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Interval mapping of quantitative trait loci for reproductive, morphological, and seed traits of soybean (*Glycine max* L.)

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Abstract. Quantitative trait loci (QTL) were mapped in segregating progeny from a cross between two soybean (*Glycine max* (L.) Merr.) cultivars: 'Minsoy' (PI 27.890) and 'Noir 1' (PI 290.136). The 15 traits analyzed included reproductive, morphological, and seed traits, seed yield and carbon isotope discrimination ratios ($^{13}C/^{12}C$). Genetic variation was detected for all of the traits, and transgressive segregation was a common phenomenon. One hundred and thirty-two linked genetic markers and 24 additional unlinked markers were used to locate QTL by interval mapping and one-way analysis of variance, respectively. Quantitative trait loci controlling 11 of the 15 traits studied were localized to intervals in 6 linkage groups. Quantitative trait loci for developmental and morphological traits (R1, R5, R8, plant height, canopy height, leaf area, etc.) tended to be clustered in three intervals, two of which were also associated with seed yield. Quantitative trait loci for seed oil were separated from all the other QTL. Major QTL for maturity and plant height were linked to RFLP markers R79 (31% variation) and G173 (53% variation). Quantitative trait loci associated with unlinked markers included possible loci for seed protein and weight. Linkage between QTL is discussed in relation to the heritability and genetic correlation of the traits.

Key words: DNA – RFLP – QTL – Genetic map – Soybean

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Introduction

In all crops, including soybean, traits of agronomic and economic importance result from the joint action of multiple genes and the environment. Such polygenic, quantitative traits exhibit phenotypes with continuous distributions that are difficult to analyze. Sax (1923) introduced the concept of using qualitative genes to locate genes of lesser effects controlling quantitative traits. Thoday (1961) used single gene morphological markers to conduct detailed studies of quantitative traits in *Drosophila melanogaster*. More systematic attempts to resolve quantitative traits into their individual genetic components were initially limited by a lack of polymorphic qualitative markers that could cover large parts of the genome. These limitations have been partly overcome by the use of isozymes (Tanksley et al. 1982; Edwards et al. 1987) and later by restriction fragment length polymorphisms (RFLPs), which have provided a virtually inexhaustible source of markers with many desirable attributes (Paterson et al. 1988, 1991).

Lander and Botstein (1989) introduced interval mapping, an analytical method that localizes the effect of a quantitative trait locus (QTL) to a genomic segment located between pairs of qualitative markers rather than associating the effect with an individual locus. Because a double cross-over is necessary to diassociate an interval from a QTL, interval mapping of QTL more efficiently exploits information obtained from genetic linkage maps. Furthermore, software has been developed (Mapmaker-QTL, Lincoln and Lander 1990; see also Lander et al. 1987) to implement interval mapping. The synergism of coupling RFLP maps to computer-assisted analysis of quantitative characters has been demonstrated by Paterson et al.

(1988, 1991), who partitioned economically important traits in tomato into several individual QTL. In the most common approach to mapping QTL, two parents, of the same genus but often of different species, are chosen to represent extremes of variation (Tanksley et al. 1982; Graef et al. 1989; Suarez et al. 1991; Keim et al. 1990; Diers et al. 1992; Paterson et al. 1988, 1990, 1991). However, breeders rely heavily on crosses of high-yielding lines exhibiting similar phenotypes to obtain improved, transgressive segregants. Thus, mapping QTL of progeny from parents of similar phenotypes but different genotypes can uncover alternative genetic solutions to the same agronomic problem. To determine this, it is necessary to evaluate segregating progeny and map the distribution of QTL among them. Once these data have been obtained, it is possible to predict the cost-effectiveness (in terms of which traits show variation and locating possible QTL) of a much more extensive genetic analysis, such as the production and analysis of a large recombinant inbred population.

We have studied a population derived from two soybean cultivars of similar phenotype. Their progeny, nevertheless, show a high degree of transgressive variation thereby yielding many offspring that surpass either parent for various reproductive, morphological, and seed traits, as well as seed yield. We then have used a RFLP genetic map (Lark et al. 1993) and interval mapping to localize possible QTL controlling these traits.

Materials and methods

In these studies, we have used progenies from an intraspecific cross of two soybean cultivars: PI 27.890 ('Minsoy') and PI 290.136 ('Noir 1'). A genetic linkage map (Lark et al. 1993) consisting of 132 loci was used for the interval mapping of QTL.

Measurement of quantitative traits and mapping of QTL

Genetic material for measuring quantitative traits

Field experiments were conducted using F_5 families derived from the same 69 F_2 plants used by Lark et al. (1993) to construct a genetic linkage map. Because of insufficient F_3 seed to conduct replicated field experiments, F_5 families were derived as follows. F_2 plants were grown during the summer of 1988 near Ames, Iowa, and 35 F_3 seeds from each F_2 plant were planted at the Iowa State University–University of Puerto Rico winter nursery at Isabela, Puerto Rico in October of 1988. These $F_2:F_3$ families included between 18 and 35 F_3 plants. F_4 seeds were used to obtain the next generation at the Puerto Rico location in January of 1989. (From $F_2:F_3$ families with fewer than 25 plants, 3 F_4 seeds per F_3 plant were used. In those with more than 25 F_3 plants 2 seeds were used). In almost all of the $F_2:F_4$ families, a minimum of 40 F_4 plants reached maturity. In five cases only 30–39 plants reached maturity. Each F_4 plant was threshed individually, and in each family an approximately equal number of seeds from each F_4 plant were bulked to conduct the field experiments.

Field experiments

Field experiments were conducted using a randomized complete block design with three replications at each of two locations: the Iowa State University Agronomy and Agricultural Engineering Research Center and the Burkey Farm near Ames, Iowa. Each replication consisted of 69 F_5 families and six plots of each parent. Plots consisted of paired rows 4.6 m long, with a row spacing of 69 cm and 102 cm spacing between plots. The seeding rate was 120 seeds per plot. Both locations were planted May 20, 1989.

Quantitative traits

Fifteen traits were scored, including reproductive stages (Fehr and Caviness 1977), morphological characters, seed traits, seed yield, and carbon isotope discrimination ($^{13}C/^{12}C$) (Farquhar et al. 1989; Ehleringer 1990).

The reproductive stages measured were: R1, beginning bloom or the number of days after May 31 when an open flower was found at any node on the main stem; R5, beginning seed or the number of days after June 30 when a 3-mm-long pod was found at one of the four uppermost nodes that had a fully developed leaf; R8, maturity or the number of days after July 31 when 95% of the normal pods on the main stem had reached their mature pod color; seed filling period or R8–R5; and reproductive period or R8–R1 (both calculated on the basis of days after planting). All of the reproductive stages were scored when 50% of the plants on the plot had reached that particular stage.

The morphological characters evaluated were: leaf area, the area of a fully developed leaf on the main stem, taken from each of 6 plants in the plot between R5 and R6 and measured using a planimeter; plant height, the height in centimeters of the main stem from the unifoliolate node to the fifth trifoliolate node on 6 plants per plot; lodging score, the average angle the plants in the plot made with the soil surface, with 1 being fully erect and 5 all plants prostrate; canopy height, the height of the canopy in centimeters. All of the morphological traits were scored at R8.

The seed traits were: seed weight expressed in milligram, $seed^{-1}$ based on a 200 seed sample per plot; percentage protein and oil on a dry weight basis measured on a 7-g sample of whole seed taken from each plot (analysis made at the USDA Northern Regional Research Center at Peoria, Ill. with a model 1255 Food and Feed Analyzer Infratec NIR grain analyzer). For seed yield, the plots were first end-trimmed to 3 m at R8 and then machine harvested. Seed yield was expressed as kg ha^{-1} on a 13% moisture basis. Carbon isotope discrimination ($^{13}C/^{12}C$) was measured on samples of F_2 leaves that had been dried and ground to powder. Carbon isotope analyses were performed at the Stable Isotope Ratio Facility for Environmental Research at the University of Utah.

Statistical analysis

Standard procedures for analysis of variance were used to partition the total variance among families into genetic and environmental components as well as genetic by environmental interaction effects. Families and locations were considered to be random effects. Means and standard deviations across locations for parents and progenies were computed for each trait. Genetic variance, heritability in the broad sense, and genetic correlations were obtained using the variance component estimates from the analysis of variance (Johnson et al. 1955).

Qualitative marker-QTL associations

These associations were obtained by interval mapping (Lander and Botstein 1989) with Mapmaker-QTL version 0.9 (Lincoln

and Lander 1990) in the case of linked markers and analysis of variance for unlinked markers (see below).

Interval mapping

For this study, the means for each F_2:F_5 family were computed for each trait across locations, and interval mapping analysis (Lander and Botstein 1989) using Mapmaker-QTL (Lincoln and Lander 1990) was used to obtain QTL maximum likelihood scans for each trait. Scans with a log of likelihood (LOD) score of at least 2.5 were used to define intervals containing QTL associated with the traits of interest.

Mapmaker-QTL describes the phenotype of an individual as the sum of the QTL that individual possesses for a particular trait. It allows either additive or additive dominance models to be applied to the observed data (for details see Lander and Botstein 1989; Lincoln and Lander 1990; Paterson et al. 1988, 1991). With the exception of ($^{13}C/^{12}C$), in which an additive-dominance model was fit, the rest of the traits were analyzed assuming an additive model. This is because our progenies were in the F_5 generation, and the dominance effects that could have been present in the F_2 plants would have been largely dissipated by the three additional rounds of inbreeding that were used to produce the F_5 families. QTL likelihood profiles were produced as described by Paterson et al. (1991).

Analysis of single markers by one-way analysis of variance

The degree of association between 24 unlinked markers and the QTL controlling the quantitative traits under study was investigated by standard analysis of variance in which marker-genotype groups were used as class variables (Osborn et al. 1987; Keim et al. 1990). Significant differences in the trait means across locations for marker genotype groups were considered to be a preliminary indication of linkage between a marker and a QTL for 1 of the traits. The proportion of the phenotypic variance explained by segregation of the marker was determined by the R^2 value. The results obtained by Mapmaker-QTL were also confirmed by analysis of variance.

Results

Segregation of quantitative traits

Table 1 presents means, ranges, and heritabilities for all of the traits measured in the F_2:F_5 families. 'Minsoy' and 'Noir 1' had almost identical values for R1, R8, seed weight, and seed yield; however, extensive transgressive variation occurred among segregants for all of these traits, indicating that the two parental genotypes had achieved similar phenotypes through different gene combinations. For example, the range for R8 among progenies was at least 12 times the range exhibited by the parents. The analysis of variance among the segregant progeny showed that significant ($P < 0.05$) genetic variation occurred for all traits. The genetic variation among progeny families for all traits was highly heritable, with H^2 values ranging from 0.72 for leaf area to 0.98 for R8 (Table 1). The analysis of variance detected significant ($P < 0.05$) genotype by environment interactions for only 3 traits, R1, R5, and R8–R1 (data not shown).

Seed yield was highly heritable in this cross ($H^2 = 0.86$), which was not surprising since it was also genetically correlated with R1 ($rg = 0.70 \pm 0.06$), R5 ($rg = 0.80 \pm 0.04$), R8 ($rg = 0.80 \pm 0.04$), and plant height ($rg = 0.68 \pm 0.06$), all of which are traits known to have high heritability (Burton 1987). Leaf area was also highly correlated to the growth stages R1, R5, and R8 and to seed yield (rg = 0.60, 0.45, 0.71 and 0.48, respectively) but not to the other measured traits. As expected, seed yield had a negative genetic correlation with seed protein content ($rg = 0.55 \pm 0.08$) but sur-

Table 1. Means, standard deviations (SD), ranges (Rng), and broad sense heritability (H^2) for traits measured in 'Minsoy', 'Noir 1', and F_5 families

Trait	*Minsoy*			*Noir 1*			*F_5 families*			
	Mean	SD[c]	Rng[c]	Mean	SD	Rng	Mean	SD	Rng	H^2
R1[a] (days)	32	0.01	0.03	33	0.01	0.04	33	0.08	0.41	0.92
R5 (days)	27	0.07	0.19	30	0.04	0.10	28	0.15	0.61	0.92
R8 (days)	30	0.02	0.05	31	0.02	0.05	34	0.14	0.62	0.98
Seed filling[b] (days)	34	0.07	0.2	33	0.03	0.07	37	0.09	0.42	0.85
Reproductive period (days)	59	0.01	0.03	59	0.01	0.01	63	0.06	0.27	0.91
Leaf area (mm^2)	418	0.001	0.002	574	0.03	0.04	486	0.01	0.06	0.72
Plant height (cm)	66	0.05	0.08	86	0.02	0.05	66	0.16	0.77	0.93
Node length (mm)	113	0.04	0.08	131	0.05	0.12	120	0.08	0.40	0.73
Lodging (score 1–5)	3.8	0.08	0.2	2.8	0.08	0.24	2.8	0.22	1.1	0.76
Canopy height (cm)	42	0.08	0.21	61	0.07	0.19	51	0.12	0.65	0.71
Seed weight (mg)	24.7	0.02	0.06	24.5	0.01	0.03	24.8	0.07	0.34	0.94
Seed protein (%)	39.5	0.003	0.01	41.2	0.01	0.03	40.3	0.02	0.12	0.83
Seed oil (%)	18.7	0.01	0.03	20.4	0.01	0.04	19.1	0.04	0.18	0.88
Seed yield (kg ha^{-1})	2668	0.03	0.08	2601	0.08	0.19	2728	0.13	0.66	0.86

[a] R1, days after May 31; R5, days after June 30; R8, days after July 31

[b] R8–R5 (seed filling period) and R8–R1 (reproductive period) are based on days after planting

[c] Standard deviations and ranges were divided by their means to obtain the values reported here

prisingly, it was not correlated with seed oil content ($rg = 0.03 \pm 11$). (See also mapping QTL below). In fact, seed oil content was not correlated to any of the other traits. In contrast, seed protein content had a negative genetic correlation with seed yield and those traits that were highly correlated to seed yield (R1, R5, R8, and plant height). It should be noted that seed weight was inherited independently of most of the other traits with the highest correlation being with R1 ($rg = 0.39 \pm 0.10$). No correlations were attempted with the carbon discrimination ratio, because this trait was measured separately in single determination using leaves from the F_2 plants.

Mapping of quantitative trait loci

Interval mapping

Quantitative trait loci controlling 11 of the 14 traits listed in Table 1 (as well as $^{13}C/^{12}C$) were localized to intervals within 6 of the 31 linkage groups described by Lark et al. (1993) (see Fig. 1 and Table 2). Possible QTL are reported at a LOD score of 2.5 or greater [except seed yield where one LOD score was 2.4 (see, however, Mansur et al. 1993)]. Overall, the most striking results were the tendency of the QTL for developmental and morphological traits (R1, R5, R8, plant height, canopy height, leaf area, etc.) to be clustered in three intervals, two of which were also associated with seed yield (linkage groups 2, 15, and 16, Fig. 1) and the separation of QTL for seed oil from the loci for other traits, notably the yield-determining traits (R1, R5, R8, leaf area, plant height, and lodging).

QTL for 6 traits were closely associated with marker R79 in linkage group 14: R1 (first flowering), R8 (maturity), reproductive period (R8–R1), leaf area, canopy height, and seed yield (Fig. 1, Table 2). QTL for 5 traits (R1, R5, R8, leaf area, and seed yield) were mapped to the 6.7-cM interval defined by markers A397 and BLT29 in linkage group 2. Although 4

Table 2. Intervals containing quantitative trait loci (QTL) with a log of likelihood (LOD) of 2.5 or higher

Interval[a]	Linkage group	Length (cM)	QTL[d] position	Effect[e] add	Variance explained	LOD
R1 (days after May 31)						
A397-BLT29	2	6.7	0	1.7	0.22	3.4
A584-R79	15	29.2	28	−1.5	0.17	2.8
A385-G173	16	18.4	18	−1.4	0.18	2.8
R5 (days after June 30)						
A397-BLT29	2	6.7	2	3.1	0.25	3.7
A385-G173	16	18.4	18	−2.4	0.19	3.1
R8 (days after July 31)						
A584-R79	15	29.2	28	−3.5	0.31	5.1
Reproductive period[b] (R8–R1)						
A397-BLT29	2	6.7	2	2.9	0.18	2.85
A584-R79	15	29.2	28	−2.0	0.17	2.6
Leaf area (mm^2)						
A397-BLT29	2	6.7	4	38	0.20	2.9
A584-R79	16	29.2	28	−39	0.25	4.2
Plant height (cm)						
A385-G173	1	18.4	18	−10	0.53	10.9
Lodging (score 1–5)[c]						
A385-G173	16	18.4	18	−0.6	0.45	8.9
Canopy height (cm)						
A584-R79	15	29.2	28	−3.7	0.19	3.0
Oil (%)						
T153a-A111	3	17.6	2	−0.7	0.36	5.5
BCI-A315	9	26.3	20	−0.5	0.24	2.9
Seed yield (kg ha^{-1})						
A109a-A397	2	6.7	9	237	0.24	2.4[f]
A584-R79	15	17.6	4	−241	0.20	3.2

[a] Mapmaker-QTL interval mapping output corresponding to an additive model. Because the progenies used to measure the quantitative traits were F_2-derived families in the F_5 generation, it was assumed that the dominance effects would have been largely dissipated

[b] R1 and R8 were adjusted to days from planting to compute this trait

[c] Lodging score 1, erect plant; 5, all plants prostrate

[d] QTL positions correspond to the maximum LOD score for each likelihood scan within or across intervals in a linkage group

[e] A plus or minus sign indicates that the 'Minsoy' allele increases or decreases the value of the trait (see Materials and methods for details)

[f] This interval for seed yield is reported because it was close to the threshold

yield-determining traits (R1, R5, plant height, and lodging) were linked to G173 in linkage group 16, only weak evidence was obtained (LOD = 1.8) that this was also a locus for seed yield. The high LOD score for the occurrence of QTL controlling plant height near marker G173 and maturity (R8) near marker R79 was striking. In both cases, these putative QTL account for a large amount of the phenotypic variation in each of the traits (30–50%, Table 2). No QTL was found for canopy height near marker G173, which is consistent with the possibility that decreases in plant height accompanied decreases in lodging, leading to little variation in canopy height.

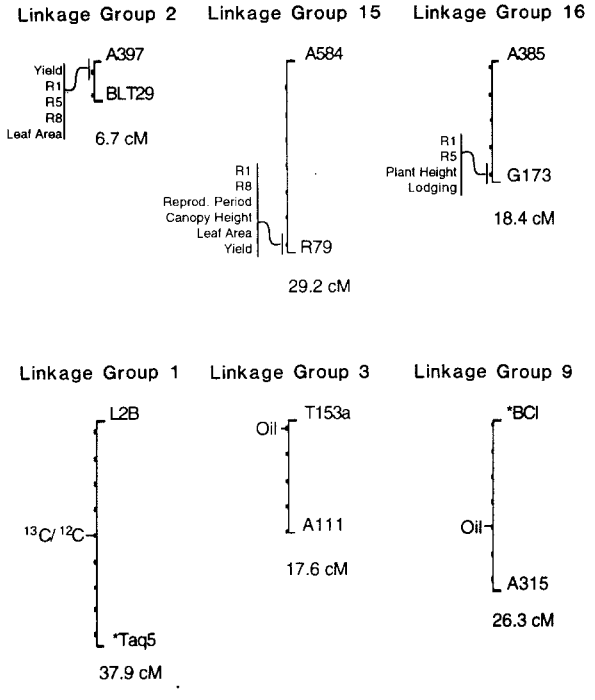

Fig. 1. Intervals from a soybean RFLP map (Lark et al. 1993) depicting the approximate location of quantitative trait loci for various traits. (For details see Materials and methods)

Table 3. Unlinked markers associated with significant phenotypic variation

Marker	Trait	R^2 (%)	$P <$
A696	Maturity	9	0.05
	Reproductive period	10	0.03
	Seed filling	12	0.01
	Yield	8	0.05
A60	Plant height	19	0.004
	Canopy height	16	0.009
K1	Oil	11	0.02
L48	Protein	20	0.004
T10	Canopy height	8	0.05
A295	Beginning seed	12	0.01
C9	Seed weight	13	0.02

Our preliminary investigation of the carbon discrimination ratio indicates that regions of the genome in the interval defined by markers L2b and *Taq5 in linkage group 1 may contain QTL that determine this trait. The locus is most likely (LOD = 3.9) 24 cM from marker L2b and could be responsible for as much as 53% of the variation present for this trait.

We found that the additive effects of QTL from one parent can either increase or decrease the value of a trait. See, for example, R1, R5, R8, and seed yield in Table 2. This would be consistent with the hypothesis that transgressive segregant progeny from this cross have arisen from a combination of different alleles from the two parents.

Analysis of unliked markers

Table 3 shows the results of the analysis of unlinked (i.e., unmapped) markers for possible association with QTL via analysis of variance. Two markers were associated with QTL for traits not previously uncovered by interval mapping: seed filling period associated with marker A676 and seed protein content with marker L48. Also, additional markers were found for traits mapped via interval mapping.

Discussion

General considerations

We have measured quantitative traits and mapped QTL in progeny from a cross between the soybean cvs 'Minsoy' and 'Noir 1'. Whereas the parents in the cross show similar values for many of the traits, the segregating progeny present a far greater range of trait values (Table 1). This transgressive behavior suggests that the similar parental phenotypes have resulted from combining different alleles for many, perhaps most, of their quantitative traits. Thus, though the parental phenotypes are similar, the diversity of the genotype makes this cross a rich source of new germ plasm, which we have now realized in the form of genetically characterized, near-inbred recombinant inbred lines (Mansur et al. 1993).

Figure 1 shows the location of QTL associated with 6 of the 31 linkage groups that are defined by the map of Lark et al. (1993). Results from interval mapping and analysis of variance are in agreement. Because of inbreeding, most of the plants in each F_5 family should be homozygous for either of the two parental alleles, justifying our assumption to disregard dominance effects.

We have found that QTL affecting related but separate traits such as the seed yield-determining traits in linkage groups 2, 15, and 16 (Fig. 1) are clustered in

discrete intervals and that these, in turn, are distinct from those controlling seed oil content. However, such a clustering of QTL could have been selected during domestication as three RFLP markers associated with R1 in the interspecific cross of *G. soja* by *G. max* (Keim et al. 1990; Diers et al. 1992) have also been found to be associated with R8, suggesting that this is the result of a previous evolutionary process. The clustering of QTL for physiologically related traits such as R1, R5, and R8 in linkage group 2, R1 and R8 in linkage group 15, and R1 and R5 and in linkage group 16 as well as the similar shapes of their respective probability curves (data not shown) suggest that the putative QTL for these traits (Table 2) may result from pleiotropic effects. Alternatively, it may be that the loci conditioning these developmental stages of the plant are genetically closely linked as a result of chromosome rearrangements selected during domestication and cultivation for agronomic traits.

Traits of agronomic interest

Previous studies relying on interspecific *G. max* by *G. soja* crosses ensure phenotypic and molecular diversity in the parents and offer the possibility of finding useful new genes that can be introgressed in *G. max* (Graef et al. 1989; Keim et al. 1990; Suarez et al. 1991; Diers et al. 1992). However, traits of agronomic importance often cannot be meaningfully evaluated in an interspecific cross. This is because soybean plants from interspecific crosses are usually trailing vines having pods with a great tendency to shatter. The progeny in this study permit the evaluation and QTL mapping of traits such as lodging, plant height, and yield that are routinely used by commercial plant breeders to select adapted, high-yielding genotypes for a particular market.

The clustering of QTL with large effects on flowering (R1), beginning seed (R5), maturity (R8), plant height, and lodging (Fig. 1, Table 2) are consistent with the high values of heritability and with the genetic correlations among these traits. Moreover, previous work has shown that these traits are in general highly heritable and genetically correlated in soybean (see Burton 1978 for a review). The high heritability and genetic correlations among these traits could be the result of single pleiotropic genes with major effects, e.g., the QTL for the reproductive and morphological traits associated with markers R79 and G173 (Fig. 1, Table 2). Alternatively, loci with relatively large effects may be the manifestation of blocks of genes that segregate as a single locus.

The heritability of complex traits, such as seed yield, can be increased through the genetic linkage or the pleiotropic effects of genes determining simpler traits that are themselves highly heritable. For example, heritability for seed yield in this cross is 0.86. This high heritability is undoubtedly due to the high genetic correlation between seed yield and simpler yield-determining traits, such as R1 ($rg = 0.7$) and R8 ($rg = 0.8$). Thus, QTL for seed yield were associated with those for R1 and R8 in the same intervals (between markers A397 and BLT 29 in linkage group 1 and linked to marker R79 in linkage group 14). The genetic correlations between the growth stages (R1 and R8) and the morphological traits (plant height and leaf area) are also explained by the fact they tend to map to the same regions of the genome (Fig. 1).

Unexpectedly, we found that in this cross, seed oil content, which usually is negatively correlated with seed protein content and seed yield, is not correlated with these traits. Consistent with this, the markers associated with the QTL explaining the major portion of the phenotypic variance for seed oil mapped to linkage group 3, which also contains the structural gene for thiol protease, a protein associated with seed oil bodies (Kalinski et al. 1990). We found no QTL for other traits in these 2 linkage groups. This finding is indicative that, to some extent, seed yield in soybean may be manipulated independently of seed oil.

To determine if the QTL we mapped are similar in a different genetic background, we compared our results to those reported by Keim et al. (1990) and Diers et al. (1992). Linkage group 3 of Lark et al. (1993) is congenic to linkage group B of Diers et al. (1992); however, Diers et al. (1992) did not report the association of any of these markers with seed oil. Moreover, marker A111, which is associated with leaf width in their cross, is not related to leaf area in our cross. There is, however, one example of a marker that appears to be associated with related traits in both crosses: marker G173 explains 24% of the variation for stem diameter in the study of Keim et al. (1990) and explains 53% and 45% of the variation for the related traits of plant height and lodging in our cross. These similarities and differences found in these two mapped genetic resources underscore the usefulness of having two distinct genetic maps to study the evolution and genetic organization of qualitative and quantitative traits in soybean.

In addition to studies of agronomic traits, this segregating population should be valuable for dissecting the $^{13}C/^{12}C$ isotope ratio. This trait deserves further research because it is related to stomatal closure and, consequently, to the ability of soybean to grow under drought conditions (Johnson et al. 1990; Ehleringer 1990). To facilitate further studies related to the physiology and genetics of soybean development and differentiation, we are preparing a genetic linkage map in a set of 284 recombinant inbred lines that are presently in the F_{10} generation (Mansur et al. 1993).

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