Theor Appl Genet (1998) 96: 786–790

B. G. Rector · J. N. All
W. A. Parrott · H. R. Boerma

Identification of molecular markers linked to quantitative trait loci for soybean resistance to corn earworm

Received: 15 October 1997 / Accepted: 4 November 1997

Abstract One hundred and thirty nine restriction fragment length polymorphisms (RFLPs) were used to construct a soybean (*Glycine max* L. Merr.) genetic linkage map and to identify quantitative trait loci (QTLs) associated with resistance to corn earworm (*Helicoverpa zea* Boddie) in a population of 103 F_2-derived lines from a cross of 'Cobb' (susceptible) and PI229358 (resistant). The genetic linkage map consisted of 128 markers which converged onto 30 linkage groups covering approximately 1325 cM. There were 11 unlinked markers. The F_2-derived lines and the two parents were grown in the field under a plastic mesh cage near Athens, Ga., in 1995. The plants were artificially infested with corn earworm and evaluated for the amount of defoliation. Using interval-mapping analysis for linked markers and single-factor analysis of variance (ANOVA), markers were tested for an association with resistance. One major and two minor QTLs for resistance were identified in this population. The PI229358 allele contributed insect resistance at all three QTLs. The major QTL is linked to the RFLP marker A584 on linkage group (LG) 'M' of the USDA/Iowa State University public soybean genetic map. It accounts for 37% of the total variation for resistance in this cross. The minor QTLs are linked to the RFLP markers R249 (LG 'H') and Bng047 (LG 'D1'). These markers explain 16% and 10% of variation, respectively. The heritability (h^2) for resistance was estimated as 64% in this population.

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

Communicated by M. A. Saghai-Maroof

B. G. Rector (✉) · J. N. All
Department of Entomology, University of Georgia, Athens, GA 30602-2603, USA

W. A. Parrott · H. R. Boerma
Department of Crop and Soil Sciences, University of Georgia, Athens, GA 30602-7272, USA

Introduction

Defoliating insects can cause significant damage to soybean plants in the southeastern USA, often requiring chemical control (Hanthrone et al. 1982). In 1991, insect damage and insecticide applications cost Georgia soybean growers $6 million (McPherson and Douce 1992). Plant resistance to insects (PRI) can be an effective component of an integrated pest-management program. Breeding elite soybean cultivars with high levels of PRI would reduce the need for chemical insecticide applications and broaden the options of the pest manager. A reduction of chemical pesticide inputs would have both environmental and economic benefits.

The main sources of defoliating insect resistant soybean germplasm are plant introductions (PIs) with low agronomic value. Three such PIs, PI171451, PI227687 and PI229358, were identified in the early 1970s (Van Duyn et al. 1971) and have shown resistance to a number of defoliating insect species (Luedders and Dickerson 1977; Lambert and Kilen 1984 b; All et al. 1989). Insect resistance in these PIs is inherited as a quantitative trait (Sisson et al. 1976; Luedders and Dickerson 1977; Rufener et al. 1989; Kenty et al. 1996).

Antibiosis, antixenosis, and tolerance are the three principal modes of PRI (Painter 1951; Kogan and Ortman 1978). The PRI in PI229358 has both antibiotic and antixenotic properties (Lambert and Kilen 1984 a; Beach et al. 1985; All et al. 1989). Bioassays can be designed to infer individual modes of PRI. The present study was undertaken to identify QTLs associated with antixenosis PRI. Heritability estimates for antixenosis PRI in PI229358 range from 55 to 81% (Sisson et al. 1976; Kenty et al. 1996). Inheritance studies indicate that there are approximately two genes controlling this trait (Kenty et al. 1996).

Screening for PRI in soybean is labor-intensive and time-consuming. Marker-assisted selection using

molecular markers tightly linked to PRI quantitative trait loci (QTLs) would greatly enhance the ability of soybean breeders to introgress high levels of PRI into elite cultivars by allowing for the selection of PRI on seedling plants and significantly reducing linkage drag (Young and Tanksley 1989).

Molecular markers have been used to mark QTLs for many agronomic traits in soybean, including seed weight (Maughan et al. 1996; Main et al. 1996 b), seed protein and oil content (Diers et al. 1992 a; Lee et al. 1996 c; Brummer et al. 1997), water-use efficiency and leaf ash (Mian et al. 1996 a), hard seededness (Keim et al. 1990), plant height, logding and maturity (Lee et al. 1996 b, c), and sensitivity to the herbicide Chlorimuron (Mian et al. 1996 c). Soybean plants resistant to *Phytophthora sojae* (Diers et al. 1992 b; Lohnes and Schmitthenner 1997), *Fusarium solani* (Hnetkovsky et al. 1996), soybean mosaic-virus (Yu et al. 1994), *Meloidogyne incognita* (Tamulonis et al. 1997), and *Heterodera glycines* (Webb et al. 1995; Concibido et al. 1996; Vierling et al. 1996) have also been tagged using molecular markers. In addition, QTLs for PRI have been studied in other crop species including maize (Schon et al. 1993), tomato (Maliepaard et al. 1995), and potato (Bonierbale et al. 1994; Yencho et al. 1996).

Our objectives in the present study were to: (1) identify QTLs in soybean associated with antixenosis to defoliating insects, (2) determine the genomic location of these QTLs, and (3) quantify their magnitude and gene action.

Materials and methods

A soybean population, derived from a cross between Cobb and PI229358, was used to construct a genetic linkage map and to evaluate insect resistance. Cobb is susceptible to defoliation-damage by the corn earworm (CEW), *Helicoverpa zea* Boddie, whereas PI229358 resists CEW damage (All et al. 1989). A total of 103 $F_{2:3}$ lines were developed from this cross. Each line originated from a single F_2 plant grown at the University of Georgia Plant Sciences Farm near Athens, Ga., in 1993. Leaves were harvested from these F_2 plants for DNA isolation. DNA isolation, Southern blotting, and hybridization procedures have been described previously (Lee et al. 1996 a, b). Approximately 400 probes from various sources, including cDNA and/or genomic clones of soybean (R. C. Shoemaker, USDA/Iowa State University; K. G. Lark, University of Utah; R. T. Nagao, University of Georgia), *Vigna radiata* (N.D. Young, University of Minnesota), *Phaseolus vulgaris* (J.M. Tohme, CIAT), *Arachis hypogaea* (G.D. Kochert, University of Georgia) and *Medicago sativa* (G.D. Kochert), were used to screen for restriction fragment length polymorphisms (RFLPs) between Cobb and PI229358. Five restriction enzymes (*Dra*I, *Eco*RI, *Eco*RV, *Hin*dIII and *Taq*I) were used to identify RFLPs. Polymorphic probes were used for genetic mapping. Linkage maps were constructed from marker data using the Kosambi map function of the MAPMAKER/EXP computer program (Lander et al. 1987). For grouping linked markers, thresholds with a minimum LOD score of 2.0 and a maximum distance of 37.2 cM were employed.

For the insect bioassay, the parents and $F_{2:3}$ lines were grown in a randomized complete block design with four replications in 1995 at the Plant Sciences Farm. Hill plots were planted 45 cm apart long rows spaced 90 cm apart. Plots were over-seeded and later thinned to six plants per hill. The entire experiment was approximately 30 m long and 12 rows wide. Each replication contained a hill of six plants from each $F_{2:3}$ line, plus six hills each of Cobb and PI229358. There was a single border row of a susceptible cultivar, DPL726, which surrounded the experiment and was distinguishable by its narrow-leaflet phenotype. A plastic, fine-meshed cage was constructed over the experiment to create conditions for an artificial insect infestation (Rowan et al. 1991).

Corn earworm eggs were infested directly onto the plants at the V4 stage of development (Fehr and Caviness 1977). The eggs were applied in a corncob grifts medium (Wiseman et al. 1980) at a rate of approximately 150 eggs per plant per week for 4 consecutive weeks. The mesh cage prevented the escape of the hatching larvae, as well as the adult moths that developed from these larvae. The cage also prevented the invasion of predatory insects. The larvae were free to feed on the plants where they hatched, or migrate to adjacent plants. Moths developing from these larvae were allowed to oviposit freely in the cage.

Visual defoliation ratings for the entire experiment were taken when the susceptible parent, Cobb, had been significantly defoliated. A percent-defoliation score was visually estimated for the combined six plants of each hill. The defoliation data were checked for normality and subjected to ANOVA (SAS 1988) using replications and lines as random effects.

The association between RFLP markers and QTLs was tested by two different procedures. QTL-mapping analysis was performed using the interval-mapping method (Lander and Botstein 1989) with the MAPMAKER-QTL computer program (Lincoln et al. 1992). A LOD score of 2.0 was chosen as the 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 each QTL 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 ($P < 0.01$) among RFLP genotypic class means using an F-test from the Type-III mean squares obtained from the General Linear Model Procedure (Proc GLM; SAS 1988). Two-factor ANOVA was used on all markers to detect epistatic effects. Three-factor ANOVA was used only on significant markers to detect a possible three-way interaction.

Results

One hundred and thirty nine polymorphic RFLP markers were screened in the F_2 population. The genetic linkage map consisted of 128 markers converged into 30 linkage groups covering approximately 1325 cM. There were 11 unlinked markers.

The range of defoliation for $F_{2:3}$ lines was from 9% to 34% (Fig. 1). The mean defoliation for the parents was 13% for PI229358 and 42% for Cobb. Thus, statistically significant transgressive segregation was not observed for either greater resistance or susceptibility than that of the parents.

Based on interval mapping, three QTLs for resistance were detected in this cross (Table 1). They were present on linkage groups (LGs) 'M', 'H', and 'D1' (Fig. 2) of the USDA/Iowa State University public soybean genetic linkage map (Shoemaker and Specht 1995). These three QTLs were linked to RFLP markers A584, R249, and Bng047 and accounted for 37, 16, and 10% of the total genetic variation for resistance, respectively.

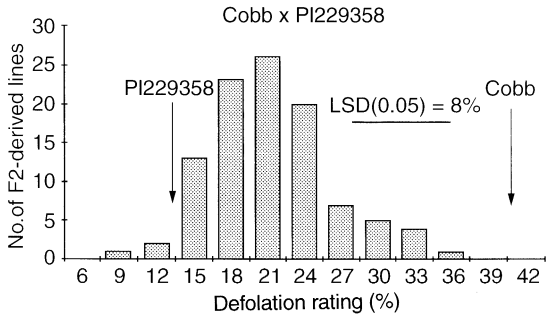

Fig. 1 Distribution of F_2-derived lines from the cross Cobb × PI229358 based on insect defoliation rating

The marker Bng047 was detected by interval mapping at a LOD score that was only slightly above the threshold of 2.0 (Fig. 2). This marker's significance was confirmed by single-factor ANOVA ($P = 0.0055$) (data not shown).

All three QTLs detected derived PRI from the allele of the resistant parent, PI229358. Each allele from PI229358 reduced defoliation by 4.1, 2.6, and 2.4% at the QTLs on LG M, H, and D1, respectively (Table 1). The degree of dominance was calculated at each of the three QTLs (Table 1). The low values for d/a indicate that each of the three QTLs acts in an additive fashion of else with a very low degree of partial dominance. No epistasis was detected when all markers were tested in two-factor and three-factor ANOVA models. While no significant epistatic interactions were detected, the three-way analysis including A584, R249, and Bng047 yielded an R^2 value of 66%. This compares favourably with the sum of the individual R^2 values from these markers ($\Sigma = 63\%$) and suggests that these markers act additively.

The heritability (h^2) for antixenosis in this population was estimated to be 64%. We feel confident that the three QTLs we have identified explain most of the genetic variation for this trait. In general, these results agree with previous estimates of gene number of this trait (Kenty et al. 1996). Single-factor ANOVA yielded similar results to those found using the interval-mapping procedure.

None of the three PRI QTLs detected in this study could be associated with each other through an analysis of soybean genome duplicated regions (Shoemaker et al. 1996). However, a comparison of these PRI QTLs with those detected in other soybean pest-resistance studies reveals that a QTL for resistance to soybean cyst nematode (SCN) has also been found on LG 'D' (Concibido et al. 1996). The SCN QTL on LG 'D' appears to lie near one end of LG 'D', whereas the PRI QTL on LG 'D1' occurs in the center of the LG. This suggests that these two QTLs are unlinked.

Attempts were made to associate the QTLs found in this study with genetically mapped insect resistance

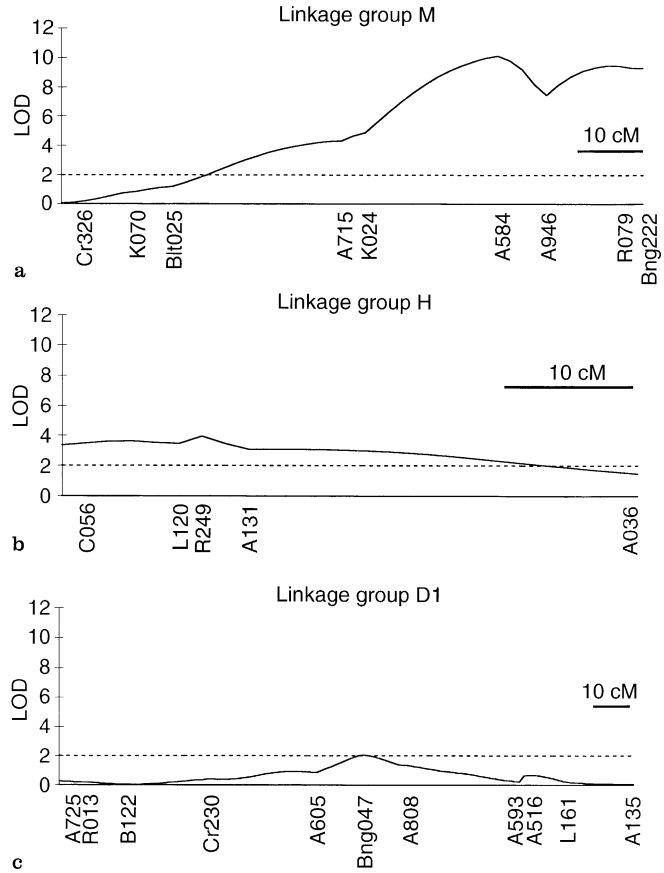

Fig. 2 QTL-likelihood maps from MAPMAKER/QTL. LOD peaks are shown for PRI.QTLs on **a** USDA LG 'M', **b** USDA LG 'H', and **c** USDA LG 'D1'. The *dotted line* in each panel represents the minimum significant LOD score of 2.0. A *bar* representing 10 cM of recombination distance is given for each panel

Table 1 RFLP markers associated with plant resistance to defoliation by *H. zea* based on MAPMAKER/QTL analysis. Effects of each marker on defoliation rating were calculated to obtain predicted marker means based on additive genetics

Linkage group	Interval	Interval length (cM)	Position of QTL[a] (cM)	LOD	a[b]	d/a	R^2 (%)
M	A584–A946.2	7.0	0.0	10.1	− 4.1	− 0.01	37
H	R249–A131	3.3	0.0	4.0	− 2.6	0.19	16
D1	Bng047–A808	16.1	1.4	2.0	− 2.4	− 0.13	10

[a] Position of LOD peak given as distance from the first marker listed in Interval
[b] Average change in defoliation for each allele from PI229358

regions in other legumes. A study comparing the genetic maps of soybean, mungbean, and common bean (Boutin et al. 1995) reveals that the gene for resistance to seed beetle in mungbean (Young et al. 1992) maps to a mungbean chromosomal region without conserved soybean linkage blocks. This mungbean chromosome also has no homologous RFLP markers from soybean LG 'M', 'H', or 'D1'. Thus it is unlikely that the mungbean resistance gene is homologous to the soybean insect resistance QTLs presented here. In addition, a pair of aphid resistance genes mapped in cowpea (Myers et al. 1996) occurred on cowpea LGs which could not be associated, through comparative mapping (Menancio-Hautea et al. 1993; Boutin et al. 1995) with the soybean LGs indicated here.

Candidate regions for disease resistance genes have been marked on the soybean genetic map, based on homology to cloned disease resistance genes from other plants (Kanazin et al. 1996; Yu et al. 1996). All three insect resistance QTLs detected in this study were on LGs which also contain resistance gene analogs (Kanazin et al. 1996).

Discussion

Genetic mapping with molecular markers enables a comparison of soybean PRI QTLs with other soybean pest resistance QTLs. Insect resistance QTLs can also be compared across legume species through comparative mapping. If borne out, these comparisons can give insight into possible relationships between pest resistance QTLs.

Insect resistance in soybean has two components: antibiosis and antixenosis. Bioassays can be designed to study these components separately. While the QTLs in this study are associated with antixenosis, QTLs for antibiosis are also being sought (experiments in progress). If independent QTLs for each of these components are found, it would suggest independent biochemical modes of action for antibiosis and antixenosis. It would also allow plant breeders to select for both components through marker-assisted selection.

The corn earworm was used in this study because of availability, low cost, and amenability to experimental use. However, previous work (All et al. 1989; Rowan et al. 1991) indicates that soybean resistance to corn earworm is highly correlated with resistance to other soybean defoliators, including the soybean looper (*Pseudoplusia includens*). Thus, introgression of the PRI QTLs identified in this study should provide resistance to a number of defoliating insect pests.

This study is concerned with PRI derived from PI229358. Lambert and Kilen (1984 b) suggested that there are likely to be further novel insect resistance QTLs in the other two major soybean insect resistance sources, PI171451 and PI227687. If this is true, soybean breeders may be able to combine QTLs from all three sources into highly resistant genotypes. Until now, the polygenic nature of insect resistance, the linkage drag associated with these genes, and perhaps the lack of simultaneous selection for both antibiosis and antixenosis, have largely prevented the successful exploitation of PRI in a soybean breeding program. With the availability of molecular markers, it is becoming possible to capitalize on the full potential of these three plant introductions as sources of insect resistance.

In this study we have been able to successfully interval map one major and two minor QTLs associated with PRI in PI229358 and determine their locations on the public soybean genetic linkage map. Our results have confirmed previous gene number estimates for PRI in soybean. The markers associated with insect resistance in this study should allow soybean breeders to utilize marker-assisted selection for PRI.

Acknowledgements The authors thank Dale Wood, Clay Stephens, Gina Rowan, Barbara Stewart, and Berry Tanner for technical assistance. This research was supported by funds allocated by the Georgia Agricultural Experiment Stations and grants from the United Soybean Board and the University of Georgia Biotechnology Research Fund.

References

All JN, Boerma HR, Todd JW (1989) Screening soybean genotypes in the greenhouse for resistance to insects. Crop Sci 29:1156–1159

Beach RM, Todd JW, Baker SH (1985) Antibiosis of four insect-resistant soybean genotypes to the soybean looper. Environ Entomol 14:531–534

Bonierbale MW, Plaisted RL, Pineda O, Tanksley SD (1994) QTL analysis of trichome-mediated insect resistance in potato. Theor Appl Genet 87:973–987

Boutin SR, Young ND, Olson TC, Yu ZH, Shoemaker RC, Vallejos CE (1995) Genome conservation among three legume genera detected with DNA markers. Genome 38:928–937

Brummer EC, Graef GL, Orf J, Wilcox JR, Shoemaker RC (1997) Mapping QTLs for seed protein and oil content in eight soybean populations. Crop Sci 37:370–378

Concibido VC, Denny RL, Lange DA, Orf JH, Young ND (1996) RFLP mapping and marker-assisted selection of soybean cyst nematode resistance in PI209332. Crop Sci 36:1643–1650

Diers BW, Keim P, Fehr WR, Shoemaker RC (1992 a) RFLP analysis of soybean seed protein and oil content. Theor Appl Genet 83:608–612

Diers BW, Mansur L, Imsande J, Shoemaker RC (1992 b) Mapping *Phytophthora* resistance loci in soybean with restriction fragment length polymorphism markers. Crop Sci 32:377–383

Fehr WR, Caviness CE (1977) Stages of soybean development. Iowa Coop Ext Serv Spec Rep 80

Hanthorne M, Osteen C, McDowell R, Robertson L (1982) 1980 Pesticide use on soybeans in the major producing states. AGES 820106 USDA-ARS Washington, D.C.

Hnetkovsky N, Chang SJC, Doubler TW, Gibson PT, Lighfoot DA (1996) Genetic mapping of loci underlying field-resistance to soybean sudden-death syndrome (SDS). Crop Sci 36:393–400

Kanazin V, Marek LF, Shoemaker RC (1996) Resistance gene analogs are conserved and clustered in soybean. Proc Natl Acad Sci USA 93:11746–11750

Kenty MM, Hinson K, Quesenberry KH, Wofford DS (1996) Inheritance of resistance to the soybean looper in soybean. Crop Sci 36:1532–1537

Keim P, Diers BW, Shoemaker RC (1990) Genetic analysis of soybean hard seededness with molecular markers. Theor Appl Genet 79:465–469

Kogan M, Ortman EE (1978) Antixenosis – a new term proposed to replace Painter's 'Nonpreference' modality of resistance. Bull Ent Soc Am 24:175–176

Lambert L, Kilen TC (1984 a) Insect resistance factor in soybean PI227687 and PI229358 demonstrated by grafting. Crop Sci 24:163–165

Lambert L, Kilen TC (1984 b) Multiple insect resistance in several soybean genotypes. Crop Sci 24:887–890

Lander ES, Botstein D (1989) Mapping Mendelian factors underlying quantitative traits using RFLP linkage maps. Genetics 121:185–199

Lander ES, Green P, Abrahamson J, Barlow A, Daly MJ, Lincoln SE, Newburg L (1987) MAPMAKER: an interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. Genomics 1:174–181

Lee SH, Bailey MA, Mian MAR, Carter TE, Ashley DA, Hussey RS, Parrott WA, Boerma HR (1996 a) Molecular markers associated with soybean plant height, lodging, and maturity across locations. Crop Sci 36:728–735

Lee SH, Bailey MA, Mian MAR, Shipe ER, Ashley DA, Parrott WA, Hussey RS, Boerma HR (1996 b) Identification of quantitative trait loci for plant height, lodging, and maturity in a soybean population segregating for growth habit. Theor Appl Genet 92:516–523

Lee SH, Bailey MA, Mian MAR, Carter TE, Shipe ER, Ashley DA, Parrott WA, Hussey RS, Boerma HR (1996 c) RFLP loci associated with soybean seed protein and oil content across populations and locations. Theor Appl Genet 93:649–657

Lincoln S, Daly M, Lander E (1992) Mapping genes controlling quantitative traits with MAPMAKER/QTL. Whitehead Institute Tech Rep, 2nd edn, [E1], Cambridge, MA

Lohnes DG, Schmitthenner AF (1997) Position of the *Phytophthora* resistance gene *Rps 7* on the soybean molecular map. Crop Sci 37:555–556

Luedders VD, Dickerson WA (1977) Resistance of selected soybean genotypes and segregating populations to cabbage looper feeding. Crop Sci 17:395–396

Maliepaard C, Bas N, van Heusden S, Kos J, Pet G, Verkerk R, Vrielink R, Zabel P, Lindhout P (1995) Mapping of QTLs for glandular trichome densities and *Trialeurodes vaporarium* (greenhouse whitefly) resistance in an F_2 from *Lycopersicon esculentum* × *Lycopersicon hirsutum* f. *glabratum*. Heredity 75:425–433

Maughan PJ, Saghai Maroof MA, Buss GR (1996) Molecular-marker analysis of seed-weight: genomic locations, gene action, and evidence for orthologous evolution among three legume species. Theor Appl Genet 93:574–579

McPherson RM, Douce GK (1992) Summary of losses from insect damage and costs of control in Georgia, 1991. Georgia Agricultural Experiment Stations, College of Agricultural and Environmental Sciences, University of Georgia, special publication no. 81

Menancio-Hautea D, Fatokun CA, Kumar L, Danesh D, Young ND (1993) Comparative genome analysis of mungbean (*Vigna radiata* L. Wilczek) and cowpea (*V. unguiculata* L. Walpers) using RFLP mapping data. Theor Appl Genet 86:797–810

Mian MAR, Bailey MA, Ashley DA, Wells R, Carter TE, Parrott WA, Boerma HR (1996 a) Molecular markers associated with water-use efficiency and leaf ash in soybean. Crop Sci 36:1252–1257

Mian MAR, Bailey MA, Tamulonis JP, Shipe ER, Carter TE, Parrott WA, Ashley DA, Hussey RS, Boerma HR (1996 b) Molecular markers associated with seed weight in two soybean populations. Theor Appl Genet 93:1011–1016

Mian MAR, Shipe ER, Alvaernaz J, Mueller JD, Ashley DA, Boerma HR (1996 c) RFLP analysis of Chlorimuron Ethyl sensitivity in soybean. J Hered 88:38:41

Myers GO, Fatokun CA, Young ND (1996) RFLP mapping of an aphid resistance gene in cowpea (*Vigna unguiculata* L. Walp) Euphytica 91:181–187

Painter RH (1951) Insect resistance in crop plants. Macmillan and Co., New York, USA

Rowan GB, Boerma HR, All JN, Todd J (1991) Soybean cultivar resistance to de-foliating insects. Crop Sci 31:678–682

Rufener GK, St. Martin SK, Cooper RL, Hammond RB (1989) Genetics of antibiosis resistance to Mexican bean beetle in soybean. Crop Sci 29:618–622

SAS (1988) SAS/STAT User's Guide version 6.03. SAS Institute, Cary, North Carolina, USA

Schon CC, Lee M, Melchinger AE, Guthrie WD, Woodman WL (1993) Mapping and characterization of quantitative trait loci affecting resistance against second-generation European corn borer in maize with the aid of RFLPs. Heredity 70:648–659

Shoemaker RC, Specht JE (1995) Integration of the soybean molecular and classical genetic linkage maps. Crop Sci 35:436–446

Shoemaker RC, Polzin K, Labate J, Specht J, Brummer EC, Olson T, Young N, Concibido V, Wilcox J, Tamulonis JP, Kochert G, Boerma HR (1996) Genome duplication in soybean (*Glycine* subgenus *Soja*). Genetics 144:329–338

Sisson VA, Miller PA, Campbell WV, Van Duyn JW (1976) Evidence of inheritance of resistance to the mexican bean beetle in soybeans. Crop Sci 16:835–837

Tamulonis JP, Luzzi BM, Hussey RS, Parrott WA, Boerma HR (1997) RFLP mapping of resistance to southern root-knot nematode in soybean. Crop Sci 37:1903–1909

Van Duyn JW, Turnipseed SG, Maxwell JD (1971) Resistance in soybean to the Mexican bean beetle. Crop Sci 11:572–573

Vierling RA, Faghihi J, Ferris VR, Ferris JM (1996) Association of RFLP markers with loci conferring broad-based resistance to the soybean cyst nematode (*Heterodera glycines*). Theor Appl Genet 92:83–86

Webb DM, Baltazar BM, Rao-Arelli AP, Schupp J, Clayton K, Keim P, Beavis WD (1995) Genetic mapping of soybean cyst nematode race-3 resistance loci in the soybean PI437.654. Theor Appl Genet 91:574–581

Wiseman BR, Davis FM, Campbell JE (1980) Mechanical infestation device used in fall armyworm plant resistance programs. Fla Entomol 63:425–438

Yencho GC, Bonierbale MW, Tingey WM, Plaisted RL, Tanksley SD (1996) Molecular markers locate genes for resistance to the Colorado potato beetle, *Leptinotarsa decemlineata*, in hybrid *Solanum tuberosum* × *S. berthaultii* potato progenies. Entomol Exp Appl 81:141–154

Young ND, Tanksley SD (1989) RFLP maps and the concept of graphical genotypes. Theor Appl Genet 77:95–101

Young ND, Kumar L, Menancio-Hautea D, Danesh D, Talekar NS, Shanmugasundarum S, Kim DH (1992) RFLP mapping of a major bruchid resistance gene in mungbean. Theor Appl Genet 84:839–844

Yu YG, Saghai Maroof MA, Buss GR, Maughan PJ, Tolin SA (1994) RFLP and microsatellite mapping of a gene for soybean mosaic-virus resistance. Phytopathology 84:60–64

Yu YG, Buss GR, Saghai Maroof MA (1996) Isolation of a superfamily of candidate disease-resistance genes in soybean based on a conserved nucleotide-binding site. Proc Natl Acad Sci USA 93:11751–11756