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QTL analysis of soybean seed weight across multi-genetic backgrounds and environments

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Abstract Seed weight, measured as mass per seed, is an important yield component of soybean and is generally positively correlated with seed yield (Burton et al, Crop Sci 27:1093, 1987). In previous reports, quantitative trait loci (QTL) associated with seed weight, were identified in single genetic background. The objective of the present study was to identify QTL and epistatic QTL underlying soybean seed weight in three RIL populations (with one common male parent 'Hefeng25') and across three different environments. Overall, 18, 11, and 17 seed weight QTL were identified in HC ('Hefeng25' × 'Conrad'), HM ('Hefeng25' × 'Maple Arrow'), and HB ('Hefeng25' × 'Bayfield') populations, respectively. The amount of phenotypic variation explained by a single QTL underlying seed weight was usually less than 10 %. The environment and background-independent QTL often had higher additive (*a*) effects. In contrast, the environment or background-dependent QTL were probably due to weak expression of QTL. QTL by environment interaction effects were in the opposite direction of *a* effects and/or epistasis effects. Four QTL and one QTL could be identified ($2.0 < \text{LOD} < 9.06$) in the HC and HB populations, respectively, across three environments (swHCA2-1, swHCC2-1, swHCD1b-1, swHCA2-2 (linked to Satt233, Satt424, Satt460, Satt428, respectively) and swHBA1-1(Satt449). Seven QTL could be identified in all three RIL populations in at least one location. Two QTL could be identified in the three RIL populations across three environments. These two QTL may have greater potential for use in marker-assisted selection of seed weight in soybean.

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Introduction

Seed weight, measured as mass per seed, is an important yield component of soybean and was generally positively correlated with seed yield (Burton et al. 1987). Seed weight is a quantitative trait, which is mainly inherited with the additive effect (Brim and Cockerham 1961). Most of the breeding strategies for developing soybean cultivars take advantage of additive gene actions (Hartwig 1973; Fehr 1987; Cooper 1990). However, traditional plant improvement has relied on phenotypic selection of populations from crosses between commercial cultivars and/or experimental lines (Stuber et al. 1992; Specht et al. 1999; Stefaniak et al. 2005).

The development of consensus molecular maps in soybean (Song et al. 2004; Choi et al. 2007; Hyten et al. 2010; Song et al. 2010) has facilitated the identification of common quantitative trait loci (QTL) controlling important quantitative traits in many soybean populations (Hyten et al. 2004). Through molecular genetic linkage maps and QTL analysis, it is possible to estimate the number of QTL controlling genetic variation. Statistical analyses, such as ANOVA and interval mapping, can estimate the gene actions and phenotypic effects (Lander et al. 1987; Basten et al. 1996). Combined analyses allowed pleiotropic and/or

epistatic interactions to be estimated (Lark et al. 1995; Yan 2001). Through selection with molecular markers, the results of QTL analyses can be used in soybean breeding, referred as marker-assisted selection (MAS). A common approach in MAS is to map QTL in a small sample of progeny from a cross, choose a marker linked to the targeted QTL, and apply MAS in a larger set of progeny from the same cross (Prabhu et al. 1999; Ken et al. 2005). This has been done for many traits, including agronomic traits in barley (Zhu et al. 1999), disease resistance in soybean (Prabhu et al. 1999), and for blight resistance in chickpea (Millan et al. 2003) and rice (Davierwala et al. 2001). However, many studies have shown that the effects of QTL underlying agronomic traits are not always detected in other genetic backgrounds for soybean (Specht et al. 1999; Hyten et al. 2004) and many other crops (McKendry et al. 1996; Toojinda et al. 1998; Ken et al. 2005). This phenomenon is a major obstacle to the efficient use of MAS in plant breeding.

In the past two decades, many studies have focused on mapping of QTL influencing soybean seed weight [reviewed by Hyten et al. (2004)]. In most of these reports, the phenotypic values of traits in single genetic background were used for QTL analysis. Few of these studies have used common parents among their multiple genetic backgrounds (Orf et al. 1999; Hyten et al. 2004), which is a very important factor influencing quantitative traits like yield components (Specht et al. 1999; Liao et al. 2001; Hyten et al. 2004; Zhang et al. 2004). Many results indicated that yield of soybean is controlled by a series of QTL with different expression in different genetic populations or environments. Though genetic background effects on quantitative traits have been well documented in many crops including tomato (Tanksley and Hewitt 1988), rice (Li et al. 1997, 1998), soybean (Lark et al. 1995; Orf et al. 1999), and maize (Doebley et al. 1995), the QTL associated with seed weight had been less frequently reported in multi-genetic background by 2011 (Orf et al. 1999; Hyten et al. 2004).

The objective of this study was to identify stable QTL and epistatic QTL effects for seed weight of soybean in different genetic backgrounds and environments, using three populations with one common male parent, 'Hefeng 25', to compare the number and location of QTL and epistatic QTL mapped across different populations and environments, and to determine QTL × environment interactions.

Materials and methods

Plant materials

'Hefeng 25' × 'Conrad' (HC, 140 RILs of $F_{4:5}$), 'Hefeng 25' × 'Maple Arrow' (HM, 149 RILs of $F_{5:6}$), and 'Hefeng 25' × 'Bayfield' (HB, 144 RILs of $F_{5:6}$) were used to evaluate seed weight across multiple environments. 'Hefeng 25', a local variety in Northeastern China, was selected as the common parent of the three soybean populations due to higher seed weight and other good agronomic traits. The RILs and their parents were grown in a randomized complete block design at Harbin in three locations during 2007, 2008, and 2009 in four row plots. The rows were 3 m long, 90 cm apart, and there was a space of about 6 cm between two plants in a row. In each plot, 20 plants from one genotype were grown as seed donors that were later used to analyze seed weight after maturity. Seeds were dried for 30 min in oven at 105 °C and then continuously dried at 50–70 °C until the seed weight was stable. All dried samples were weighed.

Genetic linkage map

The genetic map of the HC RIL population constructed with 164 SSR markers encompassed 12 linkage groups (LGs) (Li et al. 2010a). The HC map covered about 3160.28 cM of the soybean genome with a mean distance of 19.27 cM between markers. The HM RIL population map is composed of 19 LGs constructed with 109 SSRs with a mean distance of 16.96 cM between markers (Li et al. 2009). The HB RIL population map included 107 SSRs in 20 LGs with a mean distance of 14.21 cM between markers (Li et al. 2010b).

Data analysis

QTL were identified by single-factor analysis of variance (PROC. GLM. SAS), interval mapping (Lander et al. 1987) and composite interval mapping (Basten et al. 1996) as described by Primomo et al. (2005). Significant QTL (LOD > 2.0) were recorded based on the mean value of individual environment.

For interactions locus main effects were considered for linear models if they were significant at $P \leq 0.01$. Significant loci on the same LG were tested by two-factor analysis of variance without interactions. If both loci were significant at $P \leq 0.05$ in the two-factor model, they would both be considered for linear models. Otherwise, the locus with the larger individual R^2 value was chosen to represent the effect of the putative QTL on the LG.

Two-way analysis of variance was also used to detect significant ($P < 0.01$) epistatic interactions between markers. The nomenclature of QTL included four parts. For example, QTL swHCA1-1 is composed of sw (seed weight), HC (the RIL population), A1 (the linkage group), and one (the first QTL in the LG).

GT (Genotype by Trait) biplot methodology (Yan 2001) was employed to analyze the interactions between QTL

and different environments in the HC, HM, and HB populations, based on the formula: $T_{ij}-T_j/S_j = \lambda_1\zeta_{i1}\tau_{j1} + \lambda_2\zeta_{i2}\tau_{j2} + \varepsilon_{ij}$, where T_{ij} is the average value of QTL_i for environment j; T_j is the average value of environment j over all QTL of single population, S_j is the standard deviation of environment j among the QTL average; ζ_{i1} and ζ_{i2} are the PC1 (first principle component) and PC2 (second principle component) scores, respectively. For QTL_i; τ_{j1} and τ_{j2} are the PC1 and PC2 scores, respectively, for environment j; and ε_{ij} is the residual of the model associated with the QTL_i in environment j.

Results

Phenotypic variation

Phenotypic values of 100-seed weight among different populations across three environments are shown in Table 1. The differences between the two parents were significant in the three different populations across three environments. The seed weight for 'Hefeng 25' was 2–5 g higher than those of 'Conrad', 'Maple Arrow' and 'Bayfield'. In contrast, 100-seed weight variations among the RIL populations were not significantly different. Both skewness and kurtosis values of 100-seed weight distributions were less than 1.0 for the three RIL populations in most environments, suggesting that the segregations of this trait fit a normal distribution model.

Analysis of QTL in different environments and genetic backgrounds

Eighteen, 11, and 17 QTL were found to be associated with seed weight in HC, HM, and HB populations, respectively (Table 2). The QTL in HC, HM, and HB populations could explain 3.86–31.09, 5.75–23.89, and 3.23–32.76 % of the phenotypic variations at Harbin in 3 years, respectively. QTL swHCB1-1 (Sat_123), swHMK-1 (Satt555), and swHBD1a-1 (Satt168) explained the largest amount of phenotypic variation (31.09, 23.89, and 32.76 %). Four QTL swHCA2-1; swHCC2-1; swHCD1b-1; swHCA2-2 (linked to Satt233, Satt424, Satt460, Satt428, respectively) in the HC population, and one QTL swHBA1-1(Satt449) in the HB population could be identified in all three environments.

In the present work, eight QTL that derived beneficial alleles from 'Hefeng 25', could be detected in three different populations [Satt233 located in LG A2 (Chromosome (Gm) 8), Satt460 in LG C2 (Gm 6), Satt428 in LG D1b (Gm 2), Satt302 in LG H (Gm 12), Satt354 in LG I (Gm 20), Satt555 in LG K (Gm 9), Satt527 in LG L (Gm 19), and Satt153 in LG O (Gm 10)].

Six QTL of Conrad origin associated with Sat_181 in LG A2 (Gm8), Sat_123 in LG B1 (Gm 11), Satt489 in LG C2 (Gm 6), Satt277 in LG C2 (Gm 6), Satt301 in LG D2 (Gm 17), and Satt380 in LG J (Gm 16).

One QTL (Satt150 in LG M, Gm 7) from 'Maple Arrow' was detected, and five QTL from 'Bayfield' [Satt449 in LG A1 (Gm 5), Satt596 in LG B2 (Gm 14), Satt190 in LG C1 (Gm 4), Satt277 in LG C2 (Gm 6), and Satt168 in LG D1a (Gm 1)] were found.

QTL × environment interaction across multi-environments and genetic backgrounds

Eighteen, 11, and 17 QTL in HC, HM, and HB population had additive main effect (*a*) and/or additive × environment interaction effect (*ae*) at some specific environments in 14, 11, and 17 LGs (Table 3).

Eight QTL (swHCA2-1, swHCA2-2, swHCC2-1, swHCD1b-1, swHCD2-1, swHCH-1, swHCK-1, swHCO-

Table 1 Statistical analysis of seed weight (100-seed weight) for parents and the three RIL populations at different environments

Populations	Environments	Parents		Recombinant inbred lines				
				Range	Mean	CV	Skewness	Kurtosis
Hefeng 25 × Conrad		Hefeng 25	Conrad					
	2007 Harbin	20.57	17.04	11.24–23.92	18.74	54.39	−1.29	0.78
	2008 Harbin	21.01	18.13	13.76–24.32	19.12	37.89	0.86	0.59
	2009 Harbin	20.34	17.56	11.29–22.39	18.84	47.89	0.30	0.77
Hefeng 25 × Maple Arrow		Hefeng 25	Maple Arrow					
	2007 Harbin	20.57	18.49	14.67–22.58	17.89	38.97	1.03	0.94
	2008 Harbin	21.01	16.02	10.87–22.39	18.87	57.39	0.97	0.67
	2009 Harbin	20.34	16.98	12.39–21.28	17.76	44.76	0.82	−0.74
Hefeng 25 × Bayfield		Hefeng 25	Bayfield					
	2007 Harbin	20.57	15.47	11.78–22.28	18.20	57.30	0.76	0.95
	2008 Harbin	21.01	18.53	12.73–22.76	17.32	62.29	−0.84	0.96
	2009 Harbin	20.34	16.98	14.39–23.37	18.32	58.39	0.89	0.79

Table 2 QTL associated with seed weight (100-seed weight) in different populations across different environments

QTL source	QTL	LG (Chromosome)	Marker interval	Population	E1[a]			E2[b]			E3[c]		
					LOD	D	R^2 (%)	LOD	D	R^2 (%)	LOD	D	R^2 (%)
Hefeng 25	swHCA2-1	A2 (Ch[d] 8)	Satt233–Satt538	HC	6.67	12.45	28.76	4.36	8.69	8.79	6.40	14.59	12.29
Hefeng 25	swHMA2-1		Satt233–Satt177	HM							6.43	23.76	21.63
Hefeng 25	swHBA2-1		Satt538–Satt233	HB	3.45	16.48	8.60				5.49	20.30	10.29
Hefeng 25	swHCC2-1	C2 (Ch 6)	Satt100–Satt460	HC	3.40	2.40	18.89	4.49	8.89	22.30	6.87	5.84	13.59
Hefeng 25	swHMC2-1		Satt100–Satt460	HM	5.54	15.54	6.67	9.76	27.98	5.76			
Hefeng 25	swHBC2-1		Satt460–Satt202	HB	3.87	2.17	10.87	5.76	6.78	8.86			
Hefeng 25	swHCD1b-1	D1b (Ch 2)	Satt579–Satt428	HC	2.65	15.65	27.86	3.97	13.83	10.65	7.64	12.74	5.76
Hefeng 25	swHMD1b-1		Satt282–Satt428	HM							5.45	6.67	12.64
Hefeng 25	swHBD1b-1		Satt282–Satt428	HB	3.65	14.65	7.89	8.76	13.64	18.86			
Hefeng 25	swHCH-1	H (Ch 12)	Satt181–Satt302	HC	5.97	21.08	15.86						
Hefeng 25	swHMH-1		Satt253–Satt302	HM	3.97	19.89	21.06				6.86	12.64	14.45
Hefeng 25	swHBH-1		Satt293–Satt302	HB				3.76	0.89	12.76			
Hefeng 25	swHCI-1	I (Ch 20)	Satt354–Satt571	HC	6.75	10.31	5.79	2.05	11.63	4.43			
Hefeng 25	swHMI-1		Satt354–Satt419	HM	5.76	15.76	15.65						
Hefeng 25	swHBI-1		Satt354–Satt440	HB	3.76	37.65	15.97						
Hefeng 25	swHCK-1	K (Ch 9)	Satt349–Satt555	HC	4.78	0.54	7.74				6.65	0.64	15.76
Hefeng 25	swHMK-1		Satt555–Satt046	HM				3.06	5.86	23.89			
Hefeng 25	swHBK-1		Satt555–Satt046	HB	7.97	1.87	4.65				4.65	1.65	5.53
Hefeng 25	swHCL-1	L (Ch 19)	Satt527–Satt561	HC	5.98	4.76	21.75						
Hefeng 25	swHML-1		Satt527–Sct_010	HM	3.76	0.54	6.68				3.89	0.43	6.42
Hefeng 25	swHBL-1		Satt527–Satt561	HB				9.75	0.98	10.76			
Hefeng 25	swHCO-1	O (Ch 10)	Satt479–Satt153	HC	3.75	17.54	6.90	4.86	12.67	4.54			
Hefeng 25	swHMO-1		Satt153–SattSat_106	HM				6.59	21.86	5.75	7.65	26.97	14.76
Hefeng 25	swHBO-1		Satt153–Satt109	HB	8.75	5.76	4.74						
Hefeng 25	swHCA1-1	A1 (Ch 5)	Satt382–Satt211	HC	5.64	10.87	5.38				4.08	17.64	7.77
Hefeng 25	swHBA1-2		Satt454–Satt382	HB	3.60	4.61	14.56	3.45	4.75	13.29			
Hefeng 25	swHCA2-2	A2 (Ch 8)	Satt424–Satt390	HC	4.21	8.76	6.65	5.54	8.76	10.65	7.65	4.86	8.70
Hefeng 25	swHBA2-2		Satt177–Satt424	HB	4.67	14.45	10.76	5.56	8.89	7.87			
Hefeng 25	swHMB1-1	B1 (Ch 11)	Sat_123–Satt583	HM	2.86	38.97	12.53						
Hefeng 25	swHBB1-1		Satt583–Sat_096	HB	5.32	2.10	6.23						
Hefeng 25	swHCD1a-1	D1a (Ch 1)	Satt383–Satt468	HC							3.97	6.87	21.05
Hefeng 25	swHMD1a-1		Satt502–Satt383	HM				4.65	17.76	12.86			
Hefeng 25	swHCE-1	E (Ch 15)	Satt263–Satt491	HC				6.87	10.40	28.76			
Hefeng 25	swHBE-1		Satt263–Satt268	HB	9.06	32.98	5.98						
Conrad	swHCA2-3	A2 (Ch 8)	Sat_181–Satt409	HC	2.37	3.45	10.32						
Conrad	swHCB1-1	B1 (Ch 11)	Satt453–Sat_123	HC	4.45	14.45	5.87	7.65	8.76	31.09			
Conrad	swHCC2-2	C2 (Ch 6)	Satt489–Satt557	HC	6.54	13.65	3.86				3.09	7.87	8.54

Table 2 continued

QTL source	QTL	LG (Chromosome)	Marker interval	Population	E1[a]			E2[b]			E3[c]		
					LOD	D	R^2 (%)	LOD	D	R^2 (%)	LOD	D	R^2 (%)
Conrad	swHCC2-3	C2 (Ch 6)	Satt307–Satt277	HC	3.39	5.78	7.52						
Conrad	swHCD2-1	D2 (Ch 17)	Satt615–Satt301	HC	5.86	0.86	10.86						
Conrad	swHCJ-1	J (Ch 16)	Satt380–Satt183	HC	2.76	4.67	17.72						
Maple Arrow	swHMM-1	M (Ch 7)	Satt150–Satt201	HM	2.06	2.78	8.76	2.98	4.56	15.83			
Bayfield	swHBA1-1	A1 (Ch 5)	Satt449–Satt454	HB	2.70	2.45	20.70	3.47	1.89	16.67	5.79	3.29	20.28
Bayfield	swHBB2-1	B2 (Ch 14)	Satt070–Satt596	HB				5.54	12.83	7.53	7.86	7.64	9.65
Bayfield	swHBC1-1	C1 (Ch 4)	Satt190–Satt195	HB	4.47	8.87	21.67				6.65	12.43	3.23
Bayfield	swHBC2-2	C2 (Ch 6)	Satt277–Satt376	HB	5.87	4.76	15.98				3.87	2.06	8.76
Bayfield	swHBD1a-1	D1a (Ch 1)	Satt198–Satt168	HB	5.74	8.86	32.76						

[a] at Harbin in 2007

[b] at Harbin in 2008

[c] at Harbin in 2009

[d] Chromosome number

1) from HC population, four QTL (swHMC2-1, swHMI-1, swHML-1 and swHMM-1) from HM population, and nine QTL (swHBA1-2, swHBA2-1, swHBC1-1, swHBC2-1, swHBC2-2, swHBD1b-1, swHBH-1, swHBK-1, swHBL-1) from HB population, contributed the allele that increased seed weight through significant *a* effects. Three QTL (swHCB1-1, swHCC2-2, swHCI-1) originating from HC population, four QTL (swHMB1-1, swHMD1a-19, swHMH-1 and swHMO-1) origininating from HM population, and two QTL (swHBA2-2 and swHBB2-1) originating from HB population, contributed the allele that decreased seed weight through significant *a* effects, respectively.

The impact of *ae* effects on QTL was different at different years for these three populations. For example, QTL swHCA2-1 of HC population, increased seed weight at Harbin in 2007 and 2009, but decreased seed weight at Harbin in 2008. Six QTL (swHCA2-3, swHCC2-3, swHCD1a-1, swHCE-1, swHCJ-1, swHCL-1) of HC population, three QTL (swHMA2-1, swHMD1b-1 and swHMK-1) of HM population, and five QTL (swHBB1-1, swHBD1a-1, swHBE-1, swHBI-1, swHBO-1) of HB population, had only significant *ae* effects, but no significant *a* effects. Other QTL in these three populations had both significant *a* effects and significant *ae* effects.

Epistatic analysis of QTL across multi-environments

Forty, 16. and 20 epistatic pairwise QTL were detected in HC, HM, and HB population in different environments, respectively (Table 4). Of them, 18, 5 and 5 epistatic pairs of QTL, derived from HC, HM and HB populations, were beneficial for the increase of seed weight through significant *aa* effects. Seven, five and four epistatic pairs of QTL trended to decrease seed weight through significant *aa* effects in HC, HM, and HB population, respectively (Table 4).

The epistasis × environment interaction effect (*aae*) was an important component of the total QTL × environment (QE) interaction effects. Six, four, and five pairs of QTL were found with only epistatic effects (*aa*) in HC, HM, and HB populations, respectively. Fifteen, five, and eleven pairs had only *aae* effects in HC, HM, and HB populations, and other pairs of epistatic QTL had both *aa* and *aae* effects (Table 4).

Stability evaluation of QTL derived from 'Hefeng 25'

In this study, additive effects of eight QTL, linked to Satt233, Satt460, Satt428, Satt302, Satt354, Satt555, Satt527, and Satt153) from 'Hefeng25', were detected in three different populations. (Table 3). The scale of *a* effect of QTL, derived from 'Hefeng 25', was diverse in different populations. For example, *a* effect of QTL, associated with

Table 3 Additive and additive × environment interaction effect of QTL associated with seed weight at different populations

QTL source	QTL	LG (Chromosome)	Marker interval	Population	a^{d}	$a \times E1^{a}$	$a \times E2^{b}$	$a \times E3^{c}$
Hefeng 25	swHCA2-1	A2 (Ch 8)	Satt233–Satt538	HC	0.27*	0.11*	−0.17*	0.32*
Hefeng 25	swHMA2-1		Satt233–Satt177	HM				0.39*
Hefeng 25	swHBA2-1		Satt538–Satt233	HB	0.62**	0.76**		0.17*
Hefeng 25	swHCC2-1	C2 (Ch 6)	Satt100–Satt460	HC	2.01**	0.40*	−0.89*	0.87*
Hefeng 25	swHMC2-1		Satt100–Satt460	HM	0.69**		0.39*	
Hefeng 25	swHBC2-1		Satt460–Satt202	HB	0.79**	0.26*	−0.27*	
Hefeng 25	swHCD1b-1	D1b (Ch 2)	Satt579–Satt428	HC	1.64**	−1.02**	0.19*	0.76**
Hefeng 25	swHMD1b-1		Satt282–Satt428	HM				0.30*
Hefeng 25	swHBD1b-1		Satt282–Satt428	HB	1.34**	0.65**	0.76**	
Hefeng 25	swHCH-1	H (Ch 12)	Satt181–Satt302	HC	0.30 *	−0.37*		
Hefeng 25	swHMH-1		Satt253–Satt302	HM	−0.19*	0.38*		−0.69**
Hefeng 25	swHBH-1		Satt293–Satt302	HB	0.49*			
Hefeng 25	swHCI-1	I (Ch 20)	Satt354–Satt571	HC	−0.87**	0.88**	−0.32*	
Hefeng 25	swHMI-1		Satt354–Satt419	HM	0.22*	0.16*		
Hefeng 25	swHBI-1		Satt354–Satt440	HB		0.58 **		
Hefeng 25	swHCK-1	K (Ch 9)	Satt349–Satt555	HC	1.34**	0.67**		1.20**
Hefeng 25	swHMK-1		Satt555–Satt046	HM			−0.28*	
Hefeng 25	swHBK-1		Satt555–Satt046	HB	0.78**	−0.89**		−1.25**
Hefeng 25	swHCL-1	L (Ch 19)	Satt527–Satt561	HC		0.59**		
Hefeng 25	swHML-1		Satt527–Sct_010	HM	1.04**	0.45**		−1.02**
Hefeng 25	swHBL-1		Satt527–Satt561	HB	0.55**			
Hefeng 25	swHCO-1	O (Ch 10)	Satt479–Satt153	HC	0.79**	−0.87**	−0.95**	
Hefeng 25	swHMO-1		Satt153–SattSat_106	HM	−0.67**		0.20*	
Hefeng 25	swHBO-1		Satt153–Satt109	HB		−0.17*		
Hefeng 25	swHCA1-1	A1 (Ch 5)	Satt382–Satt211	HC	−0.76**			−0.48**
Hefeng 25	swHBA1-2		Satt454–Satt382	HB	0.97**	0.28*	−0.59**	
Hefeng 25	swHCA2-2	A2 (Ch 8)	Satt424–Satt390	HC	1.34**	0.21*	0.56**	−0.67**
Hefeng 25	swHBA2-2		Satt177−Satt424	HB	−0.30*	−0.49**	0.89**	
Hefeng 25	swHMB1-1	B1 (Ch 11)	Sat_123–Satt583	HM	−0.20*			
Hefeng 25	swHBB1-1		Satt583–Sat_096	HB		−0.87**		
Hefeng 25	swHCD1a-1	D1a (Ch 1)	Satt383–Satt468	HC				0.89**
Hefeng 25	swHMD1a-1		Satt502–Satt383	HM	−0.31*			
Hefeng 25	swHCE-1	E (Ch 15)	Satt263–Satt491	HC			0.30*	
Hefeng 25	swHBE-1		Satt263–Satt268	HB		−0.98**		
Conrad	swHCA2-3	A2 (Ch 8)	Sat_181–Satt409	HC		−0.15*		
Conrad	swHCB1-1	B1 (Ch 11)	Satt453–Sat_123	HC	−0.79**	−0.88**	1.09**	
Conrad	swHCC2-2	C2 (Ch 6)	Satt489–Satt557	HC	−0.97*	−0.66**		−0.59**
Conrad	swHCC2-3	C2 (Ch 6)	Satt307–Satt277	HC		0.33*		
Conrad	swHCD2-1	D2 (Ch 17)	Satt615–Satt301	HC	0.32*	−0.49*		
Conrad	swHCJ-1	J (Ch 16)	Satt380–Satt183	HC		−0.30*		
Maple Arrow	swHMM-1	M (Ch 7)	Satt150–Satt201	HM	0.98**	−1.17 *		
Bayfield	swHBA1-1	A1 (Ch 5)	Satt449–Satt454	HB	1.29**	1.21**	−0.98**	0.63**
Bayfield	swHBB2-1	B2 (Ch 14)	Satt070–Satt596	HB	−0.27*		−0.83**	−1.07*
Bayfield	swHBC1-1	C1 (Ch 4)	Satt190–Satt195	HB	0.20*	0.67**		0.80**
Bayfield	swHBC2-2	C2 (Ch 6)	Satt277–Satt376	HB	0.95**	0.94 **		−0.91**
Bayfield	swHBD1a-1	D1a (Ch 1)	Satt198–Satt168	HB		0.25*		

[a] at Harbin in 2007

[b] at Harbin in 2008

[c] at Harbin in 2009

[d] additive effect

Satt460, was 2.01 in the HC population, 0.69 in the HM population, and 0.79 in the HB population, respectively (Table 3). The impact of different environments on *ae* effect of QTL was higher than that of different populations.

In the present study, both the *aa* and *aae* effects of the QTL derived from 'Hefeng 25' were identified in the 3 or 2 of the three populations, and the number of QTL epistatic with other QTL was different across different populations (Table 4). For example, six, three, and three epistatic pairwise QTL interacting with the QTL linked to Satt233 was found in HC, HM, and HB populations, respectively. The *aa* and *aae* effect of the epistatis QTL were 0.23–0.45, 0.16–0.87, 0.25–1.07, and 0.17–0.45, 0.17–0.37, 0.19–0.89, respectively.

GT biplot analysis (Yan 2001) showed the 13 QTL with beneficial alleles from 'Hefeng 25' detected in three or two populations explained 73 % of the total variation. Figure 1 indicated that two QTL (Satt428 and Satt460) had highest performance and stability across multiple environments and populations. The QTL linked to Satt555, Satt424, Satt382, Satt354, and Satt183 also had above-average performance and stability across multiple environments and populations. The QTL linked to Satt383, Satt583, Satt233, Satt263, Satt302, and Satt527 had the lowest-average performance and stability across multi-environments and multi-populations. Furthermore, the performance of different QTL on each environment or population was evaluated. With the QTL linked to Satt460, Satt555, Satt383, Satt263, Satt527, and Satt153 as the corner QTL, three environments and two populations (HC and HM) fell in the sector in which two QTL (linked to Satt460 and Satt428) were the strongest for these three environments and two populations, respectively (Fig. 2). Two QTL (linked to Satt383 and Satt555) were the strongest for the HB population.

Discussion

Rapid advances in genomics have identified and analyzed about 36,000 genes in soybean (Schmutz et al. 2010; Severin et al. 2010). However, the usefulness of genomics data for crop breeding and improvement was dependent upon the identification of candidate gene markers for MAS via map-based cloning or association analyses (Varshney et al. 2005; Lightfoot 2008; Guttierez-Gonzalez et al. 2010). Seed weight is an important yield component of soybean (Burton et al. 1987). Hence, there was interest in understanding the genetic control of seed weight in soybean, especially the beneficial alleles from 'Hefeng 25', a superior cultivar in Heilongjiang Province of China. Because seed weight of soybean was affected by environments and genetic backgrounds, increasing the genotype selection intensity by MAS could improve the selection efficiency.

To be useful to a breeding program, QTL need to be stable across environments and genetic backgrounds (Brummer et al. 1997). Stability can be assessed by evaluating many populations across several environments to determine if a particular QTL is detected in each population or environment. In this study, three sets of RIL populations with one common male parent ('Hefeng 25') were analyzed for QTL that associated with seed weight across multi-environments. A total of 18, 11, and 17 QTL were identified in HC, HM, and HB populations, respectively. An individual QTL explained phenotypic variations ranged from 3 to 28 % for seed weight in different environments and populations. However, most loci explained less than 10 % of the variation (Table 2). The low level of phenotypic variation explained by these QTL indicated the quantitative nature of seed weight, which was similar to the findings of other studies (Mansur et al. 1996; Mian et al. 1996; Hyten et al. 2004; Zhang et al. 2004). QTL specific to one environment were also reported by other studies for different traits (Price et al. 2002; Li et al. 2003). Many instable QTL detected in different environments or genetic backgrounds were detected (Table 2) in this study, which was due to weak expression of the QTL, QTL by environment interaction in the opposite direction to *a* effects and/or epistasis (Table 3, 4). For example, swHCE-1 and swHCA2-2 were subject to these effects. Therefore, the information of QTL by environment interaction should be considered if MAS was to be applied to the manipulation of quantitative traits.

Four QTL swHCA2-1, swHCA2-2, swHCC2-1, and swHCD1b-1 linked to Satt233, Satt424, Satt460, and Satt428, respectively, in the HC population across all three environments. The QTL swHCA2-1 was reported previously in V71-370 × PI407162, Noir 1 × Archer (Hyten et al. 2004). The QTL swHCA2-1 was reported previously in Minsoy × Noir 1 (Hyten et al. 2004). The QTL swHCC2-1 was also reported previously in Young × PI416937; Noir 1 × Archer; and Essex × Williams (Hyten et al. 2004). The QTL swHCD1b-1 was also reported previously in Essex × Williams (Hyten et al. 2004).

The sole QTL swHBA1-1 (linked to Satt449) in the HB population that could be found in all three environments was reported previously in Noir 1 × Archer (Hyten et al. 2004). Therefore, all the QTL stable across environments have been confirmed, which adds to their usefulness in MAS even across multi- environments.

Seven QTL (Satt460, Satt428, Satt302, Satt354, Satt555, Satt527, Satt153) could be detected in all three populations in some environments. These QTL might be useful for MAS in a particular location.

Table 4 QTL epistatic effects associated with seed weight (100-seed weight) at different populations

QTLi Source	QTLi	LG (Chromosome)	Marker interval	Marker	LG (Chromosome)	QTLj Source	QTLj	Marker interval	Population	*aa*[d]	*aa* × E1[a]	*aa* × E2[b]	*aa* × E3[c]
Hefeng 25	swHCA2-1	A2 (Ch 8)	satt233–satt538	satt233	A2 (Ch 8)	'Hefeng 25'	swHCA2-2	satt424–satt390	HC	0.45*	0.87**	−0.36*	0.17*
					C2 (Ch 6)	'Hefeng 25'	swHCC2-1	satt100–satt460	HC		−0.89**		
					C2 (Ch 6)	'Conrad'	swHCC2-2	satt489–satt557	HC			0.23*	
					D2 (Ch 17)	'Conrad'	swHCD2-1	satt615–satt301	HC	0.48*	0.59**		
					I (Ch 20)	'Hefeng 25'	swHCI-1	satt354–satt571	HC				−0.49*
					O (Ch 10)	'Hefeng 25'	swHCO-1	satt479–satt153	HC	0.23*		−0.16*	
Hefeng 25	swHMA2-1	A2 (Ch 8)	satt233–satt177	satt233	C2 (Ch 6)	'Hefeng 25'	swHMC2-1	satt100–satt460	HM	1.07**		0.43*	
					K (Ch 9)	'Hefeng 25'	swHMK-1	satt555–satt046	HM		0.17*		
					O (Ch 10)	'Hefeng 25'	swHMO-1	satt153–sattsat_106	HM	0.25*			
Hefeng 25	swHBA2-1	A2 (Ch 8)	satt538–satt233	satt233	A2 (Ch 8)	'Hefeng 25'	swHBA2-2	satt177–satt424	HB		0.45*		−0.29*
					C2 (Ch 6)	'Hefeng 25'	swHBC2-1	satt460–satt202	HB	0.17*	0.89**	0.19*	0.21*
					O (Ch 10)	'Hefeng 25'	swHBO-1	satt153–satt109	HB	0.37*			
Hefeng 25	swHCC2-1	C2 (Ch 6)	satt100–satt460	satt460	C2 (Ch 6)	'Conrad'	swHCC2-3	satt307–satt277	HC	0.56**	0.40*	0.49*	−0.59**
					J (Ch 16)	'Conrad'	swHCJ-1	satt380–satt183	HC	−0.67**			
Hefeng 25	swHMC2-1	C2 (Ch 6)	satt100–satt460	satt460	D1b (Ch 2)	'Hefeng 25'	swHMD1b-1	satt282–satt428	HM		0.54**	−0.76**	
					M (Ch 7)	'Maple Arrow'	swHMM-1	satt150–satt201	HM	1.23**			−0.59**
Hefeng 25	swHBC2-1	C2 (Ch 6)	satt460–satt202	satt460	C2 (Ch 6)	'Bayfield'	swHBC2-2	satt277–satt376	HB		0.17*	−0.90**	
Hefeng 25	swHCD1b-1	D1b (Ch 2)	satt579–satt428	satt428	E (Ch 15)	'Hefeng 25'	swHCE-1	satt263–satt491	HC	0.47*	0.65**	0.97**	0.76**
Hefeng 25	swHMD1b-1	D1b (Ch 2)	satt282–satt428	satt428	L (Ch 19)	'Hefeng 25'	swHML-1	satt527–sct_010	HM				0.67**
Hefeng 25	swHBD1b-1	D1b (Ch 2)	satt282–satt428	satt428	E (Ch 15)	'Hefeng 25'	swHBE-1	satt263–satt268	HB		0.82**		
Hefeng 25	swHCH-1	H (Ch 12)	satt181–satt302	satt302	J (Ch 16)	'Conrad'	swHCJ-1	satt380–satt183	HC	0.86**	0.67**		
					O (Ch 10)	'Hefeng 25'	swHCO-1	satt479–satt153	HC			0.47*	
Hefeng 25	swHMH-1	H (Ch 12)	satt253–satt302	satt302	I (Ch 20)	'Hefeng 25'	swHMI-1	satt354–satt419	HM	0.78**	0.89**		0.45*
					M (Ch 7)	'Maple Arrow'	swHMM-1	satt150–satt201	HM	−0.56**			
Hefeng 25	swHBH-1	H (Ch 12)	satt293–satt302	satt302	I (Ch 20)	'Hefeng 25'	swHBI-1	satt354–satt440	HB	0.22*			
Hefeng 25	swHCI-1	I (Ch 20)	satt354–satt571	satt354	K (Ch 9)	'Hefeng 25'	swHCK-1	satt349–satt555	HC	0.56**	0.75**	0.43*	
Hefeng 25	swHMI-1	I (Ch 20)	satt354–satt419	satt354	K (Ch 9)	'Hefeng 25'	swHMK-1	satt555–satt046	HM		0.65**		
Hefeng 25	swHBI-1	I (Ch 20)	satt354–satt440	satt354	K (Ch 9)	'Hefeng 25'	swHBK-1	satt555–satt046	HB		0.97**		

Table 4 continued

QTLi Source	QTLi	LG (Chromosome)	Marker interval	Marker	LG (Chromosome)	QTLj Source	QTLj	Marker interval	Population	*aa*[d]	*aa* × E1[a]	*aa* × E2[b]	*aa* × E3[c]
Hefeng 25	swHCK-1	K (Ch 9)	satt349–satt555	satt555	L (Ch 19)	'Hefeng 25'	swHCL-1	satt527–satt561	HC		0.78**		−0.64**
Hefeng 25	swHMK-1	K (Ch 9)	satt555–satt046	satt555	L (Ch 19)	'Hefeng 25'	swHML-1	satt527–sct_010	HM			1.06**	
					M (Ch 7)	'Maple Arrow'	swHMM-1	satt150–satt201	HM	−0.99**			0.17*
Hefeng 25	swHBK-1	K (Ch 9)	satt555–satt046	satt555	L (Ch 19)	'Hefeng 25'	swHBL-1	satt527–satt561	HB	−1.13**	0.65**	0.18*	0.53**
Hefeng 25	swHML-1	L (Ch 19)	satt527–sct_010	satt527	M (Ch 7)	'Maple Arrow'	swHMM-1	satt150–satt201	HM		0.77**		0.96**
Hefeng 25	swHCA1-1	A1 (Ch 5)	satt382–satt211	satt382	A2 (Ch 8)	'Hefeng 25'	swHCA2-2	satt424–satt390	HC	0.25*	0.17*		−0.47**
					A2 (Ch 8)	'Conrad'	swHCA2-3	sat_181–satt409	HC		−0.22*		
					B1 (Ch 11)	'Hefeng 25'	swHCB1-1	satt453–sat_123	HC	−0.59**			0.19*
					C2 (Ch 6)	'Hefeng 25'	swHCC2-1	satt100–satt460	HC	0.68**			
					D2 (Ch 17)	'Conrad'	swHCD2-1	satt615–satt301	HC				−0.18*
Hefeng 25	swHBA1-2	A1 (Ch 5)	satt454–satt382	satt382	A2 (Ch 8)	'Hefeng 25'	swHBA2-1	satt538–satt233	HB	0.19*	−0.60**	0.75**	0.48*
					B1 (Ch 11)	'Hefeng 25'	swHBB1-1	satt583-sat_096	HB	−0.45*			
					H (Ch 12)	'Hefeng 25'	swHBH-1	satt293–satt302	HB		0.30*		
Hefeng 25	swHCA2-2	A2 (Ch 8)	satt424–satt390	satt424	C2 (Ch 6)	'Hefeng 25'	swHCC2-1	satt100–satt460	HC	0.21*			0.86**
					E (Ch 15)	'Hefeng 25'	swHCE-1	satt263–satt491	HC		−0.65*		
					J (Ch 16)	'Conrad'	swHCJ-1	satt380-satt183	HC			−0.70**	
					K (Ch 9)	'Hefeng 25'	swHCK-1	satt349–satt555	HC	0.59**			
Hefeng 25	swHBA2-2	A2 (Ch 8)	satt177–satt424	satt424	C2 (Ch 6)	'Hefeng 25'	swHBC2-1	satt460–satt202	HB		−0.76**	0.87**	
					K (Ch 9)	'Hefeng 25'	swHBK-1	satt555–satt046	HB	−0.22*			
Hefeng 25	swHMB1-1	B1 (Ch 11)	sat_123–satt583	satt583	H (Ch 12)	'Hefeng 25'	swHMH-1	satt253–satt302	HM	−0.86**			
					M (Ch 7)	'Maple Arrow'	swHMM-1	satt150–satt201	HM	−1.01**		0.97**	0.53**
Hefeng 25	swHBB1-1	B1 (Ch 11)	satt583–sat_096	satt583	H (Ch 12)	'Hefeng 25'	swHBH-1	satt293–satt302	HB		−0.23*		
Hefeng 25	swHCD1a-1	D1a (Ch 1)	satt383–satt468	satt383	D2 (Ch 17)	'Conrad'	swHCD2-1	satt615–satt301	HC	−0.49*			0.97**
					J (Ch 16)	'Conrad'	swHCJ-1	satt380–satt183	HC	0.58**			
Hefeng 25	swHMD1a-1	D1a (Ch 1)	satt502–satt383	satt383	H (Ch 12)	'Hefeng 25'	swHMH-1	satt253–satt302	HB	−0.65**		0.76**	
Hefeng 25	swHCE-1	E (Ch 15)	satt263–satt491	satt263	I (Ch 20)	'Hefeng 25'	swHCI-1	satt354–satt571	HC			0.87**	
Hefeng 25	swHBE-1	E (Ch 15)	satt263–satt268	satt263	I (Ch 20)	'Hefeng 25'	swHBI-1	satt354–satt440	HB		0.98**		0.76**
Conrad	swHCA2-3	A2 (Ch 8)	sat_181–satt409	sat_181	C2 (Ch 6)	'Conrad'	swHCC2-2	satt489–satt557	HC	−0.23*	0.45*		
					H (Ch 12)	'Hefeng 25'	swHCH-1	satt181–satt302	HC	−0.19*	0.57**	0.66**	−0.58**
					L (Ch 19)	'Hefeng 25'	swHCL-1	satt527–satt561	HC	0.45**			

Table 4 continued

QTLi Source	QTLi	LG (Chromosome)	Marker interval	Marker	LG (Chromosome)	QTLj Source	QTLj	Marker interval	Population	*aa*[d]	*aa* × E1[a]	*aa* × E2[b]	*aa* × E3[c]
Conrad	swHCB1-1	B1 (Ch 11)	satt453–sat_123	sat_123	C2 (Ch 6)	'Hefeng 25'	swHCC2-1	satt100–satt460	HC		−0.87**		
					K (Ch 9)	'Hefeng 25'	swHCK-1	satt349–satt555	HC	0.72**		0.76**	
Conrad	swHCC2-2	C2 (Ch 6)	satt489–satt557	satt489	C2 (Ch 6)	'Bayfield'	swHCC2-3	satt307–satt277	HC		0.54**		0.18*
					I (Ch 20)	'Hefeng 25'	swHCI-1	satt354–satt571	HC	−0.17*			
Conrad	swHCC2-3	C2 (Ch 6)	satt307–satt277	satt277	D1b (Ch 2)	'Hefeng 25'	swHCD1b-1	satt579–satt428	HC	0.31*	0.45*		
					H (Ch 12)	'Hefeng 25'	swHCH-1	satt181–satt302	HC			0.67**	
					K (Ch 9)	'Hefeng 25'	swHCK-1	satt349–satt555	HC		0.56**		
					O (Ch 10)	'Hefeng 25'	swHCO-1	satt479–satt153	HC	−0.70**		0.57**	
Conrad	swHCD2-1	D2 (Ch 17)	satt615–satt301	satt301	E (Ch 15)	'Hefeng 25'	swHCE-1	satt263–satt491	HC		0.86**		
					K (Ch 9)	'Hefeng 25'	swHCK-1	satt349–satt555	HC	0.89**		−0.45*	
Conrad	swHCJ-1	J (Ch 16)	satt380–satt183	satt380	K (Ch 9)	'Hefeng 25'	swHCK-1	satt349–satt555	HC		−0.72**		
Bayfield	swHBB2-1	B2 (Ch 14)	satt070–satt596	satt596	C2 (Ch 6)	'Hefeng 25'	swHBC2-1	satt460–satt202	HB			0.53**	−0.87**
Bayfield	swHBC1-1	C1 (Ch 4)	satt190–satt195	satt190	K (Ch 9)	'Hefeng 25'	swHBK-1	satt555–satt046	HB	0.40*	0.67**		0.23*
Bayfield	swHBC2-2	C2 (Ch 6)	satt277–satt376	satt277	D1b (Ch 2)	'Hefeng 25'	swHBD1b-1	satt282–satt428	HB		0.98**		1.06**
					H (Ch 12)	'Hefeng 25'	swHBH-1	satt293–satt302	HB	−0.24*			
					O (Ch 10)	'Hefeng 25'	swHBO-1	satt153–satt109	HB		−0.64**		

[a] at Harbin in 2007

[b] at Harbin in 2008

[c] at Harbin in 2009

[d] additive × additive effect

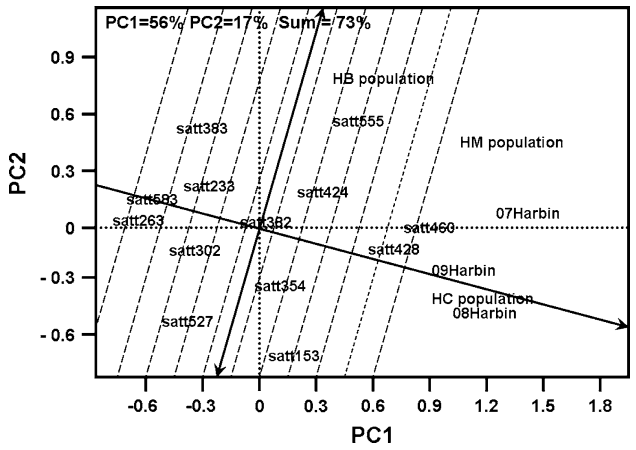

Fig. 1 A biplot showing the mean and stability of QTL in three different environments and populations. Each environment is a year-site combination, e.g. 07Harbin referring to Harbin in 2007. HC refers to Hefeng 25' × 'Conrad' population, HM refers to 'Hefeng 25' × 'Maple Arrow' population, HB refers to 'Hefeng 25' × 'Bayfield' population. The single-arrowed line points to high mean performance across environments and populations, and the double-arrowed lines point to mean performance of population regardless of direction

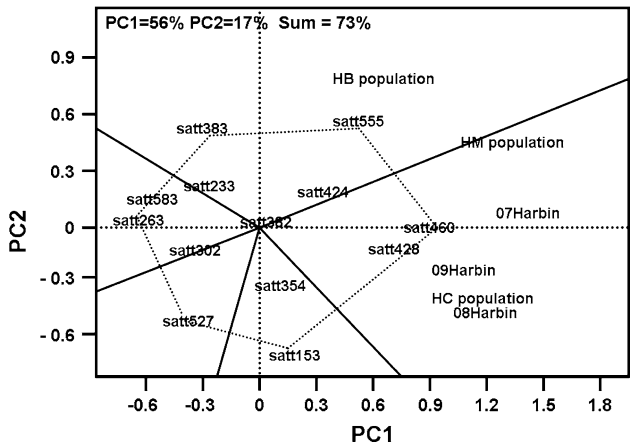

Fig. 2 GT biplot analysis for the relatedness of QTL and environment/population. PC1: first principle component; PC2: second principle component. Each environment is a year-site combination, e.g. 07Habin referring to Harbin in 2007. HC refers to Hefeng 25' × 'Conrad' population, HM refers to 'Hefeng 25' × 'Maple Arrow' population, HB refers to'Hefeng 25' × 'Bayfield' population

Two QTL (Satt460 and Satt428) could be identified across three environments and three RIL populations. The QTL swHCC2-1 and swHCD1b-1 had been reported previously (Hyten et al. 2004). These two QTL will be the primary targets for MAS to improve soybeans in China and the US. The gene underlying the QTL could be cloned based on its map position.

Teng et al. (2008) analyzed seed weight in six different stages with a RIL population derived from a cross between 'Dongnong 594' and 'Charleston', and found the QTL swHCC2-1 associated with Satt460 could be detected across six different developmental stages and three environments. It should be noted that the germplasm reported by Teng et al. (2008) was of different parentage. This suggests the QTL linked to Satt460 was weakly influenced by genetic background and environment and might be more effective in MAS.

The stable QTL were responsible for large *a* effects. As suggested by Tanksley (1993) and Zhuang et al. (1997), QTL with higher *a* effects are more likely to be stable across multiple environments (Table 3).

The importance of epistatic action of gene expression in complex traits had been demonstrated in previous studies (Li et al. 1997; Li et al. 1998; Ohno et al. 2000; Guttierez-Gonzalez et al. 2010). Our results indicated that epistatic effect accounted for a significant component of seed weight QTL in the three populations, similar to the findings of previous reports (Carlborg et al. 2005; Wilfert and Schmid-Hempel 2008) (Table 4). Because of the obvious contribution by epistatic interaction, QTL with significant epistatic effects should be considered during seed weight breeding in soybean.

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