·45	
	2006	5·99 ± 1·91	11·60 ± 1·98	3·08–18·95	11·73 ± 2·97	25·32	0·06	−0·28	
60D	2004	7·27 ± 2·03	14·30 ± 2·62	5·21–17·45	10·94 ± 2·42	22·15	0·37	0·09	0·60
	2005	12·84 ± 2·92	16·76 ± 2·26	9·16–22·53	15·59 ± 2·48	15·89	−0·37	−0·03	
	2006	12·67 ± 2·21	18·30 ± 2·47	10·33–23·04	15·57 ± 2·30	14·80	0·35	0·69	
70D	2004	10·44 ± 3·24	15·93 ± 3·01	8·88–19·82	14·07 ± 2·25	15·99	0·16	0·60	0·66
	2005	14·32 ± 2·82	19·08 ± 1·89	13·10–25·90	17·45 ± 2·06	11·81	0·48	0·53	
	2006	15·41 ± 3·14	19·37 ± 1·73	12·04–24·07	16·99 ± 2·13	12·56	0·57	1·00	
80D	2004	11·91 ± 3·93	19·33 ± 2·12	11·03–24·56	16·07 ± 2·31	14·37	0·43	0·86	0·57
	2005	15·65 ± 2·22	19·85 ± 1·92	13·45–27·27	18·33 ± 2·06	11·24	0·45	0·94	
	2006	15·82 ± 2·23	19·45 ± 1·28	12·27–24·14	17·87 ± 2·05	11·48	0·15	0·74	

CV, coefficient of variation.

3. Results

(i) *Phenotypic variation*

Phenotypic values of 100-seed weight at different developmental periods across diverse environments were evaluated at Harbin, China, for 2004, 2005 and 2006 (Table 1). The differences between the two parents were significant at all stages measured across environments. The trait values for 'Dong Nong 594' were higher than those of 'Charleston' across environments. In contrast, 100-seed weight variation for 143 RILs across diverse environments was not significant. Both skew and kurtosis values of 100-seed weight were less than 1·0 at all growth stages measured in diverse environments, suggesting that the segregation of this trait fits a normal distribution model. Broad-sense heritability of 100-seed weight for 30D to 80D stages was 0·58, 0·52, 0·62, 0·60, 0·66 and 0·57, respectively.

(ii) *Analysis of QTL epistasis effects during seed development*

Both *aa* and *aae* effects were analysed using QTL-Mapper version 1.0 along with *a* and *ae* effects. A total of 35 epistatic pairwise QTLs were identified by conditional mapping in different developmental stages (Table 2). Of them, epistatic effects of three pairs of QTLs (swC2_1-swD1b_2 at 40D, 60D and 70D; swC2_1-swL_1 at 50D, 60D and 80D; and swC2_3-swD1b_1 at 30D, 40D and 60D) were detected at three stages. Epistatic effects of seven pairs of QTLs (swA1_1-swC2_3 at 40D and 70D; swC2_1-swC2_3 at 30D and 40D; swC2_1-swD1b_1 at 30D and 40D; swC2_1-swD1b_3 at 30D and 80D; swC2_3-swD1b_3 at 30D and 80D; swC2_3-swE_2 at 40D and 70D; and swD1b_1-swE_2 at 60D and 70D) were identified at two stages. Others could be identified at only one stage. This might indicate that *aa* effect existed mostly for a short time period, so that they would hardly be observed during different developmental stages. This was implied by the fact that *aa* effects were contributed by transient gene expression, but *a* effects were contributed by continuous gene expression.

aae was an important component of the total QE interaction effects. A total of 35 pairs of QTLs were detected with conditional epistatic effects, 16 pairs having only *aae* effect, and five pairs having only *aa* effect. Other pairs had both *aa* and *aae* effects (Table 2). These results indicated that environment could greatly affect the gene expression with epistatic effects during quantitative trait development.

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Table 2. *Estimated epistatic* (*aa*) *and epistasis × environment interaction* (*aae*) *effects of seed weight QTL at six different stages for 2004, 2005 and 2006 at Harbin, China*

						aae effect		
QTL_i	$Interval_i$	QTL_j	$Interval_j$	Stage	*aa* effect	2004	2005	2006
swA1_1	Satt300–Satt200	swC2_3	Satt460–Satt134	40D	0·67**	−0·15*	0·56**	0·46**
				70D	0·57**	−0·34**	−1·34**	
		swC2_1	OPK14_70– Satt202	70D	1·43**		0·12*	−0·87**
		swE_1	Satt355–Satt452	80D	0·13*	−0·12*	0·21*	0·45**
swA1_2	Satt155–Satt449	swC1_1	Satt164 –OPAO19_1	80D		−0·11*	−0·91**	0·78**
		swD1b_3	Satt271–Satt274	80D		−0·68**	−0·45**	
swC1_1	Satt164–OPAO19_1	swE_1	Satt355–Satt452	50D			0·98**	−1·24**
		swE_2	Satt263–Satt117	60D		−0·23*		0·67**
		swF_2	Satt335–Sat_120	60D		−0·78**	−0·93**	−1·45**
		swG_1	Satt138–Sat_088	50D			−0·56**	
		swL_1	Satt182–Satt495	80D		1·43**		
swC2_1	OPK14_70–Satt202	swC2_3	Satt460–Satt134	30D	−0·45**		−0·23*	0·54**
				40D	−0·89**	−0·34**		−0·11*
		swD1b_1	Satt157–Satt266	30D	0·45**	−0·67**	−0·16*	−1·27**
				40D		−0·24*	−0·15*	
		swD1b_2	Satt537–Sat_135	40D	0·47**	−0·96**	−0·31**	−0·69**
				60D	−0·16*	−0·86**		−0·12*
				70D	−0·14*		−0·25*	−0·41**
		swD1b_3	Satt271–Satt274	30D	−0·23*	−0·09*	−0·16*	
				80D	2·13**		0·19*	0·98**
		swL_1	Satt182–Satt495	50D			−0·19*	−0·98**
				60D	−0·45**		−0·20*	
				80D	−0·29*	−0·11*	−0·76**	−0·67**
swC2_3	Satt460–Satt134	swD1b_1	Satt157–Satt266	30D	0·14*			−1·01**
				40D	−0·32**	−0·45**	−0·14*	
				60D		−0·23*	0·16*	0·37**
		swD1b_3	Satt271–Satt274	30D	−0·19*	−0·93**	−0·34*	−1·45**
				80D	0·11*	0·78**	−0·14*	−0·26*
		swE_2	Satt263–Satt117	40D			−0·87**	0·69**
				70D		0·59**	−0·37**	
swD1b_1	Satt157–Satt266	swD1b_3	Satt271–Satt274	30D				0·27*
		swD1b_2	Satt537–Sat_135	40D			−0·16*	
		swM_1	Satt150–Satt220	40D		−0·15*		
		swE_2	Satt263–Satt117	60D		−0·58**		0·67**
				70D		−0·45**		
swD1b_2	Satt537–Sat_135	swM_1	Satt150–Satt220	40D	−0·13*			
		swF_2	Satt335–Sat_120	60D	−0·43**			
		swL_1	Satt182–Satt495	60D	−0·17*			
		swG_1	Satt138–Sat_088	70D	−0·78**			
swD1b_3	Satt271–Satt274	swF_1	Sct_188–Satt335	80D		−1·04**		
		swL_1	Satt182–Satt495	80D	−0·18*		−0·69**	
swE_1	Satt355–Satt452	swG_1	Satt138–Sat_088	50D	0·52**			−0·34**
		swF_1	Sct_188–Satt335	50D		−0·21*		−0·88**
swE_2	Satt263–Satt117	swG_1	Satt138–Sat_088	70D	−0·58**			
swF_1	Sct_188–Satt335	swG_1	Satt138–Sat_088	50D			−0·17*	
		swL_1	Satt182–Satt495	80D	−0·41**		−0·47**	
swG_1	Satt138–Sat_088	swL_1	Satt182–Satt495	50D		0·12*		−0·17*

* $P<0·01$.
** $P<0·005$.

(iii) *Analysis of QE interaction during seed development*

A total of 17 QTLs with conditional *a* and/or *ae* effects at some specific stages were identified in ten linkage groups by conditional mapping (Table 3). Of them, 13 QTLs had significant *a* effect at the 0·01 or 0·005 level. Five QTLs (swA1_2 at 50D and 80D stages; swC2_2 from 30D to 80D stages; swC2_3 at 30D, 40D, 60D and 70D stages; swD1b_2 at 40D

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Table 3. *Estimated additive* (*a*) *and additive* × *environment interaction* (*ae*) *effects of seed weight QTL at six different stages for 2004, 2005 and 2006 at Harbin, China*

QTL	Marker interval	Stage	Mean ± S.E.M. for RILs with allele from[a]		*a* effect	*ae* effect		
			'Dong Nong 594'	'Charleston'		2004	2005	2006
swA1_1	Satt300–Satt200	40D	2·98 ± 0·19	3·02 ± 0·17		1·35**	0·94**	
		70D	17·23 ± 0·95	18·52 ± 1·03	−0·69**	1·65**		−0·45*
		80D	20·32 ± 1·86	22·97 ± 1·99	−0·79**	0·95**		
swA1_2	Satt155–Satt449	50D	10·47 ± 0·83	9·83 ± 0·79	1·45**			
		80D	21·84 ± 1·90	20·97 ± 1·98	0·35*			
swA2_1	Satt538–Sct_067	40D	3·23 ± 0·15	4·14 ± 0·22	−0·35*	0·87**	0·76**	−1·36**
		50D	10·39 ± 0·90	11·20 ± 0·80	−0·98**	1·47**	−2·01**	
		70D	17·84 ± 1·13	19·03 ± 1·42	−1·23**			0·98**
swC1_1	Satt164–OPAO19_1	50D	10·24 ± 0·93	10·14 ± 0·32		−0·56**	−0·47*	−1·45**
		60D	15·76 ± 1·49	15·63 ± 1·54			1·34**	0·86**
		80D	21·79 ± 1·84	21·93 ± 1·09		−1·54**		0·98**
swC2_1	OPK14_70–Satt202	30D	2·77 ± 0·18	1·84 ± 0·15	0·79**	1·56**	−0·98**	
		40D	3·03 ± 0·10	3·96 ± 0·43	−1·47**		0·76**	
		50D	10·93 ± 0·79	11·34 ± 0·88	−0·39*	1·23**	−0·89**	−0·97**
		60D	16·22 ± 1·03	16·42 ± 1·52		−2·97**		
		70D	18·63 ± 1·21	18·44 ± 1·14	0·32*	1·13**	−0·76**	
		80D	19·98 ± 2·04	20·04 ± 1·94		1·68**		−2·31**
swC2_2	Satt202–Satt460	30D	2·42 ± 0·14	2·23 ± 0·20	0·57**	0·45*	1·57**	−3·45**
		40D	4·04 ± 0·30	3·53 ± 0·25	0·87**	1·45**	2·06**	1·97**
		50D	12·16 ± 1·03	10·98 ± 0·70	0·79**	−0·67**	1·66**	
		60D	16·76 ± 1·38	15·63 ± 1·63	0·54**	1·37**	0·87**	2·21**
		70D	18·95 ± 1·49	18·32 ± 1·28	0·83*	−0·79**	0·87**	0·64**
		80D	23·49 ± 1·93	22·96 ± 1·84	1·47**		1·58**	
swC2_3	Satt460–Satt134	30D	2·56 ± 0·22	2·32 ± 0·15	0·96**	−0·59**		
		40D	4·62 ± 0·17	3·95 ± 0·39	0·72**	1·12**	1·19**	
		60D	17·69 ± 1·57	16·78 ± 1·68	1·26**			−1·17**
		70D	19·43 ± 0·95	19·98 ± 1·21	1·35**			1·10**
swD1b_1	Satt157–Satt266	30D	2·44 ± 0·28	2·27 ± 0·24		0·96**	−0·88**	−0·93**
		40D	5·93 ± 0·33	5·92 ± 0·27			−0·85**	1·21**
		60D	16·89 ± 1·73	17·03 ± 1·82		0·45*		−1·12**
		70D	19·05 ± 1·89	19·14 ± 1·55		1·56**		0·85**
swD1b_2	Satt537–Sat_135	40D	4·04 ± 0·30	3·53 ± 0·25	1·42**		1·24**	
		60D	15·55 ± 1·49	15·36 ± 1·58		−0·83**	1·01**	−1·48**
		70D	19·87 ± 1·83	18·93 ± 1·59			0·55**	−0·86**
swD1b_3	Satt271–Satt274	30D	2·65 ± 0·24	2·45 ± 0·20		0·45*	−0·87**	1·79**
		80D	21·73 ± 1·78	21·93 ± 2·03		1·56**	−0·95**	
swE_1	Satt355–Satt452	50D	10·89 ± 1·05	11·56 ± 0·94	−1·40**			
		80D	20·97 ± 2·43	21·85 ± 2·03	−0·69**			
swE_2	Satt263–Satt117	40D	3·99 ± 0·29	4·24 ± 0·37	−1·23**	0·79**		1·34**
		60D	15·85 ± 1·26	16·04 ± 1·78	−2·67**	1·56**		0·94**
		70D	18·29 ± 0·90	18·29 ± 1·00		2·60**		
swF_1	Sct_188–Satt335	50D	10·32 ± 0·79	10·28 ± 1·42		−1·34**	0·79**	−0·89**
		80D	21·54 ± 1·93	21·74 ± 1·77			0·67*	
swF_2	Satt335–Sat_120	60D	16·78 ± 1·62	17·10 ± 1·69	−0·96**		−1·11**	−1·45**
swG_1	Satt138–Sat_088	50D	9·47 ± 1·02	10·29 ± 0·84	−1·56*			
		70D	18·47 ± 1·87	20·03 ± 1·89	−2·31**			
swL_1	Satt182–Satt495	50D	11·20 ± 0·73	11·30 ± 0·79		0·45*		
		60D	17·94 ± 1·55	15·69 ± 1·78	1·45**	1·32**	−1·29**	
		80D	22·43 ± 1·86	20·97 ± 2·41		2·66**		0·41**
swM_1	Satt150–Satt220	40D	5·21 ± 0·42	3·63 ± 0·36	0·48*			

* $P < 0{\cdot}01$.
** $P < 0{\cdot}005$.
[a] S.E.M.: mean ± S.D./$\sqrt{N}$, where N is the number of each allele.

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stage; swL_1 at 60D stage; and swM_1 at 40D stage) had positive effects on seed development and six QTLs (swA1_1 at 70D and 80D stages; swA2_1 at 40D, 50D and 70D stages; swE_1 at 50D and 80D stages; swE_2 at 40D and 60D stages; swF_2 at 60D stage; and swG_1 at 50D and 70D stages) had negative effects on seed development, whereas others inconsistently had positive or negative effects at different stages. Four QTLs (swA1_2 at 50D and 80D stages; swE_1 at 50D and 80D stages; swG_1 at 50D and 70D stages; and swM_1 at 40D stage) had significant *a* effect, but no significant *ae* effect, and only QTL swC2_2 (from 30D to 80D stages) had significant *a* effect, which affected seed development during all development stages. The higher seed weight parent, 'Dong Nong 594', contributed alleles (QTL swC2_2, QTL swC2_3 and QTL swM_1) for increasing seed weight at different stages, but QTL swA1_1 and QTL swA2_1 decreased seed weight at different stages. QTL swC2_1 increased seed weight at 30D and 70D stages, but decreased seed weight at 40D and 50D stages, suggesting that the impact of some QTLs was different at the different development stages.

A total of 13 QTLs possessed significant *ae* effect at the different developmental stages (Table 3). Of them, eight QTLs (swA2_1 at 40D stage; swC1_1 at 50D stage; swC2_1 at 50D stage; swC2_2 at 30D, 40D, 60D and 70D stages; swD1b_1 at 30D stage; swD1b_2 at 60D stage; swD1b_3 at 30D stage; and swF_1 at 50D stage) had significant *ae* effect at different stages in all three environments, 12 QTLs (swA1_1 at 40D and 70D stages; swA2_1 at 50D stage; swC1_1 at 60D stage; swC2_1 at 30D, 70D and 80D stages; swC2_2 at 50D stage; swC2_3 at 40D stage; swD1b_1 at 40D, 60D and 70D stages; swD1b_2 at 70D stage; swD1b_3 at 80D stage; swE_2 at 40D and 60D stages; swF_2 at 60D stage; and swL_1 at 60D and 80D stages) had significant *ae* effect in two environments, and nine QTLs (swA1_1 at 80D stage; swA2_1 at 70D stage; swC2_1 at 40D, 60D and 80D stages; swC2_2 at 80D stage; swC2_3 at 30D, 60D and 70D stages; swD1b_2 at 40D stage; swE_2 at 70D stage; swF_1 at 80D stage; and swL_1 at 50D stage) had *ae* effect only in one environment. Four QTLs (swC1_1 at 50D, 60D and 80D stages; swD1b_1 at 30D, 40D, 60D and 70D stages; swD1b_3 at 30D and 80D stages; and swF_1 at 50D and 80D stages) had significant *ae* effect but no significant *a* effect. Five QTLs (swA1_1 at 40D, 70D and 80D stages; swA2_1 at 40D and 50D stages; swD1b_1 at 30D, 60D and 70D stages; swE_2 at 40D, 60D and 70D stages; and swL_1 at 50D, 60D and 80D stages) contributed a positive *ae* effect in seed weight increment at different developmental stages. One QTL (swC1_1 at 50D and 80D stages) showed a negative *ae* effect and other QTLs showed positive or negative *ae* effect on seed development in 2004. Three QTLs (swC2_2 from 30D to 80D stages; swD1b_2 at 40D, 60D and 70D stages; and swF_1 at 50D and 80D stages) showed increased *ae* effect, four QTLs (swD1b_1 at 30D and 40D stages; swD1b_3 at 30D and 80D stages; swF_2 at 60D stage; and swL_1 at 60D stage) showed decreased *ae* effect and other QTLs showed increased or decreased *ae* effect in 2005. Two QTLs (swE_2 at 40D and 60D stages; and swL_1 at 80D stage) showed increased *ae* effect, four QTLs (swA1_1 at 70D stage; swC2_1 at 50D and 80D stages; swF_1 at 50D stage; and swF_2 at 60D stage) showed decreased *ae* effect and other QTLs showed increased or decreased *ae* effect in 2006. Only one QTL (swE_2 at 40D and 60D stages) showed increased *ae* effect at different developmental stages in 2 years (2004 and 2006).

A total of nine QTLs (swA1_2 at 70D and 80D stages; swA2_1 at 40D and 50D stages; swC2_1 at 30D, 40D, 50D and 70D stages; swC2_2 from 30D to 80D stages; swC2_3 from 30D to 70D stages; swD1b_2 at 40D stage; swE_2 at 40D and 60D stages; swF_2 at 60D stage; and swL_1 at 60D stage) were detected with both *a* and *ae* effects at different developmental stages (Table 3).

4. Discussion

The conventional statistics revealed that the development of some quantitative traits like morphological traits was controlled by the interactions of many genes that might behave differentially during different growth periods, and that gene expression was modified by interactions with other genes and by environment (Atchley & Zhu, 1997; Vodkin *et al*., 2004). Previous works on QTL analysis of seed quantitative traits of soybean have concentrated on QTLs and QE interaction measured at the harvesting stage (Mansur *et al*., 1996; Mian *et al*., 1996). But no information has been available so far on the impact of epistasis and QE epistasis on seed weight at different developmental stages of soybean. In the present study, QTLs with *a* and *aa* effects as well as with their environmental interaction effects, were shown to vary at different stages of seed development of soybean.

QE interaction was an important component affecting quantitative traits. Understanding QE interaction is of importance to the breeding programme and to marker-assisted selection and to map-based gene cloning. Usually, QE interaction effect is treated as random effect, especially in different years. This implies that QTLs would be affected by different environments. QE interaction has been reported by comparing QTLs detected in specific environments (Paterson *et al*., 1991; Stuber *et al*., 1992; Lu *et al*., 1997). However, QTLs detected separately in each environment was not the real QE interaction (Jansen *et al*., 1995). The mixed model approaches for QTL

mapping can provide unbiased prediction on QE interaction when the experiment was conducted under multiple environments (Zhu, 1999). Regarding 100-seed weight during seed development, four QTLs (swA1_2, swE_1, swG_1 and swM_1) had only *a* effect in different developmental stages, and four QTLs (swC1_1, swD1b_1, swD1b_3 and swF_1) had only significant *ae* effect. Other QTLs had both *a* and *ae* effects at different developmental stages. QTLs with only QE effects were mainly determined by environments; therefore marker-assisted selection (MAS) using this type of QTL was ineffective. This suggested that QTLs with *a* effect should be applied in MAS rather than QTLs with QE effects.

A total of six QTLs with significant *a* effect (swA1_2, swC2_2, swC2_3, swD1b_2, swL_1 and swM_1) were positive with seed sizing up, and six QTLs (swA1_1, swA2_1, swE_1, swE_2, swF_2 and swG_1) were negative with seed development at different stages. The *a* effect of other QTLs varied with seed development. For example, QTL swC2_1 was served to increase seed weight at 30D and 70D stages, but to decrease seed weight at 40D and 50D stages. The finding that QTL with significant *a* effect was positive/negative to the development of seed weight seemed to meet different breeding goals in MAS than other types of QTLs. The parent (Dong Nong 594, with bigger seed) contributed alleles for increasing seed weight at QTLs swC2_2, swC2_3 and swM_1 at different developmental stages, but for decreasing seed weight at QTLs swA1_1 and swA2_1 at different developmental stages. If all of QTLs affecting the development of seed weight is in the same direction, it will greatly promote selection accuracy in seed weight by the accumulation of gene effects.

Epistasis among different loci played an important role in plant evolution (Lynch, 1991; Orr, 1995; Hutter, 1997). Recently, QTL mapping suggested that epistasis was the main genetic basis of complex traits (Li *et al*., 1997; William & Paul, 2002; Hyten *et al*., 2004; Kulwal *et al*., 2005). In the present study, 35 pairs of QTLs with epistasis effect were detected; five pairs of them (swD1b_2-swM_1, swD1b_2-swF_2, swD1b_2-swL_1, swD1b_2-swG_1 and swE_2-swG_1) showed only *aa* effect and 16 pairs of them showed only *aae* effect at different developmental stages (Table 3). This result further indicated that epistasis on seed weight of soybean was ubiquitous. In the present study, most of the QTLs shared epistasis effect with other QTLs. However, swC2_2 with both *a* and *ae* effects was not associated with other QTLs and independently affected the development of seed weight.

In the past, the phenotypic values of 100-seed weight were only measured at the final stage for QTL analysis in soybean (Mansur *et al*., 1996; Mian *et al*., 1996; Hoeck *et al*., 2003; Hyten *et al*., 2004; Zhang *et al*., 2004*a*; Panthee *et al*., 2005). Hoeck *et al*. (2003) used three populations to identify seed weight QTL and found that Satt322 in MLG C2 was associated with seed weight. The QTL swC2_3 in the present study was located at chromosomal locations similar to those identified by Hoeck *et al*. (2003). Watanabe *et al*. (2004) identified QTLs associated with seed weight near Satt157 in MLG D1b + W, which was similar to swD1b_1 in the present study.

For marker-assisted selection, the simultaneous application of many markers, taking into account epistasis, will lead to a highly effective selection of phenotype (Watanabe *et al*., 2004). The epistasis impact on some traits of soybean has been reported earlier (Tukamuhabwa *et al*., 2002; Watanabe *et al*., 2004; Primomo *et al*., 2005). Tukamuhabwa *et al*. (2002) studied pod shattering using diallel cross of ten pure breeding lines; the results showed that epistatic effect remarkably influenced pod shatter in soybean. Primomo *et al*. (2005) analysed isoflavone content in soybean seed through 207 RILs from the cross between 'AC756' and 'RCAT Angora' using SSR markers; the results suggested that 23 pairs of epistatic QTLs remarkably affected isoflavone content. Watanabe *et al*. (2004) studied reproductive development and seed quality trait through F_8 derived RILs from the cross between 'Misuzudaizu' and 'Moshidou gong 503' using SSR markers; the results indicated that somes pair of epistatic QTLs influenced flower time, maturity and reproductive period, especially two pairs of epistatic QTLs impacting seed weight.

When a population of small size becomes separated from a larger parental population, the founding event will be effective to produce a new genetic environment that leads the separated population to better adapt to the population bottleneck (Templeton, 1979, 1980; Gavrilets & Hastings, 1996). This phenomenon in which, physiologically, interaction genes re-adapt to one another in new genetic alignments is called the genetic 'revolution' by Mayr (1954). Once genotypic frequencies in the populations are disturbed by selection, or population bottleneck, such a cryptic molecular variation can act as a potential source of strong phenotypic effects via epistasis (Carson & Templeton, 1984; Goodnight, 1987, 1988, 1995; Tachida & Cockerham, 1989; Whitlock *et al*., 1995). Most of the QTLs identified in different developmental stages have epistatic effect with other QTLs in the same or different linkage map in the present study (Tables 2 and 3). Although epistatic effect impacting seed development of a population was not accurately estimated, the results of the present study demonstrated that epistatic effect impacted seed development, not only at the harvest period but also at different development periods.

The simulations of 95% confidence interval associated with the estimation of QTL position for F2, DH and RIL populations fell below 30 cM and ranged from 4 to 55 cM (Bandaranayake *et al*., 2004). For example, the QTLs in an RIL population of *Arabidopsis thaliana* having a narrow confidence interval (4·6 cM for plant height, and 6·3 cM for days to flowering) controlled a large proportion of the variability for a given trait (73% variability of plant height at 47 days and 75% variability at days to flowering). However, other QTLs having a large confidence interval (23 cM) only explain a small amount of the variation (16%) for a given trait. In the present study, average distance between markers was 15·65 cM with the longest distance being 48·8 cM and the shortest distance being 0·5 cM and mostly fell below the range of 95% confidence interval for RIL population, which made the results of the present study reliable, although the position and variability of some QTLs, located in large confidence interval, may imprecisely be estimated.

In general, QTL mapping based on data collected from a relatively small population is likely to detect the loci with large effects and to miss the loci with small effects (Edwards *et al*., 1992; Tanksley, 1993), which may lead to type I error to a certain extent. Therefore, the number of the putative QTLs identified in the present study should be considered the minimum of all those segregating in the population. Moreover, the non-normal distribution of trait can lead to a type I error (Allison *et al*., 1999). In general, both skew and kurtosis values of 100-seed weight were less than 1·0 at all growth stages measured in diverse environments in the present study, suggesting that the segregation of this trait fits a normal distribution model (Table 1). However, the segregation of 100-seed weight did not absolutely fit a normal distribution model (in a few cases, both skew and kurtosis values were 1·0), which may lead to type I error to a certain extent. Furthermore, erroneously assuming a normal distribution can lead to a biased estimate of the major gene (QTL) effect (Shete *et al*., 2004). Densely spaced markers (close markers) were required for detecting accurate QTLs. A relatively sparse marker was used to detect QTL, especially to small effect QTL, which also could lead to type I error (Zhang *et al*., 2004*b*).

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