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Identification of quantitative trait loci for plant height, lodging, and maturity in a soybean population segregating for growth habit

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Abstract The use of molecular markers to identify quantitative trait loci (QTLs) has the potential to enhance the efficiency of trait selection in plant breeding. The purpose of the present study was to identify additional QTLs for plant height, lodging, and maturity in a soybean, *Glycine max* (L.) Merr., population segregating for growth habit. In this study, 153 restriction fragment length polymorphisms (RFLP) and one morphological marker (*Dt1*) were used to identify QTLs associated with plant height, lodging, and maturity in 111 F_2-derived lines from a cross of PI 97100 and 'Coker 237'. The F_2-derived lines and two parents were grown at Athens, Ga., and Blackville, S.C., in 1994 and evaluated for phenotypic traits. The genetic linkage map of these 143 loci covered about 1600 cM and converged into 23 linkage groups. Eleven markers remained unlinked. Using interval-mapping analysis for linked markers and single-factor analysis of variance (ANOVA), loci were tested for association with phenotypic data taken at each location as well as mean values over the two locations. In the combined analysis over locations, the major locus associated with plant height was identified as *Dt1* on linkage group (LG) L. The *Dt1* locus was also associated with lodging. This locus explained 67.7% of the total variation for plant height, and 56.4% for lodging. In addition, two QTLs for plant height (K007 on LG H and A516b on LG N) and one QTL for lodging (cr517 on LG J) were identified. For maturity, two independent QTLs were identified in intervals between R051 and N100, and between B032 and CpTI, on LG K. These QTLs explained 31.2% and 26.2% of the total variation for maturity, respectively. The same QTLs were identified for all traits at each location. This consistency of QTLs may be related to a few QTLs with large effects conditioning plant height, lodging, and maturity in this population.

Key words Soybean · *Glycine max* · QTL · RFLP

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Introduction

In most crop-breeding programs, much emphasis is placed on quantitatively inherited traits because of their importance in agricultural productivity (Paterson et al. 1991a; Edwards 1992). Most earlier quantitative genetic studies were limited to estimating the heritability and the effective number of QTLs, and to describing average gene action (Tanksley 1993). The use of molecular markers has provided the potential to construct saturated plant genetic maps and to provide insights into the genomic location and gene action of individual QTLs (Lander and Botstein 1989; Tanksley et al. 1989).

Molecular-marker analysis for the identification of QTLs has been performed mainly by one of two different procedures, single-factor analysis of variance and interval mapping. Interval mapping (Lander and Botstein 1989) allows full exploitation of the information provided by a genetic linkage map and evaluation of the probable chromosomal positions of putative QTLs. Recently, two computer programs, Mapmaker (Lander et al. 1987) and its companion Mapmaker-QTL (Lincoln et al. 1992), have been developed to construct genetic maps and to implement interval mapping.

Several important QTLs associated with morphological and physiological traits have been genetically mapped in a number of crops, including *Hordeum vulgare* (Backes et al. 1995), *Zea mays* (Beavis et al. 1991; Veldboom et al. 1994), *Sorghum bicolor* (Pereira and Lee 1995), *Brassica oleracea* (Kennard et al. 1994), *Brassica rapa* (Song et al. 1995), *Lycopersicon esculentum* (Paterson et al. 1991b),

Vigna unguiculata and *Vigna radiata* (Fatokun et al. 1992). In soybean, two initial public RFLP genetic maps were constructed independently (Keim et al. 1990 b; Lark et al. 1993). On the basis of each soybean genetic map, several quantitative traits, such as seed protein and oil content (Diers et al. 1992) and seed hardness (Keim et al. 1990 a), as well as morphological and reproductive traits (Keim et al. 1990 b; Mansur et al. 1993; Lee et al. 1996), have been investigated, and genomic regions controlling these traits have been identified by RFLP markers.

Keim et al. (1990 b) evaluated an F_2 population derived from a cross between *G. max* and *G. soja* for stem length and maturity. They found that only one marker, pK18 (unknown linkage group), was associated with stem length. For maturity, five markers on LG C1, C2, and D1 were identified (Shoemaker and Specht 1995). In another F_2-derived soybean population from the 'Minsoy' × 'Noir 1' cross, Mansur et al. (1993) reported major QTLs near G173 (LG L, Shoemaker and Specht 1995) for plant height and lodging, and near R79 for maturity. In a previous study of F_4-derived progeny from a cross of 'Young' × PI 416937, we found RFLP markers for plant height were widely distributed on LG A2, C1, D1, F, J, and L, while those for lodging were on LG A2, C1, G, K, and L (Lee et al. 1996). For maturity, markers were identified on LG B1, C1, and L. These results indicated the different genomic location of putative QTLs from different populations and provided support for the population-specificity of important QTLs for polygenic traits.

In the present paper, we identify additional QTLs associated with plant height, lodging, and maturity in an F_2-derived population from a cross between PI 97100 × Coker 237 that is segregating for growth habit.

Materials and methods

A soybean population derived from a cross of PI97100 × Coker 237 was used to construct a genetic linkage map and to evaluate phenotypic traits. PI 97100 possesses an indeterminate growth habit, and Coker 237 has a determinate growth habit. From this cross, a total of 111 lines were 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). Briefly, 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 one 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 PI 97100 and Coker 237.

Probes polymorphic with respect to the parents were used for mapping. The DNA was isolated from the two youngest fully expanded trifoliolate leaves of 111 F_2 plants, which were grown in a field near Athens, Ga. in 1993. This harvest was conducted once in July and again in August after substantial re-growth of each F_2 plant occurred. In the spring of 1994, leaves from the population derived from the F_2 plants were also harvested equally from at least 14 plants from each of the 111 F_2-derived lines in order to reconstitute the F_2 genotype and ensure a sufficient amount of DNA. Multiple sets of nylon membranes containing DNA from each of the 111 lines were screened with polymorphic probes. The linkage map was constructed with marker data using the Kosambi map function of Mapmaker (Lander et al. 1987). For grouping markers as linkage thresholds, a minimum LOD score of 3.0 and a maximum distance of 50 cM were used.

The parents and 111 lines were grown in 1994 at two locations, Athens (Univ. of Georgia Plant Sciences Farm), Ga., and Blackville (Clemson Univ. Edisto Research and Education Centre), S.C. To reduce experimental error due to soil heterogeneity within each experimental site, the 111 lines were randomly divided into three groups. The 37 lines in each group along with PI97100, Coker 237, and 'Stonewall' were placed in three separate tests. Due to seed availability, two tests were grown in four replications and one test in three replications of a randomized complete block experimental design. A fumigant nematicide (ethylene dibromide, 53.8 kg a.i./ha at Athens, and 1,3-Dichloropropene, 74.4 kg a.i./ha at Blackville) was applied prior to planting for control of the soybean cyst nematode, *Heterodera glycines* Ichinohe. In addition, a liquid nematicide, phenamiphos [ethyl 3-methyl-4-(methylthio) phenyl (1-methylethyl) phosphoramidates, 5.7 to 7.7 kg a.i./ha] was applied on the soil surface at both locations at the R2 stage of soybean development (Fehr and Caviness 1977).

Data were collected for plant height, lodging, maturity, and plant growth habit. Plant height was measured as the average length of plants from the ground to the terminal bud of the plant at maturity. Lodging ratings were 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 August 31 when 95% of the pods had reached mature pod color (Fehr and Caviness 1977). Growth habit was classified as determinate or indeterminate based on stem-termination characteristics (Bernard 1972). For standardization across the three tests, the plot values within each test for plant height, lodging, and maturity were divided by the mean of PI 97100, Coker 237, and Stonewall for the trait within that test. Replications, locations, and lines were considered random effects in the combined analysis of variance over locations.

The association between marker and QTL was tested using two different procedures. First, QTL mapping analysis was performed using the interval mapping method (Lander and Botstein 1989) with Mapmaker-QTL software (Lincoln et al. 1992). QTL analyses were performed on the standardized mean data within each location as well as across locations. A LOD score of 2.5 was chosen as a minimum to declare the presence of a QTL in a given genomic region. The LOD score peak was used to estimate the most likely QTL position on the RFLP linkage map. The percentage of variance explained by individual QTLs 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. Single-factor ANOVA was also used to determine significance ($P \leq 0.01$) among RFLP genotypic class means using an F-test from the Type-III mean squares obtained from the GLM Procedure (SAS 1988). Two-way analysis of variance was also used to detect epistatic interactions between markers with significant associations.

Results and discussion

Genetic map

A total of 153 RFLP markers were used to construct a genetic linkage map of this population. Of these 153 mark-

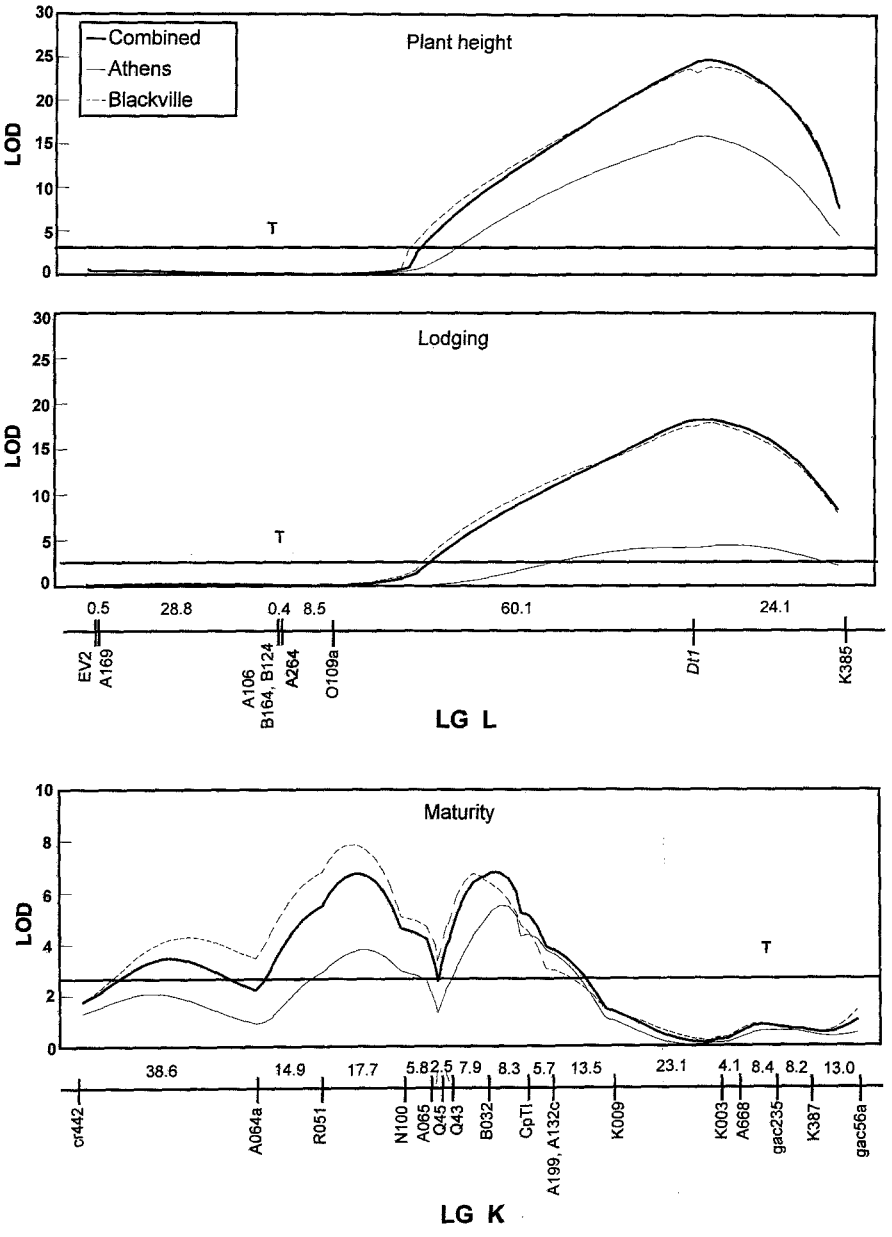

Fig. 1 QTL likelihood plots for plant height and lodging of linkage group L and for maturity of linkage group K. *Vertical axes* indicate the LOD score based on Mapmaker-QTL. The *number* between markers indicates the map distance in Kosambi cM. *T* at LOD=2.5 indicates the threshold for declaring a putative QTL

ers, 144 were expressed in a co-dominant manner. The map covered about 1600 cM with 142 markers classified into 23 linkage groups. The average distance between two adjacent marker loci was about 11 cM. Eleven of the markers remained genetically unlinked.

Classification of growth habit resulted in 24 homozygous indeterminate, 61 segregating, and 26 homozygous determinate lines. Chi-square analysis showed a good fit to a 1:2:1 mono-genic ratio (χ^2=1.16, 0.50<*P*<0.75), and indicated the presence of a single gene for growth habit. Therefore, this gene was mapped along with the RFLP markers. It mapped on LG L at the same location as the *Dt1* locus (Shoemaker and Specht 1995).

Complete marker coverage was not achieved in some regions of the genetic map. This may be due to a lack of polymorphic markers or to a high level of recombination in that region. A specific example was on LG L (Fig. 1). Mapmaker analysis of our data revealed that LG L, as described by Shoemaker and Specht (1995), was divided into two groups (one consisted of a region containing *Dt1* and K385, with the other seven markers in a region from EV2 to O109a). We attempted to identify polymorphic loci within the interval separating the two groups, but were unsuccessful. Therefore, the two groups were connected together using the Mapmaker software on the basis of a previously published map (Shoemaker and Specht 1995). Using this procedure a distance of 60.1 cM was found between *Dt1* and O109a (Figs. 1, 2).

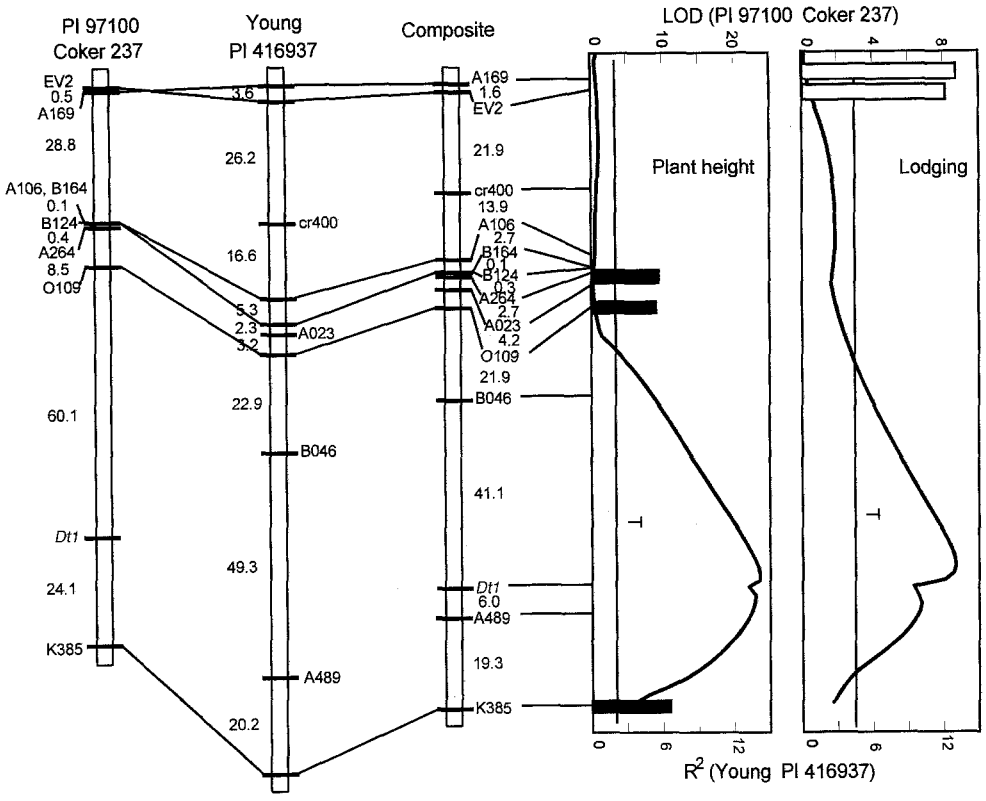

Fig. 2 Comparison of QTLs for plant height and lodging on linkage group L derived from two populations, PI 97100 × Coker 237 and Young × PI 416937. The composite map is based on the average of recombination between pairs of common markers across populations. LOD curves for plant height and lodging were derived from PI 97100 × Coker 237, and *solid* (plant height) and *open* (lodging) *bars* represent marker loci identified in Young × PI 416937. *T* at LOD=2.5 indicates the threshold for declaring a putative QTL

Plant height

PI 97100 and Coker 237 differed by 22 cm in plant height (Table 1), and wide variation (74–130 cm) occurred among the 111 F_2-derived lines. Interval-mapping analysis detected one major QTL located on LG L at both individual locations and for the combined data. Based on the LOD score peak, the most likely position of the QTL was exactly on *Dt1* at Athens, whereas it was shifted 1.6 cM from *Dt1* toward K385 at Blackville (Table 2). The log-likelihood profile for the QTL associated with plant height in the combined analysis was located at the same position as at Blackville (Fig. 1). This QTL is hereafter assumed to be the *Dt1* locus conditioning growth habit.

The *Dt1* locus affected plant height by causing a decrease of 13.8 cm for each allele from Coker 237 (*dt1*), and heterozygotes were 7.4 cm taller than predicted on the basis of additive gene action. Based on the combined data, the *dt1* allele showed a –0.5 degree of dominance (Table 2), indicating partially dominant gene action. Bernard (1972) reported that the determinate (*dt1*) gene reduced plant height by 45 to 60% compared to the indeterminate (*Dt1*) gene in near-isolines of 'Clark' and 'Harosoy'. These findings were supported by Hartung et al. (1980). In our study the homozygous *dt1* lines were an average of 32% shorter than the homozygous *Dt1* lines.

Interestingly, the LOD score for the presence of the *dt1* locus controlling plant height was high (24.8), and the percentage of phenotypic variance explained by *Dt1* was 67.7% (Table 2). The heritability (selection unit = two locations, three replications/location) for plant height was 78.3% (Table 1). Therefore, most of the genetic variation in plant height was explained by this locus. From the large amount of variation explained by this locus, it could be surmised that one major gene (*Dt1*), and possibly a few minor genes, govern the inheritance of plant height in this population.

Using single-factor ANOVA, two additional independent markers besides *Dt1* were associated with plant height (Table 3). The K007 locus on LG H, which is located on a relatively small and unsaturated linkage group, was not de-

Table 1 Means and ranges of parental and F_2-derived progeny for soybean plant height, lodging and maturity, combined over locations, and their heritabilities

Genotypes	Plant height (cm)	Lodging score[a]	Maturity (days)[b]
PI 97100	109	3.2	56
Coker 237	87	1.6	51
Progeny range	74–130	1.6–4.0	47–57
Progeny $\bar{x}$	106	2.7	54
LSD (0.05)	16.2	1.2	2.2
h^2 (%)[c]	78.3	40.6	86.8

[a] Lodging score was on a scale of 1 (plants erect) to 5 (plants prostrate)
[b] Maturity was recorded as the number of days after 31 August
[c] Selection unit = two locations, three replications/location

Table 2 Genomic location, genetic effects, and percentage of variability for soybean plant height, lodging, and maturity

Trait	Location	Linkage group[a]	Interval	Length	QTL position[b]	Genetic effects[c]			R^2 (%)	LOD[d]
						Additive (a)	Dominant (d)	d/a		
				cM		cm				
Plant height	Athens	L	*Dt1*–K385	24.1	0	–10.7	4.4	–0.4	48.7	16.1
	Blackville	L	*Dt1*–K385	24.1	1.6	–18.1	11.5	–0.7	67.9	24.0
	Combined	L	*Dt1*–K385	24.1	1.6	–13.8	7.4	–0.5	67.7	24.8
						– score –				
Lodging	Athens	L	*Dt1*–K385	24.1	5.0	–0.3	0.1	–0.3	21.6	4.5
	Blackville	L	*Dt1*–K385	24.1	1.6	–0.5	0.4	–0.8	56.0	18.0
	Combined	L	*Dt1*–K385	24.1	1.6	–0.5	0.3	–0.6	56.4	18.3
						– days –				
Maurity	Athens	K	R051–N100	17.7	10.2	–1.1	0.9	–0.8	19.3	3.8
		K	B032–CpTI	8.3	3.7	–1.3	0.6	–0.5	23.2	5.5
	Blackville	K	R051–N100	17.7	6.8	–1.9	1.2	–0.6	34.9	7.9
		K	B032–CpTI	8.3	5.9	–1.7	1.1	–0.6	26.3	6.7
	Combined	K	R051–N100	17.7	8.5	–1.5	1.1	–0.7	31.2	6.7
		K	B032–CpTI	8.3	1.8	–1.5	0.7	–0.5	26.2	6.8

[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. A negative sign indicates that the Coker 237 allele decreases the value of the trait
[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=2.5

Table 3 Markers significantly ($P \leq 0.01$) associated with soybean plant height, lodging, and maturity on the basis of single-factor analysis of variance from the combined data over two locations

Trait	Locus	Linkage group[a]	Genotypic means			R^{2c}	LOD[c]
			A/A[b]	A/B[b]	B/B[b]		
				– cm –			
Plant height	K007	H	101	109	110	8.2	1.6
	Dt1	L	116	111	89	64.1	24.8
	A516b	N	106	110	99	9.4	2.2
				– score –			
Lodging	cr517	J	2.4	2.8	2.8	11.1	1.1
	Dt1	L	3.1	2.9	2.1	53.0	18.3
				– days –			
Maturity	B032	K	55	54	52	24.0	6.8
	R051	K	55	54	52	20.8	6.7

[a] Based on the designation of Shoemaker and Specht (1995)
[b] A/A: homozygous PI 97100, A/B: heterozygous, B/B: homozygous Coker 237
[c] R^2 was on the basis of single-factor ANOVA, and LOD was the maximum value near the respective marker from the interval-mapping analysis

tected in the interval-mapping analysis. The Coker 237 allele was associated with increased plant height at the K007 locus. The second locus was A516b located on LG N. In the interval-mapping analysis, the LOD threshold is dependent on the number of linkage groups and the average spacing between RFLP markers (Lander and Botstein 1989). If a LOD score of 2.0 was chosen as the minimum for detecting a QTL position, the QTL near A516b (LOD=2.2) would have been detected. The PI 97100 allele at this QTL conditioned increased plant height.

The transgressive segregation of the progeny from this cross [lines significantly ($P \leq 0.05$) taller than PI 97100, based on Fisher's Protected LSD] supports the identification of a QTL near marker K007 at which alleles from the shorter parent, Coker 237, increase plant height. This QTL accounted for 8.2% of the variation in plant height.

All possible combinations of the putative independent markers associated with plant height were tested for two-factor interactions to detect epistasis. Epistasis was not detected for any of these markers.

The *Dt1* locus is in the same region as the QTL affecting plant height reported by Mansur et al. (1993) in F_2-derived lines from a cross between Minsoy and Noir 1. They found that 53% of the phenotypic variance was explained by this QTL near G173 (same location as *Dt1* on LG L in our study). Considering that growth habit has a significant effect on plant height, and that progeny were segregating for growth habit in both populations, it was not surprising that both studies identified this qualitative trait locus.

In our previous study (Lee et al. 1996), we found two putative independent markers (K385 and O109n) on LG L that were associated with plant height. In that study the progeny were not segregating at the *Dt1* locus. On the basis of an average of the recombination values between pairs of common markers, LG L of the two genetic maps from both present and previous studies was integrated to compare identified QTLs (Fig. 2). The LOD curve for plant height was plotted for the PI 97100 × Coker 237 population, whereas solid bars were plotted to represent data from the single-factor analysis for the Young × PI 416937 population. Since the markers B046 and A489 map between K385 and O109n, and were not associated with plant height in the Young × PI 416937 population, it could be concluded that the two putative independent markers (K385 and O109a) were different from the *Dt1* locus detected in the present study. Also, Keim et al. (1990 b) did not report the same QTLs as those identified in the present study. This different genomic location of QTLs for plant height across populations provides evidence for population specificity for important QTLs, indicating a limitation to the indiscriminate utilization of RFLP markers across populations for marker-assisted selection.

Since Robertson (1985) suggested the concept that a living organism would not have two different sets of loci for qualitative and quantitative effects, there has been much evidence in support of QTLs in close proximity to related qualitative trait loci (Beavis et al. 1991; Veldboom et al. 1994; Plaschke et al. 1995). Our results also indicate additional evidence that the QTLs for plant height were located on the same linkage group as the qualitative trait locus *Dt1*.

Lodging

PI 97100 and Coker 237 differed by a lodging score of 1.6, and lodging scores varied among F_2-derived lines from 1.6 to 4.0 (Table 1). Based on the LOD score peak, the QTL associated with lodging at Blackville was located 1.6 cM from *Dt1* and 5 cM from *Dt1* at Athens (Table 2). However, this QTL explained only 21.6% of the phenotypic variation for lodging at Athens, whereas it explained 56.0% at Blackville. This was probably due to relatively more lodging at an early growth stage at Athens (prior to flowering) than at Blackville, which resulted in less genotypic difference in lodging scores at maturity in Athens. When combined across locations, this QTL was localized to the interval between *Dt1* and K385, at the exact same QTL position detected at Blackville (Fig. 1).

At the *Dt1* locus, each Coker 237 allele (*dt1*) resulted in reduced plant lodging by a score of 0.5, and heterozygotes lodged 0.3 more than predicted based on additive gene action (Table 2). The degree of dominance was –0.6, indicating partially dominant gene action. Bernard (1972) and Hartung et al. (1980) reported greater lodging resistance in the *dt1* compared to the *Dt1* near-isolines. In our study, homozygous *dt1* lines averaged a lodging score of 1.9 compared with 3.1 for the homozygous *Dt1* lines.

Across locations, the LOD score for the *Dt1* locus was 18.3, and the amount of variation explained was 56.4% (Table 2). The heritability (selection unit = two locations, three replications/location) for lodging was 40.6%, suggesting that most of the genetic variation was explained by this QTL.

In a single-factor ANOVA for lodging, one additional independent marker at the cr517 locus was identified. The cr517 locus identified a QTL at which Coker 237 alleles were associated with increased lodging. The interaction between Dt1 and cr517 did not have a significant ($P \geq 0.01$) effect on the progeny, suggesting that there was no epistatic effect conditioning lodging in this population.

The association of the *Dt1* locus with lodging was consistent with the previous report by Mansur et al. (1993). They found the same QTL for both plant height and lodging, which was in an interval between A385 and G173 (same as LG L in our study).

In a population from Young × PI 416937 (Lee et al. 1996), two molecular markers (A169 and EV2) on LG L were associated with lodging. However, based on a comparison of the position between molecular markers identified in the Young × PI 416937 population and that of the QTL in the present study on the composite map (Fig. 2), the QTL mapped on LG L in this study is different from that of the previous study.

Maturity

PI 97100 and Coker 237 differed by 5 days in maturity, while the progeny varied by 10 days (Table 1). For maturity, interval mapping identified two peaks near R051 and B032 (Table 2, Fig. 1). To test the presence of two linked QTLs, one putative QTL near R051 was declared at a fixed location. The second QTL near B032 was also likely to be present because a scan procedure in Mapmaker-QTL still detected a substantial increase in score from 6.6 to 8.1, indicating that the two QTLs were putatively independent. Most likely, the QTL positions were localized in the interval between R051 and N100 and 1.8 cM from B032 on LG K (Table 2).

The QTL in the interval between R051 and N100 gave 1.5 days earlier maturity for each allele from Coker 237, and heterozygotes were 1.1 days later in maturity than expected based on additive gene action (Table 2). At the QTL near B032, each Coker 237 allele was also associated with 1.5 days earlier in maturity, and heterozygotes were 0.7 days later in maturity than predicted for additive gene action. The degrees of dominance were –0.7 for the QTL in the interval between R051 and N100, and –0.5 for the

QTL near B032, indicating that these two QTLs behaved in a partially dominant manner.

The amount of phenotypic variation explained was 31.2% for the QTL between R051 and N100, and 26.2% for the QTL near B032. Summed together, these two independent QTLs explained 57.4% of the total variation for maturity. The heritability (selection unit = two locations, three replications/location) for maturity was 86.8% (Table 1). The single-factor analysis did not detect additional QTLs (Table 3). None of the previous studies (Keim et al. 1990 b; Lee et al. 1996; Mansur et al. 1993) detected these QTLs for maturity. This provides evidence for additional QTLs for maturity in soybean.

In our previous study (Lee et al. 1996), transgressive variation of 36 days occurred among progenies derived from a cross of Young and PI 416937 in spite of a small parental difference of 3 days in maturity. However, the present population showed variation of only 10 days among progenies, even though Coker 237 matured 5 days earlier than PI 97100 (Table 1). The difference in the amount of variation across populations appears to be due to the combining of different alleles for several QTLs in the Young × PI 416937 population, as suggested by Mansur et al. (1993). In the present study, PI 97100 contained alleles for late maturity at both identified loci. In the Young × PI 416937 population, the alleles for late maturity were distributed in both parents. Thus, the different amount of variation among progenies across populations emphasizes the selection of diverse parent genotypes to create genetic variation in breeding programs.

As was expected, with the *Dt1* locus conditioning large differences in plant height and lodging, increased plant height showed a positive association with an increased lodging score (r=0.68***). However, maturity did not show an association with plant height (r=0.14) or lodging (r=0.08), or have any QTL in common. Given the lack of common QTLs for maturity with either plant height or lodging and the limited 10-day range in maturity among the lines, a lack of association is to be expected.

The additional QTLs detected by single-factor ANOVA compared to interval-mapping analysis may be due to the relatively low saturation of our genetic map in the present study. These results differed from the consistent detection of QTLs in maize by both methods (Stuber et al. 1992). The strengths and limitations of these two methods for detecting QTLs are discussed by Doerge et al. (1994).

The results from the present study indicated a consistency of QTLs across locations, which is supported by Stuber et al. (1992) but is in contrast to the conclusions of others (Paterson et al. 1991 b; Bubeck et al. 1993; Dudley 1993; Lee et al. 1996). Also, QTLs identified from nematicide-treated plots were in good agreement with those from untreated plots for our population (data not shown). This consistency over environments probably resulted from the control by a few loci with large effects on the quantitative traits studied in this population. In addition, a comparison of QTLs from this study with those from other soybean populations (Keim et al. 1990; Mansur et al. 1993; Lee et al. 1996) which had different genetic backgrounds indicates the population specificity of important QTLs.

RFLP mapping in our population identified the *Dt1* locus conditioning growth habit. Interval mapping identified two new QTLs for maturity (in the intervals R051-N100 and B032-CpTI) on LG K. Single-factor analysis also identified two previously undetected QTLs for plant height (K007 on LG H and A516b on LG N) and one QTL for lodging (cr517 on LG J). These QTLs add to the growing information on the genetic control of these traits.

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