

Genetic Resistance to Reniform Nematodes in Soybeans

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ABSTRACT

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A study was conducted to determine the number of genes by which four soybean (*Glycine max*) cultivars differ for resistance to the reniform nematode *Rotylenchulus reniformis*. The cultivars Davis, Bragg, Dare, and Pickett 71 are classified as susceptible, moderately susceptible, moderately resistant, and resistant, respectively. Four F₁ soybean populations had mean egg mass ratings that did not differ from those of their respective susceptible parents. Resistance to the reniform nematode in soybeans is concluded to be quantitative in nature and controlled by two pairs of genes with unequal effects. The proposed genotypes of the four parental cultivars were Davis $Rn_1 Rn_1 Rn_2 Rn_2$, Bragg $Rn_1 Rn_1 rn_2 rn_2$, Dare $rn_1 rn_1 Rn_2 Rn_2$, and Pickett 71 $rn_1 rn_1 rn_2 rn_2$.

The reinform nematode (RN) *Rotylenchulus reniformis* (Linford & Oliveira) was described in 1940 on cowpea (*Vigna sinensis* L.) in Hawaii (8). More than 80 host plants have been identified, including soybean (*Glycine max* (L.) Merr.) (9,11). The RN, which is most severe on susceptible host plants grown in fine-textured clay and silt loam soils (1), has been reported in Alabama, Georgia, Louisiana, South Carolina, and Texas (2-4,10,13).

The economic value of soybeans infested with RN is lowered because of reduced seed yield and phosphorous content of the seeds (12). The nematode may also predispose soybean plants to other diseases by opening entry points for pathogenic fungi (7).

The RN is normally controlled by use of resistant cultivars, nematicides, and crop rotation. Since nematicides and/or crop rotation are usually not economical in soybeans, genetic resistance is the most desirable control method.

Although highly resistant cultivars are available, information on the genetic basis of resistance is incomplete. According to Fontenot (5), at least one major gene is involved, with susceptibility being dominant to resistance.

The objective of this study was to determine the number of genes controlling the differential reactions of four soybean cultivars to RN.

MATERIALS AND METHODS

The soybean cultivars Bragg, Dare, Davis, and Pickett 71 were chosen as parents for a genetic study on the basics of their reactions to the RN under field and greenhouse conditions: Davis is susceptible, Pickett 71 is resistant, and Dare and Bragg are moderately resistant (6). Crosses were made between Davis and Pickett 71, Dare and Bragg, Dare and Pickett 71, and Bragg and Pickett 71. The first-mentioned cultivar was always the maternal parent.

RN-infested soil was collected from Burden Research Farm, Baton Rouge, LA. Nematodes in the soil were counted using the procedure described by Fontenot (5). A minimal soil population of 14,000 nematode larvae per liter was used. Seed were planted 2.5 cm deep in 7.5-cm-diameter plastic pots of infected

soil. The pots were placed on a layer of sand on greenhouse benches in a completely randomized design, with each pot of one seed representing an experimental unit.

Thirty days after planting, the plants were removed from the soil and gently washed. Each plant was rated for RN on a scale of 0-6, where 0 = 0% of roots bearing egg masses, 1 = 1-10%, 2 = 11-20%, 3 = 21-30%, 4 = 31-40%, 5 = 41-50%, and 6 = 51-100%.

In the first experiment, commercial seed of the parental cultivars were planted and roots were rated using the scale of 0-6. Five other experiments, each consisting of parental, F₁, and F₂ seed of a particular cross, were planted on separate dates and rated for RN. In the last experiment, 100 pots each of Dare and Bragg were planted in a completely randomized design and rated for RN.

Differences among sample means of each cultivar were analyzed by *t* tests. Results from experiments 2-6 were analyzed with chi-square goodness-of-fit tests. Data from experiment 7 were analyzed with analysis of variance.

RESULTS AND DISCUSSION

Comparisons of parental cultivars tested in the first experiment are shown in Table 1. Mean egg mass ratings were 5.09 and 1.67 for Davis and Pickett 71, respectively. Results showed Davis susceptible and Pickett 71 resistant to the RN, which supports previous findings (6). Dare and Bragg were intermediate in their reactions to the nematode. The *t* tests showed all parental means to be

Table 1. Reniform nematode ratings of four soybean cultivars

Cultivar	No. of plants	Classification	Rating mean ^y
Davis	57	Susceptible	5.09 a ^z
Bragg	84	Moderately susceptible	4.34 b
Dare	85	Moderately resistant	3.61 c
Pickett 71	42	Resistant	1.67 d

^y Rating on a scale of 0-6, where 0 = 0%, 1 = 1-10%, 2 = 11-20%, 3 = 21-30%, 4 = 31-40%, 5 = 41-50%, and 6 = 51-100% of roots bearing egg masses.

^z Means followed by different letters are significantly ($P = 0.05$) different by a *t* test.

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Table 2. Classification of parental, F₁, and F₂ plants from all crosses according to their reactions to the reniform nematode

Cross ^a	Parent or generation	No. of plants per egg mass rating ^b						Total no. of plants	Rating mean	SD	C.V.	
		0	1	2	3	4	5					6
Dare (MR) × Bragg (MS)	Dare	0	0	0	0	2	1	2	5	5.00	2.00	40.00
	Bragg	0	0	0	1	3	0	1	5	4.20	2.19	52.14
	F ₁	0	0	0	1	19	21	4	45	4.62	0.68	14.79
	F ₂	2	8	22	38	30	24	7	131	3.42	1.36	39.56
Dare (MR) × Pickett 71 (R)	Dare	0	0	1	1	2	1	0	5	3.60	2.28	63.33
	Pickett 71	1	2	2	0	0	0	0	5	1.20	1.67	139.23
	F ₁	0	3	12	16	14	1	0	46	2.96	0.97	32.64
	F ₂	6	8	29	35	21	9	4	112	2.89	1.36	47.17
Bragg (MS) × Pickett 71 (R)	Bragg	0	0	3	7	2	1	0	13	3.08	1.59	51.60
	Pickett 71	1	5	3	0	0	0	0	9	1.22	1.00	81.90
	F ₁	0	0	3	9	11	1	0	24	3.42	0.78	22.70
	F ₂	1	15	30	72	60	19	0	197	3.18	1.08	33.93
Davis (S) × Pickett 71 (R)	Davis	0	0	0	0	7	12	18	37	5.30	1.66	31.13
	Pickett 71	1	7	9	1	0	0	0	18	1.56	0.91	58.00
	F ₁	0	0	0	0	10	20	19	49	5.18	0.75	14.56
	F ₂	0	3	10	25	29	21	1	89	3.50	1.06	30.16

^a MR = moderately resistant, MS = moderately susceptible, R = resistant, and S = susceptible.

^b Rating on a scale of 0–6, where 0 = 0%, 1 = 1–10%, 2 = 11–20%, 3 = 21–30%, 4 = 31–40%, 5 = 41–50%, and 6 = 51–100% of roots bearing egg masses.

Table 3. Chi-square test of fit of F₂ segregation ratios from four crosses

Cross	Classification ^a	Observed	Expected	Rating mean	P
Dare × Bragg	Resistant (0–2)	32	25	2.77	0.538
	Susceptible (3–6)	99	106		
Dare × Pickett 71	Resistant (0–2)	43	28	1.05	0.306
	Susceptible (3–6)	88	84		
Bragg × Pickett 71	Resistant (0–2)	46	49	0.28	0.597
	Susceptible (3–6)	151	148		
Davis × Pickett 71	Resistant (0–2)	13	17	0.04	0.842
	Susceptible (3–6)	76	72		

^a Rating on a scale of 0–6, where 0 = 0%, 1 = 1–10%, 2 = 11–20%, 3 = 21–30%, 4 = 31–40%, 5 = 41–50%, and 6 = 51–100% of roots bearing egg masses.

significantly different.

Since the Dare and Bragg means indicated a significant difference between their reactions to RN, they were retested. In this experiment, Dare and Bragg had mean ratings of 3.86 and 4.63, respectively, which were significantly different. They were reclassified as moderately susceptible (Bragg) and moderately resistant (Dare) in this study.

The F₁ population of the Dare × Bragg cross was strongly skewed toward susceptibility and was similar in mean and distribution to both parents (Table 2). There was no evidence of escapes among the F₁ and parental plants. Distribution of parent and F₁ plants was in ratings 3–6, with most plants in ratings 4 and 5. The 131 F₂ plants showed continuous type distribution with ratings from 0 to 6 and some skewness toward susceptibility. Thirty-two F₂ plants were rated more resistant than rating 3; 10 of those plants were rated 0 or 1. The lack of escapes among F₁ and parent plants and the large number of F₂ plants in resistant ratings from 0 to 2 provide strong evidence for transgressive segregation and suggest that the parents were homozygous for resistant genes at different loci. Using two categories of ratings (0–2 = resistant and 3–6 = susceptible) and testing for a 13:3 ratio, a nonsignificant chi-square value of 2.77 was obtained. This fits a two-gene model,

assuming complete dominance for susceptibility at one locus and absence of dominance at the other.

The Dare × Pickett 71 cross indicated a slight overlapping of parent plants; one plant of Dare had a rating of 2 (Table 2). Ratings of 46 F₁ plants ranged from 1 to 5. The F₁ population was intermediate between the parents in distribution and had a mean slightly skewed toward the susceptible parent. The F₂ population had a normal bell shape and continuous type distribution with a mean and distribution intermediate between those of the parents (Table 2). If we assume plants with ratings of 0–2 to be homozygous resistant and correct for the heterozygous plants that also fall into their range (indicated by the F₁ population), the adjusted F₂ population closely fits a single-gene model with partial dominance for susceptibility (Table 3).

A slight overlapping of the parent plants occurred in the Bragg × Pickett 71 cross (Table 3). Three of 13 Bragg plants were rated 2; others were rated from 3 to 5. All plants of Pickett 71 were rated from 0 to 2. Ratings of the 24 F₁ plants ranged from 2 to 5 with a mode of 4 and a mean of 3.42, showing complete dominance for susceptibility. The F₂ population had a mean of 3.18 and a continuous type distribution from 0 to 5 that was distinctly skewed toward the more

susceptible parent. Considering ratings of 0–2 as resistant and 3–6 as susceptible, the observed ratio of 46:151 closely fits that for a one-gene model (Table 3).

The Davis × Pickett 71 cross represented the widest difference of the parents studied (Table 3). Ratings of the 37 Davis plants ranged from 4 to 6 with a mean of 5.30. The Pickett 71 parent ranged from 0 to 3 with a mean of 1.56; most plants were rated 1 or 2. The F₁ showed nearly identical distribution of plants and population mean to the Davis parent, thus showing complete dominance for susceptibility. Distribution of F₂ plants was continuous and symmetrical from ratings 1–6 with a mean of 3.5, about intermediate between the parents. If as in previous crosses the resistant rating is accepted as 0–2 and susceptible as 3–6, the distribution of F₂ plants (13:76) approach that of a 3:13 ratio. This is in agreement with a two-gene model in which complete dominance is expressed at one locus and absence of dominance is expressed at the other.

Data from the Dare × Bragg, Dare × Pickett 71, Bragg × Pickett 71, and Dare × Pickett 71 crosses combined with the parent evaluation studies suggest that the parents differ at two loci that have unequal effects. The proposed genotypes for the four parental cultivars are Davis *Rn₁ Rn₁ Rn₂ Rn₂*, Bragg *Rn₁ Rn₁ rn₂ rn₂*, Dare *rn₁ rn₁ Rn₂ Rn₂*, and Pickett 71 *rn₁ rn₁ rn₂ rn₂*. The *rn₁ rn₁* gene has a slightly stronger effect on resistance than the *rn₂ rn₂* gene and shows additive gene action, whereas the *rn₂ rn₂* gene shows complete recessiveness. The F₂ population of all crosses showed a continuous type distribution similar to that expected for a quantitative trait. Pickett 71 resistance to the RN in soybeans is concluded to be quantitative in nature and controlled by two pairs of genes with unequal effects; one pair showing complete recessiveness, the other pair showing absence of dominance. If the above assumptions are

true, homozygous resistant plants similar in genotype to Pickett 71 should be obtainable from the Bragg × Dare cross. This hypothesis will be tested in a later study.

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