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ORIGINAL PAPER

Genetic mapping of seed shape in three populations of recombinant inbred lines of soybean (*Glycine max* L. Merr.)

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Abstract Round soybean seeds are sought-after for food-type soybean. Also the genetic control of seed geometry is of scientific interest. The objectives of this study were to estimate heritability and map quantitative trait loci (QTLs) responsible for seed shape traits. Three densely mapped recombinant inbred populations each with 192 segregants were used, Minsoy × Archer, Minsoy × Noir1, and Noir1 × Archer. A two rep two location experiment was conducted in Los Andes, Chile, and East Lansing, MI, USA. Seed height (SH), width (SW), length (SL), and seed volume (SV) as width × height × length were measured to determine seed shape. Heritability was estimated by variance component analysis. A total of 19 significant QTLs (LOD ≥ 3.7) in ten linkage groups (LG) were detected for all the traits. Only one QTL was stable across populations and environments and six were stable in at least two populations in both environments. The amount of phenotypic variation explained by a single QTL varied from 7.5% for SH, to 18.5% for SW and at least 30% of the genetic variation for the traits is controlled by four QTL or less. All traits were highly correlated with each other in all populations with values ranging from 0.5 to 0.9, except for SL and SW that were not significantly correlated or had a low correlation in all populations. Narrow sense heritabilities for all traits ranged from 0.42 to 0.88. We note that LG u9, u11, and u14 are hot points of the genome for QTLs for various traits. The number and genomic distribution of the QTLs confirms the complex genetic control of seed shape. Transgressive segregation was observed for all traits suggesting that careful selection of parents with similar phenotypes but different genotypes using molecular markers can result in desirable transgressive segregants.

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Introduction

Soybean is one of the most important crops in the world. It is used in human and animal feeding because of its high nutritional value. In specialty soy food products, including tofu, natto, miso, and edamame, seed size and shape are important traits. Round seed is often desirable for food-type soybean, while desirable seed size ranges from large, for tofu, edamame, and miso, to small for natto production (Wilson 1995). In Japan 20% of the soybean production is used for producing traditional food like tofu, miso, and edamame (Sakai and Yonekawa 1991).

Nelson and Wang (1989) determined that seed size and shape in soybean were variable among a collection of varieties and that these traits were stable in time. Cober et al. (1997) stated that there is no correlation between seed size and seed shape. Mansur et al. (1993) introduced genetic mapping of quantitative trait loci

(QTL) using populations of recombinant inbred (RI) lines of soybean. Since then, several QTL have been identified that are associated with morphological and reproductive traits, such as leaf weight and size, days from planting to flowering, days from planting to seed set, days from planting to maturity, pod shattering, plant height and lodging, pest, disease, and nematode resistances, seed weight and size, and oil and protein content of the seed (Arahana et al. 2001; Kim et al. 2000; Orf et al. 1999; Mian et al. 1998, 1996; Rector et al. 1998; Bailey et al. 1997; Brummer et al. 1997; Lee et al. 1996; Webb et al. 1995).

Cober et al. (1997) estimated the heritabilites for seed size and shape, obtaining moderate to high values, 59–79% for seed shape and 19–56% for seed size. These results indicated that plants with round seed can be effectively selected from early generations of segregating populations.

Although much work has been done to understand the genetics of seed size and weight (Kim et al. 2000; Johnson et al. 2001; Orf et al. 1999; Mansur et al. 1993, 1996; Mian et al. 1996; LeRoy et al. 1991), few studies have been done to understand the underlying factors controlling seed shape (seed height, SH; length, SL; and width, SW) (Cober et al. 1997; Nelson and Wang 1989).

Seed size and shape are complex, polygenic traits; therefore, the use of molecular markers for indirect selection of these traits might be helpful for breeders.

In this work a genetic analysis of seed shape using molecular markers and three populations of RI lines was conducted. The aim of this study was to identify important QTL associated with seed shape and size in soybean.

Materials and methods

Germplasm and design of field experiments

Three F7-derived RI populations developed at Iowa Sate University by L. Mansur (Mansur et al. 1993) from crosses between Minsoy (PI 27890) and Noir1 (PI 290136) (MN population), Archer (PI 546487) and Minsoy (MA population), and Noir1 and Archer (NA population) were used. Due to space constraints a random sample of 192 lines per population were used although 240 MN RI lines, 233 MA RI lines, and 240 NA RI lines are available. A dense genetic map previously used by Orf et al. (1999) was facilitated for this research. The lines were planted in a completely randomized design with two replications in Los Andes, Chile in 2000 and in East Lansing, Michigan in 2001.

Phenotypic data

The variables measured were SW, SH, SL (Fig. 1), and seed volume (SV) estimated as width × height × length. The length of the seed was defined as the longest distance across the seed parallel to the hilum, the seed height as the longest distance from top to bottom of the seed, and the seed width as the longest distance across the seed perpendicular to the hilum. In the Los Andes experiment 25 seeds per replicate of each line were randomly sampled and used to record width, height, and length in millimeters using a digital vernier caliper, whereas 20 seeds per line were measured in the Michigan experiment.

Statistical methods and QTL mapping

The composite genetic map developed by Orf et al. (1999) was used as a base to locate the QTLs associated with the seed traits. QTLs were identified and analyzed for interactions using the Epistat computer program (Chase et al. 1997). Epistat detects QTLs using single marker tests and interactions between markers using pairs of markers. This program does not investigate intervals. It uses maximum likelihood methods and permutation tests for both the identification and evaluation of significance of interactions between pairs of QTLs (Chase et al. 1997).

The simple interval-mapping feature of the computer package PLABQTL (Utz and Melchinger 1996) was also used for detecting QTLs. PLABQTL is an interval-mapping program which uses flanking markers to estimate genotypes in intervals. This program does simple interval mapping (SIM) and composite interval mapping (CIM) using a fast multiple regression procedure. The interval mapping functions of PLABQTL

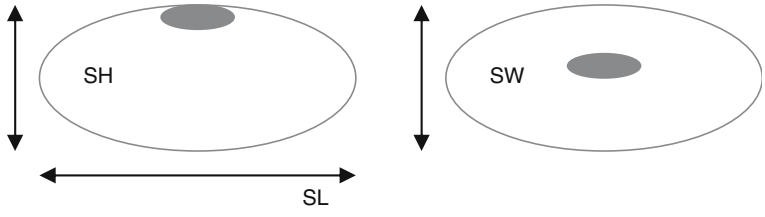

Fig. 1 Seed height (*SH*), seed length (*SL*), and seed width (*SW*)

are more powerful for detecting QTLs but the PLABQTL program does not investigate interactions.

We established empirical LOD thresholds for QTL detection using permutation tests (Churchill and Doerge 1994). Five thousand permutation tests were used to establish the empirical null distribution of maximum LOD score for a genome scan. The LOD scores from these permutation tests were approximately distributed as a log normal distribution ($\log N(\mu = 0.879, \sigma^2 = 0.061)$). LOD thresholds established from the permutation test are: suggestive (*P*-value 0.1) LOD 3.3, significant (*P*-value 0.05) LOD 3.7 and highly significant (*P*-value 0.01) LOD 4.8.

Heritability

Analyses of variance were used to partition the total variance into genetic and environmental components. Narrow sense heritability estimates were computed as follows: $h^2 = S_G/(S_G + S_e/r)$, where h^2 = heritability, S_G = genotypic variance, S_e = error and r = number of reps for the trait (Hanson et al. 1956).

Results

We measured seed dimensions traits that determine seed shape and volume or size in soybean. In all three populations these were normally distributed and inherited quantitatively, as observed by Hartwig (1973). The combined data for the parents and their RI progenies for SH, SW, and SL (Fig. 1) along with SV, from all replications and environments are shown in Table 1. The range for all traits varies from a minimum 4.7 for SH and maximum of 7.7 for SL in all three populations (Table 1).

The narrow sense heritabilities based on plot means ranged among populations between 0.72 and 0.83; 0.42 and 0.88; 0.58 and 0.85; 0.44 and 0.88 for SH, SW, SL, and SV, respectively (Table 1). These were similar to the values obtained by Cober et al. (1997) for seed shape and seed size.

Correlation coefficients between traits were calculated in each of the three RI populations across environments (Table 2). All traits were highly correlated with each other in all populations with values ranging from 0.5 to 0.9 except for the correlation between SL and SW that was either not significant or very low (0.3) in all populations.

Figure 2 and Table 3 show the genetic map locations of the QTLs detected above a LOD of 3 associated with each of the four traits in all three populations and environments.

A total of 26 QTLs (LOD ≥ 3) in 13 linkage groups (LG) were detected. One QTL for SL located in LG u22, near Satt578 was detected in all three populations across environments, this QTL was also associated with SH in MA and NA populations and with SV only in MA population.

Six QTLs (LOD ≥ 3) were detected in two populations, one was located in LG u9, near Satt489 for SL in MN population in USA, and in NA population in all environments; another one was located in LG u10, close to Satt052 and Satt181 for SW in all environments and for SL in Chile in MN and MA populations, respectively. One QTL was found in LG u11 near Satt567 associated with SH and SV across environments and with SW and SL in USA in MA population, and with SL and SV in USA in MN population. In LG u14 there are two QTLs near Satt166 (no. 21 and 22 in Table 3), these QTLs have a common region in MN population, one was detected for SH in USA and SV and SL in all environments in MA population; the other one was detected for SH, SV, and SW in all environments in NA population; and both for SL in USA and SW in Chile in MN population. Finally, in LG u22 there is one QTL located between L192_1 and Satt338 associated with all the four traits in all environments in populations MA and NA.

In the MN population 18 QTLs (LOD ≥ 3) were detected. Three of them were associated with three traits, six were associated with two traits, and nine with only one trait each. In this population, six, nine, seven and eight QTLs were detected for SH, SL, SV, and SW, respectively, explaining 56.8, 83.4, 83.8, and 62.4% of the variation in the traits.

In the MA population six QTLs (LOD ≥ 3) were detected. Two were associated with all traits, two were associated with three traits, and two with only one trait. Four, five, four, and three QTLs were detected for SH, SL, SV, and SW, respectively, explaining 41.6, 50.0, 48.4, and 32.3% of the variation in the traits.

In the NA population nine QTLs (LOD ≥ 3) were detected. One of them was associated with all traits, one with three traits, two were associated with two traits, and three were associated with only one trait. Six, five, two, and three QTLs were detected for SH, SL, SV, and SW, respectively, accounting for 52.8, 42.7, 30.4, and 40.3% of the variation in the traits.

In this study positive additive effects associated with SH were contributed by both parents, except for the MA population where Minsoy, the smallest parent, contributed solely negative additive effects. This was consistent in Chile, USA, and across environments. With respect to SW, only in the MN population both parents contributed positive additive effects, whereas

Table 1 Means, standard deviations (SD), range, and heritabilities of seed traits in the three RI populations (MN, Minsoy–Noir1; MA, Minsoy–Archer; and NA, Noir1–Archer); parental means are shown below

	RI populations														
	MA				MN				NA						
	SH[a]	SW	SL	SV	SH	SW	SL	SV	SH	SW	SL	SV			
Mean	5.1	6.4	7.7	254.2	4.7	6.2	7.7	224.5	5.1	6.5	7.7	256.0			
SD	0.3	0.4	0.7	40.2	0.3	0.3	0.7	31.8	0.4	0.3	0.4	31.0			
Range	4.3–6.0	5.2–7.4	5.9–9.8	143.6–428.7	3.9–5.6	5.1–7.0	5.9–9.5	133.3–350.1	3.9–6.1	5.6–7.3	6.4–9.5	180.1–361.7			
h^2(±SE)	0.72 (0.001)	0.68 (0.003)	0.58 (0.001)	0.62 (0.002)	0.73 (0.001)	0.42 (0.002)	0.64 (0.001)	0.44 (0.008)	0.83 (0.025)	0.88 (0.052)	0.85 (0.023)	0.88 (0.003)			
	Parents														
	Archer				Minsoy				Noir- 1						
	SH	SW	SL	SV	SH	SW	SL	SV	SH	SW	SL	SV			
Mean	5.2	6.7	8.1	282.8	4.9	6.2	7.3	225.9	4.7	6.3	7.7	227.1			

[a] Traits were: seed height (SH), seed width (SW), and seed length (SL) in mm, and seed volume (SV) in mm^3 measured in Chile and USA

Table 2 Correlation between seed height (SH), seed width (SW), seed length (SL), and seed volume (SV) in the three RI populations (MN, Minsoy–Noir1; MA, Minsoy–Archer; and NA, Noir1–Archer)

Population	Traits				
		SH	SL	SW	SV
MN	SH	–	0.5	0.6	0.9
	SL		–	NS	0.6
	SW			–	0.8
	SV				–
MA	SH	–	0.8	0.6	0.8
	SL		–	0.3	0.7
	SW			–	0.6
	SV				–
NA	SH	–	0.7	0.7	0.9
	SL		–	0.3	0.8
	SW			–	0.8
	SV				–

in the other populations the Archer allele always had a positive effect. For SL in all populations the QTL alleles contributed both ways across environments. For SV, only Archer, the largest parent, contributed positive QTL allele in all environments whereas in the MN population both parents contributed QTL alleles with positive or negative additive effects (Table 3).

Surprisingly, no epistatic interactions between QTLs were detected for the seed traits measured. The fact that epistatic interactions were not detected does not mean that they are not present. The power to detect epistatic interactions depends on the magnitude of the interacting QTLs and it is entirely possible that that seed shape in these crosses is governed by a multitude of smaller QTLs where epistasis may be present but not detected in our experiments. In such a situation the interactions between these QTLs would not show up as statistically significant.

Discussion

As would be expected the genetic control of seed shape and volume is complex and controlled by many loci. However, at least 30% of the genetic variation for the traits is controlled by four QTLs or less. This explains the medium to high heritability observed and thus we conclude that these traits are amenable to manipulation by selection without the help of molecular markers. Cober et al. (1997) stated that seed shape and seed size are not correlated, which is good when breeding for rounded, small or big seed. Our data confirmed their results, however, we observed that none of the

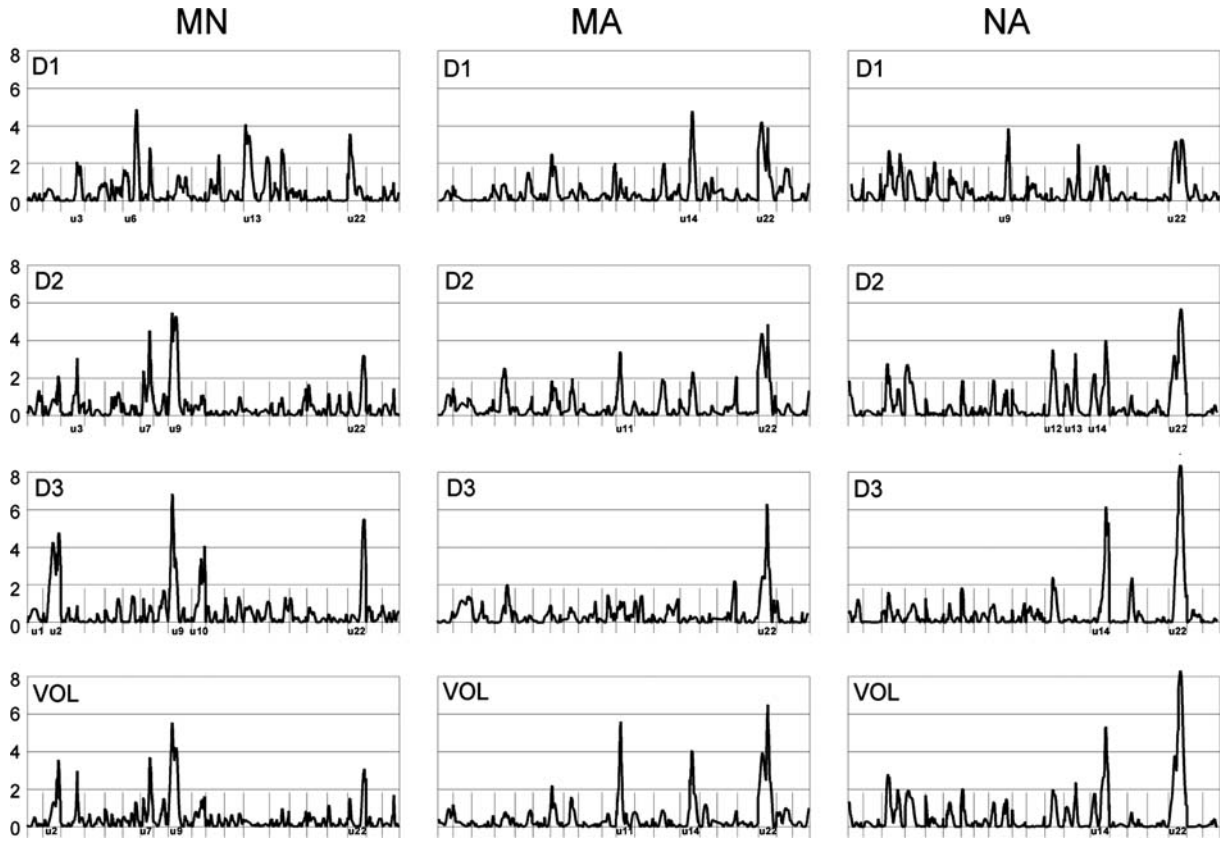

Fig. 2 QTL genome scans for four different traits in each of three RI populations. Each graph displays the complete simple interval-mapping scan for a particular population and trait. The genome position (*x*-axis) is graphed against the LOD score (*y*-axis). *Vertical lines* on the *x*-axis indicate the boundaries of linkage groups. LOD thresholds established from the permutation test are: suggestive (*P*-value 0.1) LOD 3.3, significant (*P*-value 0.05) LOD 3.7, and highly significant (*P*-value 0.01) LOD 4.8. The populations are MN = Minsoy–Noir 1, MA = Minsoy–Archer, and NA = Noir1–Archer. The traits are (D1) seed height, (D2) seed width, (D3) seed length and (VOL) seed volume (D1 × D2 × D3)

576 segregants that we examined had a round seed shape, indicating that to readily find round seed shape segregants it is necessary to start with at least one round seeded parent. Nonetheless, we observed that all RI populations showed transgressive segregation for all traits measured (Table 1). These could be explained by lines having the correct combination of the positive QTL alleles which can be donated even by the parent with the smaller value for the trait (Mansur et al. 1996; Mian et al. 1996: Orf et al. 1999), or by undetected QTLs or epistatic interactions. Therefore, breeders should not overlook the fact that using molecular markers it is possible to find transgressive segregants among parents of similar phenotype. Mansur et al. (1996) found that this could be possible for maturity and yield in the cross of Minsoy by Noir1.

It is rewarding to find that that important loci detected by us for seed shape traits, were also detected by other researchers measuring seed weight in the same or other populations in different environments. Mian et al. (1996) detected 16 QTLs for seed size located in 12 linkage groups. Six of those QTLs were located in the same linkage groups where our QTLs were located (u2, u9, u12, u13, u14, and u22). One of these QTLs Dt1 in u14 was located within the interval denoted by Satt166 and Satt006 responsible for seed height, volume, and width in population NA (Table 3).

Mansur et al. (1996) detected three markers associated with seed weight in three linkage groups (u3, u7, and u20). One of these QTLs (K_443) located in LG u3 in population MN is located less than 5 cM from a QTL detected by us (Satt508–Satt421), responsible for seed height (Table 3).

Orf et al. (1999) detected 16 QTLs associated with seed weight in 11 linkage groups. Seven of these QTLs were also detected by us for seed shape traits (Satt508, Satt277, L199_2, Satt150, L050_14, Satt527, K001_1, and L192_1) (Table 3).

Hoeck et al. (2003) examined three populations in three environments for seed size QTLs. They found 27 QTLs associated with seed size averaged across environments in 16 linkage groups. Eighteen of these QTLs

Table 3 Complete listing of all QTLs detected above a LOD of 3.0 for seed height (SH), seed width (SW), seed length (SL), and seed volume (SV) in the three RI populations (MN, Minsoy–Noir1; MA, Minsoy–Archer; and NA, Noir1–Archer)

QTL	Population	Trait	Location	Linkage group (Utah/Iowa[a])	Position	Marker 1	Marker 2	LOD	R^2	Additive effect
1	MN	SL	USA	u2/E	18	Sat_112	G214_10	3.15	7.4	11.2
	MN	SV	USA	u2/E	18	Sat_112	G214_10	3.27	7.7	658.3
2	MN	SW	Average	u2/E	74	B2	Satt573	4.26	9.9	−11.3
3	MN	SV	Average	u2/E	112	Satt369	Satt553	3.55	8.3	−578.8
	MN	SW	Average	u2/E	114	Satt369	Satt553	4.77	11.0	−7.8
4	MN	SH	Average	u3/A2	114	Satt508	Satt421	3.06	7.2	5.1
	MN	SL	Chile	u3/A2	114	Satt508	Satt421	3.69	8.6	9.7
	MN	SV	Chile	u3/A2	114	Satt508	Satt421	3.96	9.2	793.9
5	NA	SL	Chile	u3/A2	34	Satt207	Satt315	3.98	9.6	−14.7
6	NA	SH	USA	u4/B1	20	T028_1	Satt509	3.09	7.2	10.4
7	MN	SL	Average	u6/N	98	Satt234	Satt022	4.88	11.2	−12.3
8	MN	SH	Chile	u7/A1	26	A053_2	R183_1	3.02	7.1	−6.7
9	MN	SV	Average	u7/A1	68	A975_1	K636_2	3.68	8.6	−612.1
	MN	SH	Average	u7/A1	66	A975_1	K636_2	4.5	10.4	−6.3
10	MN	SH	Average	u9/C2	30	L199_2	Sat_062	5.46	12.5	7.5
	MN	SV	Average	u9/C2	30	L199_2	Sat_062	5.52	12.6	785.4
	MN	SW	Average	u9/C2	30	L199_2	Sat_062	6.84	15.4	9.7
11	MN	SH	Average	u9/C2	56	Satt291	A426_1	5.29	12.1	8.0
	MN	SW	USA	u9/C2	52	Satt291	A426_1	3.56	8.3	6.6
12	NA	SL	Average	u9/C2	120	Satt277	Satt489	3.84	8.9	10.5
	MN	SL	USA	u9/C2	122	Satt489	Satt134	4.09	9.5	12.4
13	MN	SW	Average	u10/A1	68	Satt052	Satt253	3.4	8	−6.2
	MA	SL	Chile	u10/A1	70	Satt181	Satt434	3.63	8.8	15.0
14	MN	SW	Average	u10/A1	92	Satt142	Satt434	4.06	9.4	−8.0
15	MA	SH	Average	u11/M	26	Satt150	Satt567	3.4	8.2	−7.4
	MA	SW	USA	u11/M	30	Satt150	Satt567	3.79	9.1	−6.6
	MA	SL	USA	u11/M	30	Satt150	Satt567	4	9.6	−13.8
	MA	SV	Average	u11/M	30	Satt150	Satt567	5.59	13.2	−1182.7
	MN	SL	USA	u11/M	34	Satt567	R079_1	4.92	11.3	−13.6
	MN	SV	USA	u11/M	36	Satt567	R079_1	3.8	8.8	−701.2
16	MN	SL	USA	u11/M	66	Sat_003	Satt494	3.8	8.8	−13.0
17	MA	SW	USA	u12/D2	4	L072_1	A401_2	3.5	8.5	−6.9
18	NA	SH	Average	u12/D2	28	Satt002	Satt582	3.51	8.2	6.7
19	MN	SL	Average	u13/F	18	Satt423	W1	4.08	9.5	9.3
20	NA	SH	Average	u13/F	82	L050_14	Sct_033	3.3	7.7	6.5
	NA	SL	Chile	u13/F	86	Satt335	Satt072	3.93	9.2	10.7
21	MA	SH	USA	u14/L	88	Satt527	Satt166	4.46	10.7	−7.9
	MA	SV	Average	u14/L	88	Satt527	Satt166	4.06	9.8	−1077.2
	MA	SL	Average	u14/L	90	Satt527	Satt166	4.77	11.4	−14.8
21–22	MN	SL	USA	u14/L	90	Sat_099	G173_1	3.96	9.2	−14.3
	MN	SW	Chile	u14/L	100	G173_1	Dt1	3.82	8.9	8.3
22	NA	SH	Average	u14/L	110	Satt166	Satt006	4.02	9.3	−8.7
	NA	SV	Average	u14/L	110	Satt166	Satt006	5.33	12.1	−1181.0
	NA	SW	Average	u14/L	110	Satt166	Satt006	6.17	13.9	−11.1
23	NA	SW	Chile	u19/D1b+W	30	Sat_096	Satt095	3.12	7.9	−7.6
24	MN	SL	Average	u22/C1	18	A463_1	K001_1	3.57	8.3	−9.7
	MA	SL	Average	u22/C1	24	SOYGPATR	Satt578	4.19	10.8	−26.3
	MA	SH	Average	u22/C1	28	SOYGPATR	Satt578	4.36	11.2	−15.6
	MA	SV	Average	u22/C1	32	SOYGPATR	Satt578	3.93	10.2	−2090.2
	NA	SL	Average	u22/C1	34	K001_1	Satt578	3.17	7.4	−12.7
	NA	SH	Average	u22/C1	40	K001_1	Satt578	3.22	7.5	−9.5
25	MA	SL	Average	u22/C1	68	L192_1	Satt136	3.89	9.4	−11.9
	MA	SH	Average	u22/C1	68	L192_1	Satt136	4.84	11.5	−7.6
	MA	SV	Average	u22/C1	68	L192_1	Satt136	6.49	15.2	−1245.5
	MA	SW	Average	u22/C1	70	G214_24	Satt399	6.3	14.7	−8.7
	NA	SL	Average	u22/C1	78	Sat_077	Satt338	3.25	7.6	−12.7
	NA	SV	Average	u22/C1	84	Sat_077	Satt338	8.31	18.3	−1853.8
	NA	SW	Average	u22/C1	84	Sat_077	Satt338	8.41	18.5	−16.4
	NA	SH	Average	u22/C1	88	Sat_077	Satt338	5.69	12.9	−14.2
26	MN	SW	Average	u22/C1	112	A063_1	N	5.49	12.5	9.1
	MN	SH	Average	u22/C1	112	A063_1	N	3.2	7.5	6.1
	MN	SV	Average	u22/C1	116	N	Satt338	3.06	7.2	527.9

[a] Current Iowa State Map linkage groups are the same as those in the Consensus Map (Cregan et al. 1999)

were located in the same linkage groups as those associated with seed shape traits in this study. Most importantly, there are four QTLs detected here (Table 3) that coincided very closely (less than 5 cM) with those of Hoeck et al. (2003). Satt277 in LG u9 was associated with seed length in NA and with seed size in population 2 (Hoeck et al. 2003); Sct_033 in LG u13 was detected for seed height in population NA, and Satt510 for seed size in population 1 (Hoeck et al. 2003). Two markers of Hoeck et al. (2003), controlled seed size in two of their populations and comprised an interval detected by us having a QTL for seed height, volume, and weight in NA and for seed volume and length in MA. Finally, the interval SOYGPATR to Satt578 in LG u22 was detected for seed length, height, and volume in population NA and for seed size in Hoeck's populations 2 and 3 (Hoeck et al. 2003).

The number and genomic distribution of the QTLs confirms the complexity of seed shape and shows that its genetic structure is similar to other quantitative traits investigated via molecular marker maps. That is that the QTLs are scattered in many chromosomes, usually four to six of them control at least 40% of the genetic variation, and a few QTLs are also involved in the control of many quantitative traits (Mansur et al. 1996; Orf et al. 1999; Lee et al. 1996; Zhang et al. 2004).

In regards to this last point, it has been observed that certain loci are QTL hot spots having effects on many different traits. In the first QTL mapping effort in a cross of two *Glycine max* L. cultivars, Mansur et al. 1993 detected three intervals involving the following markers A397, G173, and R079 located in the consensus map's linkage groups C2 (u9), L (u14), and M (u11), respectively (Cregan et al. 1999). Within 10 cm from the location of the A397 loci, we found Satt277 and Satt489 to be associated with seed length (Table 3). Moreover, this same region has been associated with days to flower (Mansur et al. 1993; Orf et al. 1999; Zhang et al. 2004), maturity (Mansur et al. 1993, 1996; Orf et al. 1999); reproductive period (Orf et al. 1999); plant height (Mansur et al. 1996; Orf et al. 1999; Zhang et al. 2004); lodging (Orf et al. 1999; Zhang et al. 2004); seed size (Hoeck et al. 2003); seed number (Orf et al. 1999); number of nods (Zhang et al. 2004); and yield (Mansur et al. 1993, 1996; Orf et al. 1999; Zhang et al. 2004). Similarly, within 10 cM of G173_1 there are loci associated with seed width and length in this study (Table 3), and seed size (Hoeck et al. 2003); days to flower (Mansur et al. 1993, 1996; Orf et al. 1999), plant height and lodging (Lee et al. 1996; Mansur et al. 1993, 1996; Orf et al. 1999); days to maturity (Mansur et al. 1996; Orf et al. 1999); seed protein and oil content (Mansur et al. 1996); leaf length and area, and yield (Orf et al. 1999). Finally, within 20 cM of R79 there are loci associated with seed length, width, and volume in this study as well as days to flower and maturity, leaf area, and yield (Mansur et al. 1993, 1996; Orf et al. 1999) and plant height (Mansur et al. 1996; Orf et al. 1999; Zhang et al. 2004).

It is important to note that strong loci such as the ones described above, should be further studied in detail at the molecular level in order to elucidate the gene or genes responsible for them and their mode of action.

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