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QTLs conditioning early growth in a soybean population segregating for growth habit

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Abstract There are both economic and environmental reasons for reducing the use of herbicides for weed control in soybean [*Glycine max* (L.) Merr.] fields. Optimizing crop competitiveness can reduce reliance on chemical weed control. Fast and vigorous early growth and rapid canopy development can be effective in suppressing weed infestation of crop plants. The purposes of this study were to identify and molecularly map the quantitative trait loci (QTLs) conditioning soybean plant height and canopy width during the early vegetative stages of soybean growth. A restriction fragment length polymorphism (RFLP) linkage map was created using 142 markers and 116 F_2-derived lines from a cross of 'S100' × 'Tokyo'. The parents and the 116 F_2-derived lines were evaluated in the greenhouse and in the field at Athens, Ga., in 1996 and 1997. Combined over environments, Tokyo averaged 41 and 17% taller plants than S100 at the V7 and V10 stages of development. Transgressive segregation was observed among the progeny at both stages. Based on single-factor analysis of variance (ANOVA), three and four independent RFLP loci were associated with plant height at the V7 and V10 stages, respectively. All three loci detected [on linkage groups (LGs) C2 and F, and unlinked] at the V7 stage were also detected at the V10 stage along with one additional independent locus on LG E. The Tokyo allele contributed to increased plant height at all loci except at the unlinked locus. Three QTLs (on LGs C2, E, and F) were consistent across environments, three (on LGs C2 and F, and unlinked) were consistent across stages of plant development, and two (on LGs C2 and F) were consistent both across environments and stages of plant development. Within each stage of development, there was no interaction among the independent loci, and the respective loci together explained most of the variation in the traits. Three independent RFLP loci were associated with canopy width at the V10 stage, of which one was unique to the trait, while the remaining loci (on LGs C2 and F) were in common with the independent loci for plant height. Canopy width had a strong correlation ($r = 0.87$) with plant height at the V10 stage. However, mature plant height, lodging, or seed weight had no phenotypic or QTL association with early plant height or canopy width.

Key words Soybean · *Glycine max* · RFLP · QTL · Plant height · Canopy width

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Introduction

In order to reduce production cost and to address environmental concerns, there is a strong interest in finding ways to reduce the use of herbicides for weed control in field crops. Optimizing crop competitiveness can reduce reliance on chemical weed control (King and Buchanan 1993). Harper (1957) has stated that "to control existing weeds by herbicides and to prevent re-invasion by management is the most sensible procedure." Grundy et al. (1992) found that long-straw cereal cultivars suppressed weed growth better compared to their short-straw counterparts. Richards (1989) reported that wheat (*Triticum aestivum*) cultivars that achieved the greatest ground cover competed better with weeds than did cultivars that achieved ground cover more slowly. Richards and Davies (1991) suggested that lower doses of herbicides could be used with more competitive wheat cultivars.

Soybean is typically grown in 76–100 cm rows. A number of researchers (Wax and Pendleton 1968; Kust and Smith 1969; Yelverton and Coble 1991; Derting et al. 1995) have reported that narrow-row spacings suppressed weeds better in a soybean field than the typical-row spacings. Derting et al. (1995) attributed the lower weed infestation in the narrow-row soybean field to early canopy closure and shading of the subsequent weed populations. According to Yelverton and Coble (1991) rapid and complete canopy formation reduces the amount of light reaching the soil surface, which can suppress weed resurgence. The need for the special equipment for planting and cultivation of narrow-row soybean, increased seed cost, and the absence of economically sustainable yield advantage of narrow-row soybean over the typically spaced soybean are some of the practical reasons that kept soybean growers from adopting the narrow-row planting of soybean in southern USA.

One way of avoiding the problems associated with the narrow-row planting of soybean and yet suppress weed infestation is to use soybean cultivars that are able to grow rapidly and shade the ground quickly. Utilization of such cultivars would require less herbicide application for weed control than slow-growing cultivars.

Achieving an early ground cover is especially important for herbicides that do not possess a residual effect, such as glyphosate applied to Roundup Ready soybean cultivars, and for double-cropped or late-planted soybean. Presently available Roundup Ready soybean cultivars require two or even three applications of herbicide to achieve an adequate weed control. Utilization of a soybean cutivar that can rapidly close the canopy, may reduce the need for additional application of the herbicide.

The use of molecular markers provides the opportunity to construct plant genetic maps and to give insights into the genomic location and gene action of individual QTLs (Lander and Botstein 1989; Tanksley et al. 1989). The identification of QTLs allows the analysis and selection of complex quantitative traits as a set of single-gene traits (Tanksley et al. 1989). A number of researchers (Keim et al. 1990; Mansur et al. 1993; Lee et al. 1996 a,b; Mansur et al. 1996) have identified QTLs for height in mature soybean plants. They, however, did not measure plant height during the early vegetative stages of soybean development. In several greenhouse trials for the determination of water-use efficiency, S100 produced significantly shorter plants at the V7 stage of development (Fehr and Caviness 1977) than did Tokyo (unpublished data 1994). The objectives of the present study were to identify and map the QTLs conditioning soybean plant height and canopy width during the early stages of soybean development in an F_2-derived population from a cross of S100 × Tokyo.

Materials and methods

Genotypic assay

A soybean population derived from a cross between the indeterminate soybean cultivar S100 and the determinate cultivar Tokyo was used to construct a genetic linkage map and to evaluate phenotypic traits. From this cross, a total of 116 F_2-derived lines was developed with each line originating from a different F_2 plant. DNA isolation, Southern blotting, and hybridization procedures have been described previously (Lee et al. 1996 a). In short, RFLPs were surveyed from DNA isolated from lyophilized young leaves of parents grown in the greenhouse. The DNA was isolated from leaves according to the procedure of Keim et al. (1988), and digested overnight with each of five restriction enzymes (*Dra*I, *Eco*RI, *Eco*RV, *Hin*dIII, or *Taq*I). Following electrophoresis of DNA fragments, a Southern blot was made by transfer to an uncharged nylon membrane. Nylon membranes were placed in 300 × 38-mm glass bottles containing 4–10 ml of 0.25 M Na_2PO_4 and 7% SDS, and prehybridized in a rotisserie oven for 4–6 h at 65°C. About 25 ng of isolated DNA probe were labeled with ^{32}P using a random primer procedure, and hybridization was conducted overnight. Approximately 750 probes from various sources, including cDNA and/or genomic clones of soybean (R. C. Shoemaker, USDA/Iowa State Univ.; K. G. Lark, Univ. of Utah; R. T. Nagao, Univ. of Georgia), *Vigna radiata* (N. D. Young, Univ. of Minnesota), *Phaseolus vulgaris* (J. M. Tohme, CIAT), *Arachis hypogaea* (G. D. Kochert, Univ. of Georgia) and *Medicago sativa* (G. D. Kochert), were used to screen for polymorphisms between S100 and Tokyo.

Probes polymorphic with respect to the parents were used for creating the genetic map. The DNA was isolated from young unfolded trifoliolate leaves of 10–12 plants for each of the 116 F_2 -derived lines, which were grown in a field near Athens, Ga., in 1993. Multiple sets of nylon membranes containing DNA from each of the 116 lines were screened with polymorphic probes. The nomenclature for polymorphic RFLP loci consist of a probe designation, followed by the restriction endonuclease designation [*Dra*I (D); *Eco*RI (E); *Eco*RV (V); *Hin*dIII (H); *Taq*I (T)], and a dashed-number suffix for an anchored probe or a letter (lower-case) suffix for a non-anchored probe when more than one locus was detected by that probe. A RFLP locus was accepted as an anchor when it had the same probe/enzyme combination and an identical banding pattern with the corresponding RFLP locus on the USDA/ARS-ISU map (Shoemaker and Specht 1995). The linkage map was constructed with marker data using the Kosambi map function of Mapmaker (Lander et al. 1987). For grouping markers, linkage thresholds of 3.0 for a minimum LOD score and 50 cM for a maximum distance were employed.

Greenhouse assay

In a greenhouse in Athens, Ga., 116 F_2-derived lines and the two parents were grown in plastic pots containing 3.5 kg of methyl bromide-fumigated Pacolet sandy loam soil (a member of the clayey, Kaolinitic, thermic family of Typic Hapludults) amended with sand to a texture of 800 g kg^{-1} sand, 120 g kg^{-1} silt, and 80 g kg^{-1} clay. Four seeds were planted in each pot and seedlings were thinned to one per pot 8–10 days after planting.

The experimental design was a randomized complete block with five replicates. Because of the large size of the experiment and the limitation in greenhouse space, the replicates were grown sequentially in time with 2–3 weeks between successive replicates. The experiment was started in mid April of 1995 and was completed by July of the same year. High-pressure sodium-vapor lighting (575 μmol m^{-2} s^{-1} at 20 cm above soil level) was used after dusk to maintain a 15-h light and 9-h dark cycle throughout the experiment. The same lights were also used during days with complete cloud

cover. The temperature ranged from 28 to 37°C during the day and from 19 to 23°C during the night. Plants were spaced at 20 × 25 cm to avoid the shading effect from neighboring plants. One column of border pots was included at the two ends of the experiment (along the width of the bench), but no border pots were provided on the other two sides (along the length of the bench). The pots were regularly rotated to minimize border and locational effects within the test. At the V7 stage of development, the height of each plant was measured in cm from the soil surface to the top of the growing point.

Field evaluation

The parents and the F_2-derived lines were grown in 1996 and 1997 at the Plant Sciences Farm near Athens, Ga. In both years, the lines were grown in 0.76-m wide and 3.66-m long single-row plots. To reduce experimental error due to soil heterogeneity within the experimental site, the 116 lines were randomly divided into two groups of 58. The 58 lines in each of the two groups, along with three entries of each parent, were grown in two separate tests. Each test was grown in a randomized complete block design with four replicates. In 1996, the experiment was planted on 14 June and the soil type was Wedowee coarse sandy loam, a member of the clayey, kaolinitic, thermic family of the Typic Hapludults. In 1997, the experiment was planted on 12 June, and the soil type was Appling loamy coarse sand, a member of the clayey, kaolinitic, thermic family of the Typic Hapludults.

Data were collected on plant height at the V7 and V10 stages, and canopy width was measured at the V10 stage. Plant height was measured from the soil surface to the tip of the growing point of four randomly chosen plants in each plot. The canopy width was measured with an adjustable sliding scale by averaging four random measurements per plot. Data were also collected on mature plant height, lodging, maturity, and seed weight. Mature plant height was measured as the average length of plants from the ground to the terminal bud of the plant at maturity. Lodging rating was recorded at maturity on a scale of 1 (all plants erect) to 5 (all plants prostrate). Maturity was recorded as the number of days after 31 August when 95% of the pods had reached mature pod color (Fehr and Caviness 1977). The seed weight was determined in mg seed^{-1} based on a 100-seed sample per plot.

Data analysis

The association between markers and phenotypic data was tested using two different procedures. A single-factor analysis of variance (ANOVA) was conducted to evaluate each marker locus for linkage to a presumed QTL affecting the trait by contrasting the mean performance of the three RFLP classes (homozygotes for the S100 band, homozygotes for the Tokyo band, and heterozygotes). For each of the marker loci, differences among the RFLP class means were tested for significance using an *F*-test based on the type-III means squares generated by the GLM procedure of SAS (SAS Institute 1991). The significant markers were determined by first testing all the markers for significant association with each trait at $P \leq 0.01$ based on the combined phenotypic data across environments. In order to detect consistency of the previously identified markers across environments, a relaxed probability level of $P \leq 0.05$ was used for marker association in the individual environments. The proportion of the total phenotypic variance among lines that could be explained by a marker was estimated by R^2 = (sum of squares for the markers)/(sum of squares among lines). Multi-factor analysis of variance was used to detect epistatic interactions ($P \leq 0.01$) among the independent RFLP loci conditioning each of the traits.

The QTL mapping analysis was performed using the interval-mapping method (Lander and Botstein 1989) with MAPMAKER-QTL software (Lincoln et al. 1992). A minimum LOD score of 2.4 was chosen as the significance criterion for declaring the presence of a QTL in a given genomic region. The LOD threshold of 2.4 would be equivalent to applying a significance level of $P \leq 0.01$ in this soybean population (Lander and Botstein 1989; Doerge and Rebai 1995). The LOD score peak was used to estimate the most likely QTL position on the RFLP linkage map. The percentage of phenotypic variance among lines explained by individual QTL (R^2), and the additive (a) and dominant (d) effects were estimated at the maximum-likelihood QTL position. The average degree of dominance for each QTL was calculated as the ratio d/a.

Results and discussion

Genetic map

A total of 142 polymorphic RFLP markers were used to construct the genetic linkage map of this population. Of these 142 markers, 115 segregated in a codominant fashion, while 27 markers were dominant in their expression. The map covered about 1100 cM of the soybean genome with 120 markers linked on 25 linkage groups. Twenty two of the markers remained genetically unlinked. Each RFLP locus on this map was compared with its Soybase (1995) image whenever available. Through these comparisons, 20 of the linkage groups were associated with the USDA linkage groups (Shoemaker and Specht 1995) on the basis of anchored probes.

Plant height at the V7 and V10 stages

Combined over environments, Tokyo averaged 41 and 17% taller plants than S100 at the V7 and V10 stages, respectively (Table 1). At V7, the tallest progeny line was 59% taller than the shortest progeny line, while at V10 the tallest progeny line was 50% taller than the shortest progeny line (Table 1). Transgressive segregation occurred among the progeny for the trait at both stages of development.

Single-factor ANOVA, based on combined phenotypic data over environments, detected three putative

Table 1 Mean plant height and canopy width of the parent and the extreme progeny lines for the F_2-derived population of S100 × Tokyo combined across environments

Genotypes	Traits		
	Plant height (cm)		Canopy width (cm)
	V7[a]	V10	V10
S100	17	30	46
Tokyo	24	35	49
High progeny	27	39	51
Low progeny	17	26	37
LSD (0.01)	2.5	4	5
h^2 (%)	78	76	49

[a] Stage of soybean development (Fehr and Caviness 1977)

Table 2 Putative independent RFLP loci associated with soybean plant height measured at the V7 stage of development

RFLP marker	Linkage group[a]	Combined					Environment					
		P	R^2 (%)	Alleic means (cm)[b]			Greenhouse		Field 96		Field 97	
				SS	ST	TT	*P*	R^2 (%)	*P*	R^2 (%)	*P*	R^2 (%)
K418H	C2	0.0001	21	16.9	18.2	18.9	0.004	12	0.001	14	0.0001	22
A077V-a	Unlinked	0.005	10	18.8	18.3	17.4	NS	–	0.01	8	0.004	10
HSP176H	F	0.0001	25	17.6	18.0	19.6	0.0001	24	0.002	13	0.0004	15

[a] Shoemaker and Specht (1995)
[b] SS: homozygous for S100 allele, ST: heterozygotes, TT: homozygous for Tokyo allele

independent marker loci conditioning plant height at V7 (Table 2). A putative independent locus was defined as a marker locus which was greater than 50 cM from another marker locus significantly associated with the trait, and which acted in an additive manner (i.e., no epistasis with other significant markers) with regard to explaining variation in the trait. Marker HSP176H on LG F explained the highest amount of variation in the trait ($R^2 = 25\%$) (Table 2). Marker K418H on LG C2 and the unlinked marker A077V-a explained 21 and 10% of the variation in the trait, respectively. Tokyo contributed the allele for increased plant height at marker loci HSP176H and K418H, while S100 did so at the remaining locus (Table 2). There was no epistatic interaction among the three independent marker loci. Together, the three independent loci explained 55% of the variation in the trait in a three marker-model analysis (SAS 1991). The heritability for the trait was 78% (based on four replicates and three environments). Marker loci HSP176H and K418H were consistent across the three environments; however, locus A077V-a was detected only in the two field environments and not in the greenhouse.

MAPMAKER/QTL analysis detected the presence of a QTL for plant height at V7 in the interval between markers K418H and A397D-1 on LG C2 (see Table 5 and Fig. 1). The approximate QTL position was within 1.8 cM from marker K418H and the LOD score for the presence of a QTL at this location was 5.2. A second QTL was detected on LG F in the interval between markers HSP176H and B212. The LOD score for the presence of a QTL for plant height on this LG was 6.4. The approximate location of the QTL was at marker HSP176H (See Table 5 and Fig. 1).

All three QTLs identified for plant height at V7 were also identified at V10 along with one additional QTL on LG E (marker locus Cr406V). Marker K418H explained approximately the same amount of variation in the trait as it did at the V7 stage (Table 3). However, marker HSP176H on LG F was significant at $P \leq 0.01$ and explained only 8% of the variation in the trait at V10. The same locus accounted for 25% variation in the trait at V7 (Table 2). Thus, the effect of the plant height QTL on LG F was more pronounced at V7

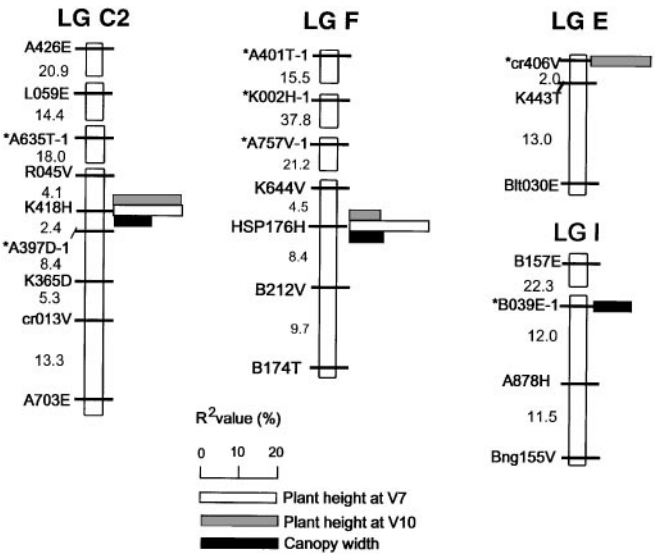

Fig. 1 RFLP linkage groups C2, E, F, and I of the S100 × Tokyo population showing marker positions and estimated map distances (cM) on the left-hand side, and USDA linkage group designation (Shoemaker and Specht 1995) on the top of each linkage group. *Lengths of horizontal bars* indicate R^2 values for the loci associated with the trait. * indicates an anchored probe which had the same probe/enzyme combination and an identical banding pattern with its SoyBase (1995) image. A marker locus is identified with a *probe designation*, followed by the *restriction endonuclease designation*, and a *dashed number suffix* for an anchored probe, or a *letter* (*lower case*) *suffix* for a non-anchored probe, when more than one locus was detected by that probe

compared to that at V10. The QTL linked to marker A077V-a had approximately the same effect on plant height at V10 as it had at V7. The independent marker locus, Cr406V on LG E was also found to be associated with plant height at V10. It explained 19% of the variation in the trait in the combined analysis. All four loci were consistent across the two field environments. Tokyo contributed alleles for increased plant height at marker loci K418H and HSP176H, while S100 did so at marker loci A077V-a and Cr406V. In a four-marker model there was no interaction among the four independent loci and together they explained 60% of the

variation in the trait. The heritability of the trait was 76% (based on four replicates and two environments).

At the V10 stage, MAPMAKER/QTL detected the same QTL on LG C2 as it did at V7 (see Table 5). The probable location of the QTL was 2.0 cM from marker K418H with a LOD score of 4.1. The QTLs on LG E and F were not detectable at V10 using a LOD score minimum of 2.4. These QTLs, however, could be detected using a LOD score minimum of 2.0 (data not shown).

Canopy width at V10

S100 and Tokyo did not differ in canopy width but the high progeny line had a 38% greater canopy width than the low progeny line (Table 1). There was no transgressive segregation for greater canopy width in the high parent (Tokyo). Three independent marker loci were associated with canopy width at V10 (Table 4). Two of these RFLP markers (K418H and HSP176H) were also associated with plant height (Tables 2, 3, and Fig. 1). For both of these loci, the alleles for greater canopy width came from the same parent that contributed the alleles for increased plant height. This observation was in agreement with the high correlation ($r = 0.87$) between plant height and canopy width at V10. These results indicate that these two marker loci are probably associated with increased plant vigor (both height and width of a plant). Marker B039E-1 on LG I was associated only with canopy width, but not with plant height (Table 4 and Fig. 1).

For canopy width, the QTL on LG C2 was detected by MAPMAKER/QTL (Table 5 and Fig. 1). The most probable location of the QTL on LG C2 was 1.8 cM from the marker K418H in the interval between K418H and A397D-1. The other two QTLs were not detectable above the minimum LOD threshold of 2.4.

Relationship with other traits

Lee et al. (1996 a,b) reported QTLs for mature plant height on USDA LGs A2, B1, C1, D1, F, H, J, L and N, while Keim et al. (1990) reported only one marker locus on an unidentified LG. Mansur et al. (1993) reported one major QTL for mature soybean plant height on LG L. Mansur et al. (1996) identified five QTLs for plant height on five separate LGs of the Minsoy × Noir1 population. Of the four QTLs for early plant height in soybean that we report here only one, on LG F, appears to be in a similar genomic region with the previously reported QTLs for mature plant height. The height locus (A186 on LG F) reported by Lee et al. (1996 a) is within 10 cM of the marker HSP176H based on the newly integrated soybean map (Shoemaker et al. 1996), and accounted for 5% of the variation in mature plant height. This lack of agreement of mature plant height QTLs with QTLs for early plant growth in this soybean population is not

Table 3 Putative independent RFLP loci associated with soybean plant height in the field, measured at the V10 stage of development

RFLP marker	Linkage group[a]	Combined					Environment			
		P	R^2 (%)	Allelic means (cm)[b]			Field 96		Field 97	
				SS	ST	TT	*P*	R^2 (%)	*P*	R^2(%)
K418H	C2	0.0001	20	27.2	28.7	29.7	0.003	12	0.0001	26
A077V-a	Unlinked	0.001	12	30.7	29.3	28.2	0.008	9	0.01	9
Cr406V	E	0.0001	19	31.0	28.9	27.9	0.003	17	0.01	11
HSP176H	F	0.01	8	28.6	29.3	30.5	0.01	9	0.03	7

[a] Shoemaker and Specht (1995)
[b] SS: homozygous for S100 allele, ST: heterozygotes, TT: homozygous for Tokyo allele

Table 4 Putative independent RFLP loci associated with soybean canopy width in the field, measured at the V10 stage of development

RFLP marker	Linkage group[a]	Combined					Environment			
		P	R^2 (%)	Allelic means (cm)[b]			Field 96		Field 97	
				SS	ST	TT	*P*	R^2 (%)	*P*	R^2 (%)
K418H	C2	0.008	10	42.6	44.0	45.0	0.03	8	0.003	12
HSP176H	F	0.01	8	43.4	44.2	45.0	0.04	6	0.01	8
B039E-1	I	0.01	10	43.2	44.4	44.7	0.01	9	0.01	10

[a] Shoemaker and Specht (1995)
[b] SS: homozygous for S100 allele, ST: heterozygotes, TT: homozygous for Tokyo allele

Table 5 Genomic location, genetic effects, and percentage of variability for early plant height and canopy width based on the combined phenotypic data across environments

Trait	Linkage group[a]	Interval	Length (cm)	QTL position (cm)[b]	Genetic effects (cm)[c]			R^2 (%)	LOD[d]
					Additive (a)	Dominant(d)	d/a		
Plant height at V7	C2	K418H – A397D-1	2.4	1.8	1.04	0.4	0.4	21	5.2
	F	HSP176H – B212	8.4	0.0	1.0	0.7	0.7	25	6.4
Plant height at V10	C2	K418H – A397D-1	2.4	2.0	1.8	0.5	0.3	20	4.1
Canopy width at V10	C2	A397D-1 – K365	2.4	1.8	1.0	0.3	0.3	12	2.8

[a] Based on the designation of Shoemaker and Specht (1995)
[b] Most likely QTL position, corresponding to the LOD score peak, which represents the distance from the left marker of the interval
[c] Genetic effects were estimated using Mapmaker/QTL
[d] LOD indicates how much more probable the data are to have arisen assuming the presence of a QTL than assuming its absence; LOD threshold = 2.4

unexpected. Since this soybean population was segregating for growth habit, most of the genetic variation in mature plant height would be due to the differences in growth habit (Lee et al. 1996 b).

Seed weight had no association with early plant height or canopy width. None of the seed weight QTLs were in common with the early plant height or canopy width QTLs in this soybean population (data not shown).

Maturity was correlated with plant height at V7 ($r = 0.50$), plant height at V10 ($r = 0.46$), and canopy width at V10 ($r = 0.43$). The plant height and canopy width QTLs (marker K418H) on LG C2 also explained 20% of the variation in maturity in this soybean population. It is difficult to explain the relationship between early growth and maturity in this study. It is most likely the result of a close linkage of a QTLs for early growth with a QTLs for maturity. Alternatively, such a relationship is also attributable to the pleiotropic effect of a QTLs on early growth as well as on maturity.

Summary

We have discovered a total of four QTLs conditioning soybean plant height and three QTLs affecting canopy width during the early stages of soybean development (V7 to V10). Two of the three QTLs for canopy width were in common with the plant height QTLs, indicating that these two are probably QTLs for early plant vigor. Two of the plant height and canopy width QTLs (on LGs C2 and F) were consistent across environments. However, one early plant height QTLs was sensitive to the environment while the expression of another one was dependent on the stage of plant development.

The information on individual QTLs for early plant height and canopy width will be valuable in breeding for soybean genotypes that can grow rapidly and have early season canopy coverage. Utilization of such a soybean genotype should suppress weed growth and minimize the amount of herbicide needed for effective weed control in soybean fields.

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