Molecular Markers Associated with Soybean Plant Height, Lodging, and Maturity across Locations

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ABSTRACT

The identification of quantitative trait loci (QTL) has the potential to improve the efficiency of selection for polygenic traits in a plant breeding program. In this study a soybean, *Glycine max* (L.) Merr., population derived from the cross of 'Young' and PI 416937 was evaluated with restriction fragment length polymorphism (RFLP) markers to identifiy QTL related to plant height, lodging, and maturity. One hundred-twenty F_4-derived lines were evaluated for segregation at 155 RFLP loci. Field data were obtained in four different locations in 1994 (Athens and Plains, GA, and Windblow and Plymouth, NC). The genetic map consisted of 137 RFLP loci which converged into 31 linkage groups and covered more than 1600 centimorgan (cM). By means of single-factor analysis of variance, 11 independent markers associated with plant height and the eight with lodging explained most of the genetic variability for these traits in combined analysis over locations. Of the 11 RFLP markers associated with plant height and the eight with lodging, only two markers for plant height (Blt043 and A063a) and one for lodging (A169) were detected in all locations, indicating either the inconsistency of these molecular markers across locations or the inability to detect putative QTL with the population size of 120 lines. However, good agreement of QTL across locations was found for maturity. Five markers were identified that explained variation in mean maturity over three locations, four of which were associated with maturity in all three locations. Results from this research indicate the level of consistency of QTL across environments is trait specific.

In soybean and many other crops, selection for major agronomic traits such as plant height, lodging, and maturity has been extensively applied in breeding programs for development of cultivars with superior performance and adaptation. This selection has been based on the association of these agronomic traits with seed yield and stability (Byth et al., 1969; Smith and Weber, 1968; Weber and Moorthy, 1952), and the high heritabilities of these traits relative to seed yield (Anand and Torrie, 1963; Kwon and Torrie, 1964). Unfortunately, a major problem in the determination of genotypic values of agronomic traits from phenotypic expression stems from the complex polygenic inheritance as well as the presence of substantial genotype × environment interaction, which may limit the value of phenotypic estimates (Byth et al., 1969).

With the development of molecular marker technology, QTL can be identified and located in the plant genome (Tanksley et al., 1989). The QTL for agronomically important traits, such as morphological traits, have been identified in many crops (Backes et al., 1995; Beavis et al., 1991; Kennard et al., 1994; Paterson et al., 1991b; Song et al., 1995). A limited number of studies have been conducted to identify QTL in the soybean genome (Shoemaker et al., 1994; Lark et al., 1993). In 60 F_2-derived lines from a cross between *G. max* and *G. soja* Siebold & Zucc., Keim et al. (1990b) detected association between RFLP markers and QTL affecting leaf width, leaf length, stem diameter, stem length, canopy height, and maturity. Also, five independent RFLP markers were found to be associated with variation in soybean seed hardness (Keim et al, 1990a). Furthermore, interval mapping of QTL for 15 reproductive, morphological, and seed traits revealed that QTL tended to be localized to intervals within three of 31 linkage groups (Mansur et al., 1993). More recently, classical markers such as pigmentation, morphological traits, and isozyme loci have been integrated into the molecular genetic map in soybean (Shoemaker and Specht, 1995), which will provide a powerful tool to facilitate marker-assisted selection, and eventually will enhance map-based cloning of agronomically important genes.

Most studies that examine the association of RFLP markers with QTL have collected phenotypic data in a single environment. A number of recent investigations have revealed inconsistencies over environments in the detection of QTL (Dudley, 1993; Paterson et al., 1991a; Tanksley, 1993). In a study of resistance to gray leaf spot (*Cercospora zeae-maydis* Theon & Daniels), a fungal disease of maize (*Zea mays* L.), QTL associated with resistance were inconsistent over environments (Bubeck et al., 1993). Only two of 20 markers associated with gray leaf spot resistance across environments were detected in all three environments. Previously, Paterson et al. (1991b) mapped 29 putative QTL affecting mass per fruit, soluble solid concentrations, and fruit pH in a tomato (*Lycopersicon esculentum* Mill. × *L. cheesmanii*) population grown in three different locations. Of these 29 QTL, only four markers (14%) were identified in all three environments, 10 markers (34%) in two environments, and 15 (52%) in a single environment. This inconsistency over environments indicates the limitation of accurately detecting QTL for a base population of environments (target environments of the breeding program) on the basis of a single environment.

The purpose of this study was to identify RFLP markers linked to additional QTL affecting plant height, lodging, and maturity in a F_4-derived population from a cross

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Abbreviations: cM, centimorgan; LG, linkage group; LOD, Likelihood of Odds; QTL, quantitative trait loci; RFLP, restriction fragment length polymorphism.

of Young and PI 416937. A secondary purpose was to examine the consistency of QTL detection across several southeastern USA locations.

MATERIALS AND METHODS

A F_4-derived soybean population from Young × PI 416937 was used to establish a RFLP linkage map and for phenotypic trait evaluation. PI 416937 was selected as a parent for its drought tolerance traits (Sloane et al., 1990) and Young was selected as a highly productive Maturity Group VI cultivar (Burton et al., 1987). This population consisted of 120 lines which were created by single-seed-descent with each line originating from a different F_2 plant. To obtain DNA for the RFLP survey of the parents, seeds of Young and PI 416937 were sown in the greenhouse, and leaves were harvested from seedlings prior to full expansion. The DNA was isolated from leaves according to the procedure of Keim et al. (1988), and digested overnight with each one of five restriction enzymes (*Dra*I, *Eco*RI, *Eco*RV, *Hin*dIII, or *Taq*I). Restriction digested DNA was separated by 0.8% agarose gel electrophoresis for 16 to 20 h at 22 V. Following electrophoresis, a Southern blot was made by transfer to Gene-Screen Plus nylon membranes (Biotechnology Systems, NEN Research Products, Boston). Nylon membranes were placed in 300- × 38-mm glass bottles containing 4 to10 mL of 0.25 *M* Na_2PO_4 and 7% SDS (sodium dodecyl sulfate), and prehybridized in a rotisserie oven for 4 to 6 h at 65°C. About 25 ηg of isolated DNA probe was randomly labeled, and hybridization was conducted overnight. Approximately 750 probes from various sources including cDNA and/or genomic clones of *Glycine max* (R.C. Shoemaker, USDA/Iowa State Univ.; K.G. Lark, Univ. of Utah; R.T. Nagao, Univ. of Georgia), *Vigna radiata* (L.) R. Wilczek (N.D. Young, Univ. of Minnesota), *Phaseolus vulgaris* L. (J.M. Tohme, CIAT), *Arachis hypogaea* L. (G.D. Kochert, Univ. of Georgia), and *Medicago sativa* L. (G.D. Kochert) were used to screen for polymorphisms between Young and PI 416937.

Probes polymorphic with respect to the parents were used for mapping. The DNA was isolated from leaves of 8 to 10 plants/line, which were grown in a field near Athens, GA, in 1993. To supplement this DNA and replace DNA samples with poor yield or low quality, leaves were collected and pooled from at least 14 additional plants from each line grown in the greenhouse in 1994. Multiple sets of nylon membranes containing DNA from each of the 120 lines were screened with polymorphic probes. The linkage map was constructed with marker data using Kosambi map function of Mapmaker (Lander et al., 1987), as if the data were derived from F_2 lines. For combining markers into linkage groups, a minimum LOD (Likelihood of Odds) of 3.0 and maximum distance of 50 cM were used.

The parents and 120 lines were grown in 1994 at two locations in Georgia, Athens (Plant Sciences Farm) and Plains (Southwest Branch Exp. Stn.), and two locations in North Carolina, Windblow (Sandhills Res. Stn.) and Plymouth (Plymouth Res. Stn.). At each location the lines were grown in multiple row plots that varied in area from 5.56 m^2 at Athens to 14.05 m^2 at Plymouth (Table 1). To reduce experimental error due to soil heterogeneity within each experimental site, the 120 lines were divided into three groups of 40 lines based on maturity (early, medium, and late). The lines in each of these groups were placed in three separate tests, with three entries of Young and and one entry of PI 416937 as reference genotypes. Each test was grown in two replications of a randomized complete block experimental design, except at Windblow, NC, which had three replications. Data were collected for plant height, lodging, and maturity. Plant height was measured as the average length of plants from the ground to the top extremity of the plant at maturity. Lodging was recorded on a scale of 1 (almost 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). Maturity data were not collected at Plains, GA. For standardization across the three tests, the plot values within each test were divided by the mean of the reference entries within that test. Replications, locations, and lines were considered random effects in the combined analysis over locations.

Table 1. Description of plots and soil classification at experimental sites.

Location	Rows/ plot	Plot spacing	Row length	Soil classification
	no.	cm	m	
Athens, GA	2	76	3.66	clayey, kaolinitic, thermic Typic Hapludults
Plains, GA	4	76	3.66	clayey, kaolinitic, thermic Typic Paleudult
Plymouth, NC	3	96	4.88	sandy, skeletal, mixed thermic Typic Umbracuult
Windblow, NC	3	96	3.05	sandy, salicious, thermic Arenic Paleudult

Plant height, lodging, and maturity data from the F_4-derived lines were compared with the RFLP data. The two homozygous RFLP classes were selected at each marker locus. For each of the 155 marker loci, the RFLP class means were compared for the determination of significant difference ($P \leq 0.05$) using an *F*-test from the type III mean squares obtained from the GLM Procedure of SAS (SAS Institute, Cary, NC). This probability level was selected to enhance our ability to detect QTL consistency across locations. Two-way analysis of variance was also used to detect epistatic interactions between markers with significant associations.

RESULTS AND DISCUSSION

The DNA of Young and PI 416937 was digested with five restriction enzymes and analyzed for polymorphisms. A RFLP was detected with 250 of the 750 probes. Thus, 33% of the probes detected a polymorphism with at least one of the five restriction enzymes, which is higher than in a previous study (Apuya et al., 1988). On the other hand, it is still low when compared with other reports by Keim et al. (1992) and Shoemaker et al. (1994). The difference in the polymorphism frequency among these studies is probably due to the amount of diversity between the soybean genotypes evaluated and the use of different types of probes.

The map contains 47 heterologous probes with 37 from *A. hypogaea*, nine from *M. sativa*, and one from *P. vulgaris*. These heterologous probes were distributed among most of the linkage groups in the soybean genome. However, none of *V. radiata* probes mapped. Mapping of heterologus probes from a wide range of legume species revealed that soybean shared common RFLP loci with other legume species. This supports a common evolutionary history of these species.

Genetic Map

A genetic map was constructed with 155 of the 250 polymorphic markers (Fig. 1). Of these 155 markers, 126 were expressed in a co-dominant manner. For the

29 dominant RFLP markers, an *n* for null was attached to the name of probes. Also, *a* or *b* was attached to the locus name when more than one polymorphism was present for the same enzyme-probe combination. In the RFLP map of this population, 137 markers were genetically linked and were placed into 31 linkage groups covering more than 1600 cM. Eighteen of the markers remained unlinked. At two loci, two of the markers co-segregated indicating in each case that these markers probed a similar DNA region. The markers cr321bn and K644 mapped to the same locus on Linkage Group (LG) 11, and the B124n and Blt49n markers mapped to the same site on LG 27 (Fig. 1).

Each RFLP locus on this map was compared with its image in SoyBase (1995) as well as with another soybean genetic map constructed from an F_2-derived population from the cross of PI 97100 × 'Coker 237' (1995, unpublished data). Through this comparison, linkage groups were assigned to their corresponding linkage group on the USDA soybean genetic map (Shoemaker and Specht, 1995) on the basis of RFLP "anchored probes." These anchored probes were used with the same restriction enzyme and had an identical banding pattern as used to construct the USDA map. Of the 31 linkage groups in this population, seven linkage groups could not be identified on the USDA map. Twenty-four linkage groups were known to correspond to the USDA map, four of which were indirectly associated with positions on the USDA map. These four linkage groups were identified with '?' following their probable LG designation (Fig. 1). Specifically, cr207 in LG 2 was linked 7.5 cM away from A588 in the map derived from PI 97100 × Coker 237. The locus A588 belongs to LG B1 of the USDA map, suggesting that our LG 2 probably corresponds to LG B1. Also, LG 3 tentatively corresponds to LG B1 on the basis that cr122 was on LG B1 in the map from PI 97100 × Coker 237. The markers K14b on LG 10 as well as K443 and A112 on LG 13 showed similar banding patterns to those in LG F and LG G of the USDA map, respectively. Further mapping with anchored probes within the unidentified linkage groups from our population will be needed to confirm the corresponding linkage groups on the USDA map.

Soybean has a chromosome number of $2n = 40$. Consequently, only 20 linkage groups should exist in a saturated soybean genetic map. In our map, LG 4 was separated from LG 5, in spite of their both being located on LG C1 in the USDA map. The corresponding USDA LG C2, H, and J were also separated into two linkage groups, as were LG B1, F, and G (Fig. 1). Based on a more saturated recent map (Shoemaker and Specht, 1995), map distances were estimated between pairs of disconnected anchor markers. These distances were 82.6 cM between K300 (LG 4) and A063 (LG 5), 82.8 cM between A122 (LG 6) and A635 (LG 7), and 89.5 cM between K14a (LG 14) and K089a (LG 15). These recombination distances resulted in the assignment of separate linkage groups. Connection of these two separated link-

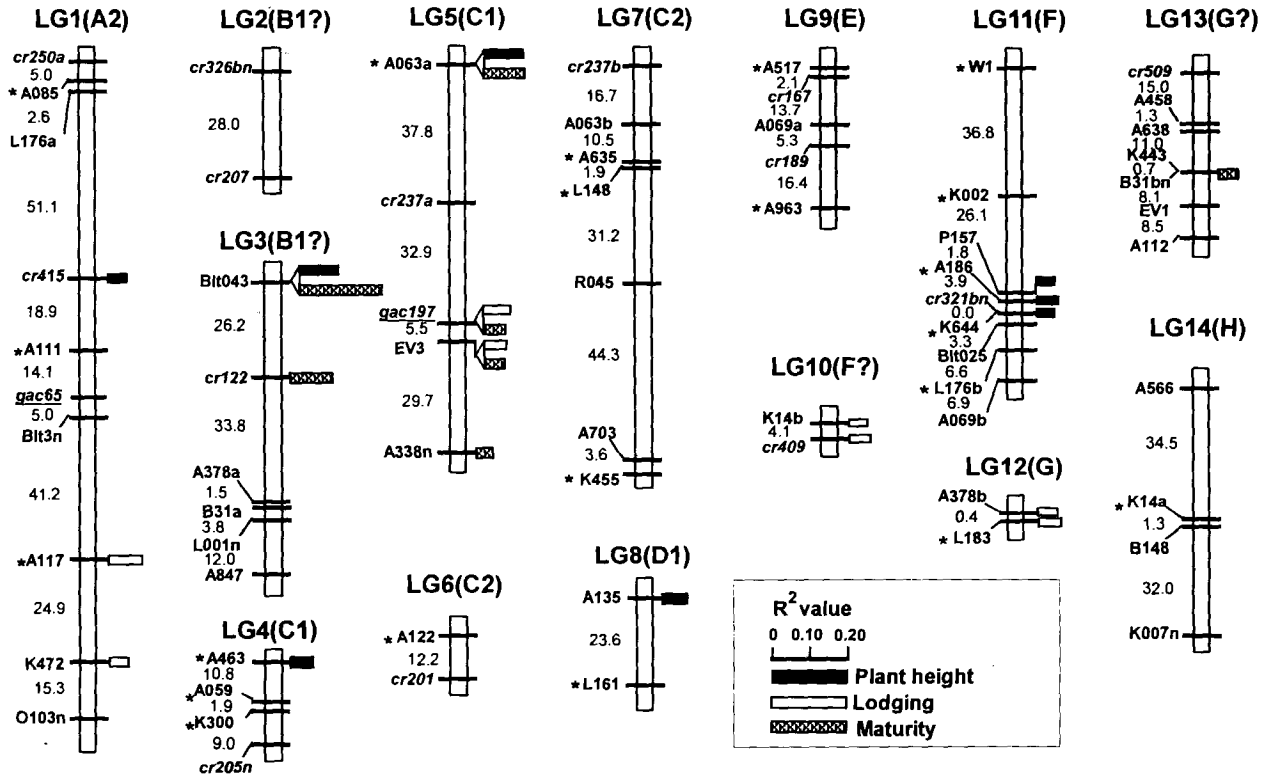

Fig. 1. Soybean RFLP genetic linkage map showing marker positions and estimated map distance (cM) on the left-hand side, and USDA linkage group (Shoemaker and Specht, 1995) in parentheses. Length of bars indicates the R^2 values for the loci associated with plant height, lodging, and maturity on the basis of combined analysis from all environments. * represents the anchored probe which had an identical banding pattern with the image in SoyBase (1995). Markers from *G. max* are depicted in regular boldface type, those from *P. vulgaris* in underlined boldface type, those from *A. hypogaea* in italicized boldface type, and those from *M. sativa* are underlined in italicized boldface type.

age groups could be made by further mapping with markers between these two disconnected linkage groups. However, a short map distance (only 29.1 cM) between A122 (LG 16) and B233 (LG 17) was detected in the map of Shoemaker and Specht (1995), indicating that LG 16 and LG 17 should be connected in our map. The cause of the lack of association between these two groups in our population could be explained by the twofold expansion of the map that exists in advanced lines when compared to the F_2 generation (Burr et al., 1988; Haldane and Waddington, 1931).

Plant Height

Young and PI 416937 differed by 45 cm in plant height. Wide variation (71–127 cm) occurred in plant height among progenies (Table 2). Individual RFLP loci were tested for association of specific RFLP bands with differences in plant height among lines by single-factor ANOVA. A total of 29 QTL were detected in at least one of the four separate locations. Of these 29 QTL, 13 were detected in more than two locations. In the combined analysis over four locations, 14 RFLP markers were associated with plant height (Table 3, Fig. 1). Eleven of these 14 represent putative independent QTL (greater than 50 cM from another marker significantly ($P > 0.05$) associated with the trait and the marker acted in an additive manner with regards to explaining variation) and individually accounted for 3.8 to 10.0% of the phenotypic variation. In all cases when two putative independent QTL were identified on the same linkage group, there was at least one RFLP marker between the putative independent QTL that was not significantly ($P \leq 0.05$) associated with plant height. At all loci, except Blt043, the Young allele increased plant height. Across the four locations, Young averaged 109 cm in plant height compared to 64 cm for PI 416937 (Table 2). The amount of variation explained by the 11 independent markers sums to 68%. The heritability (selection unit = four locations, two replications/location) for plant height was 90.8%. Thus when combined, these 11 markers explain most of the genetic variation for this trait.

Only two (A063a/K385 and A186/K385) of the possible 55 two-way epistatic interactions were significant (Table 4). The interaction between A063a/K385 loci resulted in similar plant height for lines with the PI

Table 2. Means and ranges of parental and F_4-derived progeny for plant height, lodging, and maturity combined over locations.

	Plant height	Lodging	Maturity
	cm	score†	d‡
Young	109	2.8	50
PI 416937	64	3.3	47
Progeny range	71–127	2.1–4.4	34–69
LSD (0.05)	11	0.6	9
Progeny $\bar{x}$	89	3.1	54

† Lodging score was on a scale 1 (plants erect) to 5 (plants prostrate).
‡ Maturity was recorded as the number of days after 31 August.

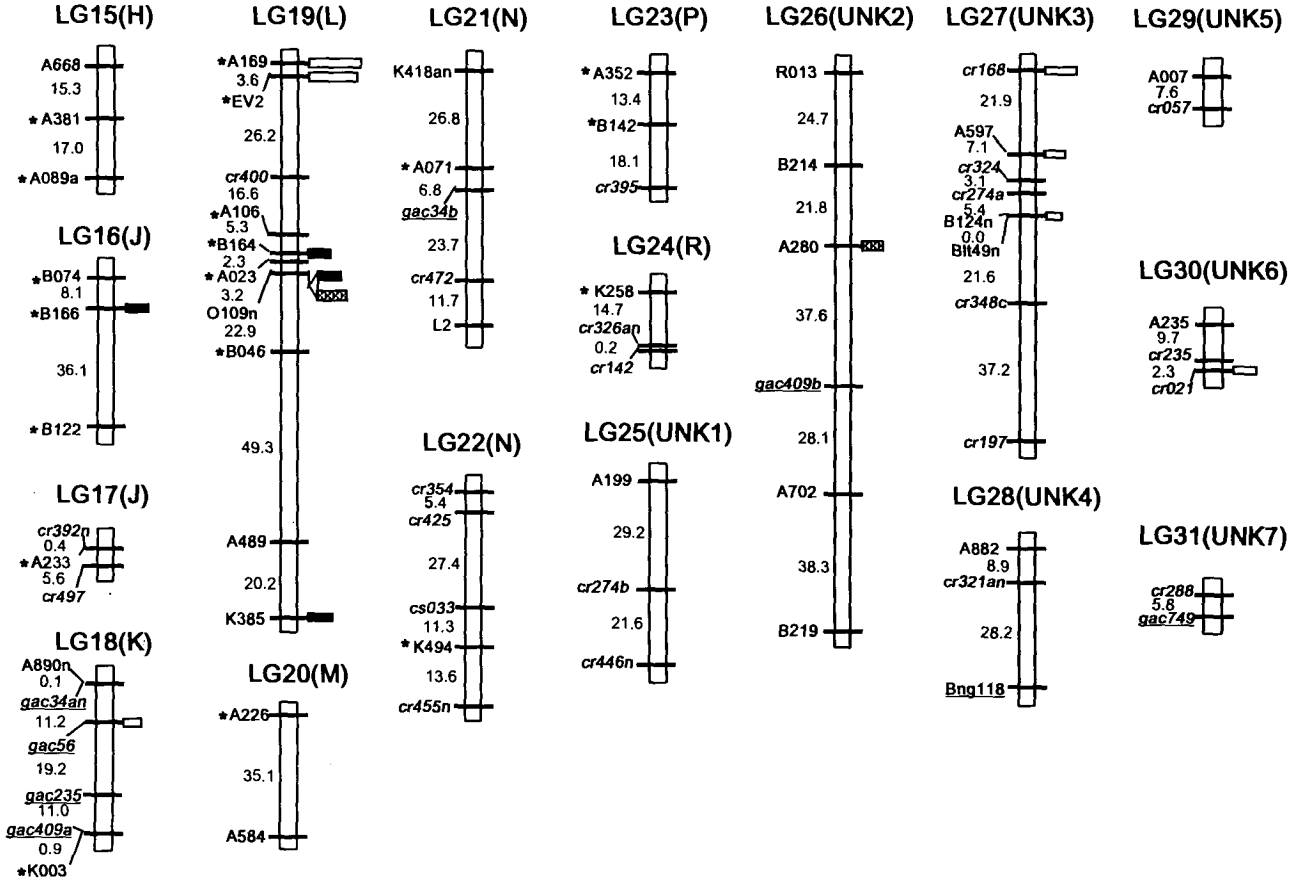

Fig. 1. Continued.

Table 3. RFLP markers associated with variation in plant height over four locations.

RFLP locus	Linkage group	Combined				Athens		Plains		Windblow		Plymouth	
				Allelic means									
		P	R^2	Young	PI 416937	P	R^2	P	R^2	P	R^2	P	R^2
			%	cm			%		%		%		%
cr415†	A2	0.034	4.3	90.8	86.2	0.037	4.2	0.020	5.2	ns	–	ns	–
Blt043†	B1?	0.002	9.9	83.6	91.4	0.006	7.7	0.013	6.3	0.004	8.1	0.001	11.4
A463†	C1	0.019	5.1	91.2	86.2	0.022	4.9	0.036	4.1	0.014	5.7	ns	–
A063a†	C1	0.001	10.0	94.3	86.4	0.001	9.9	0.025	4.6	0.001	12.5	0.004	7.7
A135†	D1	0.009	6.8	92.4	86.6	0.005	8.0	0.005	7.7	ns	–	0.037	4.4
A186†	F	0.018	5.4	91.4	86.2	ns	–	0.020	5.2	ns	–	0.050	3.7
P157	F	0.020	5.1	91.5	86.5	ns	–	0.019	5.1	ns	–	ns	–
K644	F	0.041	4.0	91.0	86.5	ns	–	0.038	4.1	ns	–	ns	–
B166†	J	0.011	6.6	91.8	86.0	0.012	6.4	ns	–	0.003	8.7	0.045	4.1
K385†	L	0.008	6.6	92.3	86.6	0.003	8.1	ns	–	0.008	6.5	0.030	3.2
O109n†	L	0.021	5.2	91.0	85.8	0.008	6.8	0.041	4.1	0.035	4.3	ns	–
B164	L	0.030	5.1	91.3	86.3	0.006	8.1	0.031	5.1	ns	–	ns	–
K375n†	Unlinked	0.020	4.7	91.1	86.2	0.007	6.3	ns	–	0.001	9.4	ns	–
K102†	Unlinked	0.047	3.8	91.3	86.9	ns	–	ns	–	ns	–	ns	–

† Putative independent QTL (greater than 50 cM from another marker significantly associated with plant height and additive gene action with regards to explaining variation).

416937/Young, Young/PI 416937, and PI 416937/PI 416937 allelic configuration at the A063a and K385 loci. For the A186 and K385 loci, the Young allele at K385 did not increase plant height when in combination with the Young allele at A186, but did when in combination with the PI 416937 allele at this locus.

Of the 11 independent markers associated with plant height in the combined analysis, only two markers (Blt043 and A063a) were detected in all four locations. These data clearly demonstrated the inconsistency of some QTL over locations, as well as a fairly large location by QTL interaction. The genotype × location variance component was 18% of the genotypic variance component. Of the markers associated with plant height at all four locations, Blt043 showed the largest effect in Plymouth, NC, whereas A063a did in Athens, GA and Windblow, NC, indicating that the QTL showing the largest effect in one location seemed likely to be detected in another location. This was consistent with the results of Tanksley (1993). On the other hand, it is interesting to note that unlinked K102 was associated with plant height in the combined analysis over four locations, even though it was not detected in any individual location (Table 3).

Table 4. Epistatic interactions between two markers associated with plant height and lodging.

RFLP locus	Allele	Allele/Locus		P	R^2
		Young	PI 416937		
		– Plant height (cm) –			%
A063a*K385				0.001	21.2
		K385			
A063a	Young	99	86		
	PI 416937	87	86		
A186*K385				0.017	15.9
		K385			
A186	Young	92	92		
	PI 416937	95	83		
		– Lodging (score)† –			
A117*cr021				0.022	16.5
		cr021			
A117	Young	2.9	3.0		
	PI 416937	3.1	3.7		
A169*L183				0.042	26.9
		L183			
A169	Young	2.8	3.3		
	PI 416937	3.2	3.3		

† Lodging score was on a scale 1 (plants erect) to 5 (plants prostrate).

Lodging

Young and PI 416937 differed by a lodging score of 0.5. However, lodging score varied from 2.1 to 4.4 among progenies (Table 2). Of the 42 RFLP loci associated with the variation in lodging in at least one of the four locations, 28 (67%) were associated with lodging only in a single location. Fifteen RFLP loci were associated with lodging in the combined analysis over four locations (Table 5, Fig. 1). Eight of these 15 loci were genetically independent markers. At six of these eight loci, the PI 416937 allele was associated with increased plant lodging (Table 5).

The total amount of variation explained by the eight independent markers was 61%. The heritability (selection unit = four locations, two replications/location) of lodging was 82.3%. This indicated that much of the genetic variation was explained by these eight markers.

Of the possible 28 two-way epistatic interactions, only two (cr201/A117 and L183/A169) were significant (Table 4). When a line contained PI 416937 alleles at both the A117 and cr021 locus, its lodging score was greater than would be expected due to additive gene action (Table 4). Lines containing the Young allele at A169 and the PI 416937 allele at L183 also lodged more than would be predicted by additive gene action at these loci.

Only one region of LG L (A169) was detected as being associated with lodging at all locations (Table 5). This RFLP marker was detected as highly significant ($P \leq 0.001$) and had the largest effect on lodging across locations ($R^2 = 13.3\%$). The cr168 locus is an exception

Table 5. RFLP markers associated with variation in lodging over four locations.

RFLP locus	Linkage group	Combined				Athens		Plains		Windblow		Plymouth	
				Allelic means									
		P	R^2	Young	PI 416937	P	R^2	P	R^2	P	R^2	P	R^2
			%	score‡			%		%		%		%
A117†	A2	0.002	9.0	3.0	3.3	0.001	9.7	ns	–	0.003	7.9	0.006	6.9
K472	A2	0.031	4.5	3.0	3.2	0.017	5.4	ns	–	0.004	7.6	0.027	4.7
gac197†	C1	0.008	7.0	3.0	3.3	ns	–	ns	–	ns	–	0.001	15.4
EV3	C1	0.024	5.4	3.0	3.3	ns	–	ns	–	ns	–	0.001	13.0
cr409†	F?	0.023	5.5	3.0	3.3	0.021	5.7	ns	–	0.001	12.6	ns	–
K14b	F?	0.044	4.2	3.0	3.3	0.023	5.4	ns	–	0.005	7.8	ns	–
L183†	G	0.009	6.7	3.0	3.3	ns	–	0.034	4.4	0.027	4.8	0.010	6.5
A378b	G	0.016	5.5	3.1	3.3	ns	–	ns	–	0.048	3.8	0.013	5.9
gac56†	K	0.024	4.7	3.3	3.1	0.036	4.1	ns	–	ns	–	0.020	5.0
A169†	L	0.001	13.3	3.0	3.3	0.001	15.9	0.045	4.2	0.002	9.9	0.001	10.9
EV2	L	0.001	12.2	3.0	3.3	0.001	13.7	0.038	4.5	0.005	7.9	0.001	10.6
cr168†	Unknown	0.048	8.6	3.4	3.0	ns	–	0.001	21.0	ns	–	ns	–
A597	Unknown	0.019	5.4	3.3	3.0	ns	–	0.004	8.1	ns	–	0.046	3.9
Blt49n	Unknown	0.041	3.8	3.2	3.0	ns	–	0.020	5.0	ns	–	ns	–
cr021†	Unknown	0.020	5.8	3.1	3.3	ns	–	ns	–	0.003	8.9	ns	–

† Putative independent QTL (greater than 50 cM from another marker significantly associated with lodging and additive gene action with regards to explaining variation).
‡ Lodging score was on a scale of 1 (plants erect) to 5 (plants prostrate).

to the generalization that a major QTL in one location would be detected in other locations. The cr168 locus accounted for 21.0% of the variation in lodging at Plains, GA, but was not detected at any other location. This suggested that cr168 was linked to a highly environment-sensitive QTL. This partially explains the genotype × location interaction for lodging score. The genotype × location variance component was more than 40% of the genotypic component.

Maturity

Young and PI 416937 differed by 3 d in maturity. However, trangressive variation of 36 d occurred among progenies (Table 2). For maturity, eight markers were detected on the basis of the combined analysis over three locations (Table 6). Five of these eight represent putative independent QTL. At all of these 5 loci, except Blt043, the Young allele was associated with late maturity.

The Blt043 marker on LG B1 explained 21.8% of the total variation for maturity. Summed together, these five independent markers explained 48.8% of the total variation for maturity. The heritability (selection unit = three locations, two replications/location) of maturity was 93.1%, suggesting either that other undetected QTL or markers more closely linked to the existing QTL, were required to explain the remaining genetic variation. There were no epistatic interactions identified among the 10 two-way combinations between two independent markers.

Of the five putative independent markers for maturity, four were detected in all three locations. Thus, the RFLP markers for maturity were consistent across the three locations. The genotype × location variance component for maturity was 18% of the genotypic variance component. Stuber et al. (1992) reported little evidence for genotype by location interaction for most QTL in maize lines grown in six diverse environments. However, our data for plant height and lodging as well as those from other studies (Bubeck et al., 1993; Paterson et al., 1991a) revealed inconsistency of some QTL over environments. These differences may be due to the heritability of traits evaluated, the specific crop species evaluated, or the level of saturation of the different genetic maps. In our study maturity was more heritable than plant height or lodging, which was in good agreement with other soybean studies (Anand and Torrie, 1963; Byth et al., 1969; Kwon and Torrie, 1964; Smith and Weber, 1968).

Table 6. RFLP markers associated with variation in maturity over three locations.

RFLP locus	Linkage group	Combined				Athens		Windblow		Plymouth	
				Allelic means							
		P	R^2	Young	PI 416937	P	R^2	P	R^2	P	R^2
			%	d‡			%		%		%
Blt043†	B1?	0.001	21.8	49.1	56.4	0.001	22.6	0.001	20.5	0.001	26.1
cr122	B1?	0.002	10.8	51.0	56.1	0.001	12.2	0.001	11.2	0.001	15.1
A063a†	C1	0.001	10.3	57.6	52.7	0.001	10.6	0.019	8.9	0.002	8.5
EV3	C1	0.036	4.7	54.9	52.4	0.041	4.4	0.015	6.3	0.044	4.3
gac197†	C1	0.024	5.1	55.8	52.5	0.027	4.9	0.024	5.2	0.043	4.1
A338n	C1	0.032	4.0	55.8	52.0	0.011	5.6	0.016	5.0	0.045	3.4
O109n†	L	0.001	6.7	55.3	51.6	0.009	6.6	0.012	6.3	0.019	5.4
A280†	Unknown	0.026	4.9	56.0	52.7	0.043	4.2	ns	–	ns	–

† Putative independent QTL (greater than 50 cM from another marker significantly associated with maturity and additive gene action with regards to explaining variation).
‡ Maturity was recorded as number of days after 31 August.

Relationship among Traits

Maturity, plant height, and lodging were interrelated in that increased plant height showed a positive association with increased lodging (r = 0.51***) and later maturity (r = 0.71***). A positive correlation was also found for late maturity and increased lodging (r = 0.51***). Several RFLP markers were also detected as being associated with two traits (Fig. 1). Specifically, Blt043 (LG B1?), A063a (LG C1), and O109n (LG L) were associated with variation in plant height and maturity. At each of these RFLP loci the allele associated with later maturity was associated with increased height (Table 3 and 6). These loci could provide the genetic basis for the correlations between plant height and maturity. The gac197 (LG C1) locus was associated with both lodging and maturity. At this locus, the PI 416937 allele conditioned earlier maturity and increased lodging (Table 5 and 6). Thus, this locus does not provide a genetic explanation for the positive association between these traits.

In an F_2 population derived from the cross between *G. max* and *G. soja*, Keim et al. (1990b) identified RFLP markers associated with stem length (same as plant height) and maturity. They found that only one marker, K18 (unknown LG), was associated with variation in stem length. For maturity, four markers located on LG C2 and D1 (formerly described as LG M and H, respectively) and one unlinked marker (K472 now mapped to LG C1) were identified (Shoemaker and Specht, 1995). Recently, Mansur et al. (1993) reported QTL for plant height and lodging were closely associated with marker G173 on LG 16 of the linkage map from the cross between 'Minsoy' and 'Noir 1'. However, our markers for plant height were widely distributed on LG A2, B2, C1, F, J, and L, and those for maturity were in LG B1, C1,and L rather than in LG C2 and D1 as reported by Keim et al.(1990b). The different genomic locations of putative QTL in this study and other studies emphasizes the polygenic inheritance of these traits and the population specificity of important QTL.

The results from this study provide evidence for additional QTL for plant height, lodging, and maturity in soybean. The data also indicate the need for the collection of phenotypic data for a polygenic trait over a range of locations from within the base population of environments to identify putative QTL. Comparison of these results with previous studies supports the population specificity of important QTL for polygenic traits.

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