

Inheritance of Resistance to *Phytophthora megasperma* f. sp. *glycinea* in a Soybean Plant Introduction

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ABSTRACT

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Inheritance of resistance to *Phytophthora megasperma* f. sp. *glycinea* was studied in a soybean (*Glycine max*) plant introduction (PI 157409) that was resistant to races 1 through 16 of the fungus. PI 157409 was crossed with Harosoy, Mukden, Sanga, PI 54615-1, Williams 82, PI 86972-1, and PRX27-108. The F₂ populations and the F₃ families of each cross were inoculated with races 1, 2, 3, 4, 5, 7, and 9 of the fungus. PI 157409 had two genes for resistance: *Rps*₁^b, which gives resistance to races 1, 3, 4, 5, 7, and 9 and susceptibility to race 2; and *Rps*₄, which gives resistance to races 1, 2, 3, and 4 and susceptibility to races 5, 7, and 9. This is the first soybean strain in which the gene combination *Rps*₁^b*Rps*₄ has been reported. The combination is useful because the genes *Rps*₁^b*Rps*₄ confer resistance to all reported races, 1 through 22, of *P. megasperma* f. sp. *glycinea*.

Nine major dominant genes for resistance to *Phytophthora megasperma* Drechs. f. sp. *glycinea* Kuan & Erwin (9) (syn. *P. megasperma* Drechs. var. *sojae* Hildeb.) have been reported in soybean (*Glycine max* (L.) Merr.). Four of these genes are allelic: *Rps*₁ from Mukden (5); *Rps*₁^b from D60-9647 (7), PI 84637 (11), or Sanga (*unpublished*) (from intercrossing Sanga, PI 84637, and D60-9647); *Rps*₁^c from Arksoy (11) or PI 54615-1 (11); and *Rps*₁^k from Kingwa (4).

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MATERIALS AND METHODS

The soybean cultivars and plant introductions Harosoy, Mukden, Sanga, PI 54615-1, Williams 82, PI 86972-1, and PRX27-108 were selected as parents because of their known genotype and their reactions to races 1 through 9 of the fungus (10). Harosoy has the *rps* gene and is susceptible to all nine races. Mukden contains *Rps*₁ and is resistant to races 1 and 2 and is susceptible to races 3, 4, 5, 7, and 9. Sanga has the *Rps*₁^b gene, which confers resistance to races 1, 3, 4, 5, 7, and 9 and susceptibility to race 2. PI 54615-1 contains *Rps*₁^c and is resistant to races 1, 2, 3, 7, and 9 and susceptible to races 4 and 5. Williams 82 has the *Rps*₁^k gene, which gives resistance to races 1 through 9. PI 86972-1 has the gene *Rps*₃ and is resistant to races 1, 2, 3, 4, 5, and 9 and susceptible to race 7. PRX27-108 contains *Rps*₄ and is resistant to races 1, 2, 3, and 4 and susceptible to races 5, 7, and 9.

Between 73 and 270 F₂ seedlings from each cross were tested with races 1, 2, 3, 4, 5, 7, and 9. Races 6 and 8 were not used because race 6 is no longer available and race 8 would give the same results as race 9. About 12 F₃ seedlings from as many as 100 F₂ plants were tested with the same seven races to verify the segregation ratios obtained in the F₂ populations. The progenies of only 25 F₂ plants were tested if the F₂ population was completely resistant. If the F₂ population segregated in a ratio of three resistant to one susceptible, the progenies from 60 F₂ plants were evaluated. The progenies

*Rps*₂ was found in the cultivar CNS and derived strains using root inoculations with races 1 and 2 (8). *Rps*₃ was found in PI 86972-1 (11) and in combination with *Rps*₁^b in Tracy (2). *Rps*₄ was reported in combination with *Rps*₁^c in PI 86050 (3) and is in PRX27-108 (*unpublished*) (selection from the cross of Mukden × PI 86050). In 1981, *Rps*₅ was reported from L62-904 (6), and in 1982, *Rps*₆ was reported in Altona (1). Athow and Laviolette in 1979 (*unpublished*) identified seven plant introductions that were resistant to the then known 16 physiologic races. To determine the inheritance of resistance in one of these plant introductions, 157409, it was crossed to Harosoy (*rps*), Mukden (*Rps*₁), Sanga (*Rps*₁^b), PI 54615-1 (*Rps*₁^c), Williams 82 (*Rps*₁^k), PI 86972-1 (*Rps*₃), and PRX27-108 (*Rps*₄). The results of inoculating the F₂ populations and the progenies from the F₂ plants from each cross with races 1, 2, 3, 4, 5, 7, and 9 are reported in this paper.

from 100 F₂ plants were tested if the F₂ population segregated in a ratio of 15 resistant to one susceptible or in a ratio of 63 resistant to one susceptible. Different progenies from the same F₂ plants were tested with each race.

The same isolate of each race was used throughout the study. Inoculum from each isolate was grown on oatmeal agar in petri plates at 22–24 C for 2–3 wk. Seedlings were grown in the greenhouse

at 24–27 C and inoculated in the greenhouse when they were 10 days old. Inoculations were done by the hypocotyl method, which consists of inserting pieces (2 × 2 mm) of inoculum in a longitudinal slit and covering with petroleum jelly to prevent desiccation of the host tissue and inoculum. Six days after inoculation, the seedlings were classified as resistant (no external symptoms) or susceptible (dead). The data were analyzed by the

chi-square test for goodness of fit to expected ratios.

RESULTS AND DISCUSSION

The F₂ population from the cross of Harosoy (*rps*) with PI 157409 segregated in a ratio of about 15 resistant to one susceptible to races 1, 3, and 4, indicating two genes for resistance to each of these races in PI 157409 (Table 1). The F₂ population from this cross segregated in a ratio of about three resistant to one susceptible to races 2, 5, 7, and 9, indicating a single dominant gene for resistance to these races in PI 157409. The chi-square value of 11.7813 for race 2 indicated a significant deviation from the expected ratio of three resistant to one susceptible. The deviation was actually only 11 excess susceptible plants. Inoculation with race 2 was repeated on 235 additional plants with precisely the same results, chi-square of 11.2355 (Table 1).

The F₂ population from the cross of Mukden (*Rps*₁) with PI 157409 segregated in a ratio of 15 resistant to one susceptible for races 2, 3, and 4 and in a ratio of three resistant to one susceptible to races 5, 7, and 9. These results substantiated the results from the previous cross, which indicated a single dominant gene for resistance to races 5, 7, and 9 and two genes for resistance to races 3 and 4 in PI 157409. The F₂ population was completely resistant to race 1, indicating that one gene in PI 157409 was allelic to *Rps*₁ from Mukden, but it was not *Rps*₁ or the F₂ population would have been resistant to race 2. This indicated that the gene in PI 157409, which was allelic to *Rps*₁, was *Rps*₁^b because *Rps*₁^b conditions susceptibility to race 2.

In the cross of Sanga (*Rps*₁^b) with PI 157409, the F₂ population segregated in a ratio of three resistant to one susceptible to race 2 (Table 1). This was compatible with the results in the previous crosses, which indicated a single dominant gene for resistance to race 2 in PI 157409. The F₂ population was resistant to races 1, 3, 4, 5, 7, and 9, indicating the other gene in PI 157409 was allelic to *Rps*₁^b. The allelic gene in PI 157409 could be *Rps*₁^b because both it and *Rps*₁^b from Sanga condition susceptibility to race 2.

The F₂ population from the cross of PI 54615-1 (*Rps*₁^c) with PI 157409 was resistant to races 1, 3, 7, and 9 (Table 1), indicating that one of the genes in PI 157409 was an allele of *Rps*₁^c. The F₂ population segregated in a ratio of 15 resistant to one susceptible to races 2 and 4 and in a ratio of three resistant to one susceptible to race 5. This indicated two genes for resistance to race 4 and one gene for resistance to race 5 in PI 157409 because *Rps*₁^c from PI 54615-1 gives susceptibility to races 4 and 5. This also showed that the gene in PI 157409, which was at the *Rps*₁ locus, was not *Rps*₁^c.

In the cross of Williams 82 (*Rps*₁^k) with PI 157409, the F₂ population was

Table 1. Segregation of F₂ populations from crosses of PI 157409 with Harosoy, Mukden, Sanga, PI 54615-1, Williams 82, PI 86972-1, and PRX27-108 inoculated with seven physiologic races of *Phytophthora megasperma* f. sp. *glycinea*

Parentage and gene	Race	Number of plants ^a			Ratio ^b	X ²	P
		Total	R	S			
PI 157409							
× Harosoy (<i>rps</i>)	1	266	243	23	15:1	2.6075	0.20–0.10
	2	250	164	86	3:1	11.7813	<0.01
		235	154	81	3:1	11.2355	<0.01
	3	260	248	12	15:1	1.1856	0.20–0.10
	4	270	246	24	15:1	3.2089	0.10–0.05
	5	217	166	51	3:1	0.2596	0.70–0.50
	7	262	198	64	3:1	0.0458	0.90–0.80
	9	226	172	54	3:1	0.1475	0.80–0.70
Mukden (<i>Rps</i> ₁)							
× PI 157409	1	247	247	0	R
	2	147	140	7	15:1	0.5555	0.50–0.30
	3	73	70	3	15:1	0.5708	0.50–0.30
	4	214	201	13	15:1	0.0112	0.95–0.90
	5	82	57	25	3:1	1.3171	0.30–0.20
	7	203	160	43	3:1	1.5779	0.30–0.20
	9	82	61	21	3:1	0.0163	0.90–0.80
PI 157409							
× Sanga (<i>Rps</i> ₁ ^b)	1	254	254	0	R
	2	240	177	63	3:1	0.2000	0.70–0.50
	3	127	127	0	R
	4	251	251	0	R
	5	167	167	0	R
	7	209	209	0	R
	9	224	224	0	R
PI 157409							
× 54615-1 (<i>Rps</i> ₁ ^c)	1	224	224	0	R
	2	232	218	14	15:1	0.0184	0.90–0.80
	3	148	148	0	R
	4	217	199	18	15:1	1.5487	0.30–0.20
	5	217	168	49	3:1	0.6674	0.50–0.30
	7	247	247	0	R
	9	232	232	0	R
Williams 82 (<i>Rps</i> ₁ ^k)							
× PI 157409	1	248	248	0	R
	2	247	228	19	15:1	0.8769	0.50–0.30
	3	146	146	0	R
	4	265	265	0	R
	5	248	248	0	R
	7	214	214	0	R
	9	221	221	0	R
PI 157409							
× PI 86972-1 (<i>Rps</i> ₃)	1	258	252	6	63:1	0.9767	0.50–0.30
	2	258	234	24	15:1	4.1023	0.05–0.02
	3	201	195	6	63:1	2.6446	0.20–0.10
	4	259	252	7	63:1	2.1892	0.20–0.10
	5	223	210	13	15:1	0.0673	0.80–0.70
	7	259	190	69	3:1	0.3719	0.70–0.50
	9	225	205	20	15:1	2.6740	0.20–0.10
PRX27-108 (<i>Rps</i> ₄)							
× PI 157409	1	256	256	0	R
	2	253	253	0	R
	3	189	189	0	R
	4	254	254	0	R
	5	267	198	69	3:1	0.1011	0.80–0.70
	7	247	181	66	3:1	0.3900	0.70–0.50
	9	241	170	71	3:1	2.5574	0.20–0.10

^aR = resistant and S = susceptible.

^bRatio = resistant to susceptible and R = resistant.

resistant to races 1, 3, 4, 5, 7, and 9 (Table 1), indicating that one of the genes in PI 157409 was an allele of *Rps1^k* from Williams 82. The segregation ratio of 15 resistant to one susceptible in the F₂ population to race 2 indicated that the allele in PI 157409 was not *Rps1^k* because *Rps1^k* gives resistance to races 1 through 9. This is additional proof that one gene in PI 157409 is *Rps1^b*, because of the four genes (*Rps1^a*, *Rps1^b*, *Rps1^c*, and *Rps1^k*) described at the *Rps1* locus, only *Rps1^b* does not condition resistance to race 2.

The F₂ population from the cross of PI 86972-1 (*Rps3*) with PI 157409 segregated in a ratio of three resistant to one susceptible to race 7 (Table 1). This single gene for resistance to race 7 was probably *Rps1^b* because *Rps3* from PI 86972-1 gives susceptibility to race 7. The F₂ population segregated in a ratio of 15 resistant to one susceptible to races 2, 5, and 9 and in a ratio of 63 resistant to one susceptible to races 1, 3, and 4. These results indicate that the two genes in PI 157409 segregate independently of *Rps3* from PI 86972-1, which gives resistance to races 1, 2, 3, 4, 5, and 9. The two genes for resistance to races 5 and 9 were *Rps3* from PI 86972-1 and *Rps1^b* from PI 157409. The two genes for resistance to race 2 were *Rps3* from PI 86972-1 and the gene other than *Rps1^b* from PI 157409. The three genes for resistance to races 1, 3, and 4 were *Rps3* from PI 86972-1 and the two genes from PI 157409, one of which was *Rps1^b*.

In the cross of PRX27-108 (*Rps4*) with PI 157409, the F₂ population segregated in a ratio of three resistant to one susceptible to races 5, 7, and 9. The single dominant resistant gene indicated was probably *Rps1^b* because *Rps4* from PRX27-108 gives susceptibility to races 5, 7, and 9, and the previous crosses suggested that the other gene in PI 157409 gives resistance to only races 1, 2, 3, and 4. The F₂ population was resistant to races 1, 2, 3, and 4, indicating the other gene in PI 157409 must be at the *Rps4* locus.

Results from the F₂ populations indicate PI 157409 contains two genes. One of these genes conditions resistance to races 1, 3, 4, 5, 7, and 9 and susceptibility to race 2. This gene is most probably *Rps1^b*. The other gene gave resistance to races 1, 2, 3, and 4 but susceptibility to races 5, 7, and 9. Both *Rps4* and *Rps6* would give the same disease reactions to these races. However, in the cross of PI 157409 with PRX27-108 (*Rps4*), the F₂ population was resistant when inoculated with races 1, 2, 3, and 4, indicating the other gene in PI 157409 is *Rps4*, not *Rps6*. Therefore, the data support the hypothesis that the genotype of PI 157409 is *Rps1^bRps4*.

The breeding behavior of the progenies from the F₂ plants in each cross (Table 2) verified the observed or expected segregation ratios in the F₂ populations (Table 1). In the cross of PI 157409 with

Harosoy inoculated with race 2, the F₂ population differed significantly from the expected ratio of three resistant to one susceptible. However, the F₂ plants as tested by their progenies (Table 2) showed 21 homozygous resistant to 49 heterozygous to 29 homozygous susceptible, indicating the F₂ population was in a ratio of three resistant to one susceptible and the deviation observed was probably the result of sampling error.

Only in the cross of Williams 82 with PI 157409 inoculated with race 2 was there a significant deviation in the segregation of F₃ families from the expected ratio of seven homozygous resistant to eight heterozygous to one homozygous susceptible. This was because of an apparent excess number of homozygous resistant F₃ families. It is not unexpected to have some error in either the homozygous resistant or heterozygous

Table 2. Breeding behavior of progenies from F₂ plants from crosses of PI 157409 with Harosoy, Mukden, Sanga, PI 54615-1, Williams 82, PI 86972-1, and PRX27-108 inoculated with seven physiologic races of *Phytophthora megasperma* f. sp. *glycinea*

Parentage and gene	Race	Number of F ₂ plants ^a				Ratio ^b	X ²	P	
		Total	R	Seg.	S				
PI 157409									
× Harosoy (<i>rps</i>)	1	100	47	50	3	7:8:1	1.9314	0.50-0.30	
	2	100	21	49	29	1:2:1	1.3000	0.70-0.50	
	3	100	47	50	3	7:8:1	1.9314	0.50-0.30	
	4	100	47	50	3	7:8:1	1.9314	0.50-0.30	
	5	60	18	34	8	1:2:1	4.4000	0.20-0.10	
	7	60	18	34	8	1:2:1	4.4000	0.20-0.10	
	9	60	18	34	8	1:2:1	4.4000	0.20-0.10	
	Mukden (<i>Rps1</i>)								
	× PI 157409	1	100	100	0	0	R
2		100	43	53	4	7:8:1	1.0029	0.70-0.50	
3		100	49	49	2	7:8:1	3.5400	0.20-0.10	
4		100	49	49	2	7:8:1	3.5400	0.20-0.10	
5		60	14	27	19	1:2:1	1.4333	0.50-0.30	
7		60	14	27	19	1:2:1	1.4333	0.50-0.30	
9		60	14	27	19	1:2:1	1.4333	0.50-0.30	
PI 157409									
× Sanga (<i>Rps1^b</i>)		1	100	100	0	0	R
	2	60	13	32	15	1:2:1	0.4000	0.90-0.80	
	3	25	25	0	0	R	
	4	25	25	0	0	R	
	5	25	25	0	0	R	
	7	25	25	0	0	R	
	9	25	25	0	0	R	
	PI 157409								
	× PI 54615-1 (<i>Rps1^c</i>)	1	100	100	0	0	R
2		100	50	43	7	7:8:1	1.9629	0.50-0.30	
3		25	25	0	0	R	
4		100	36	56	8	7:8:1	2.5829	0.30-0.20	
5		60	17	27	16	1:2:1	0.6333	0.80-0.70	
7		25	25	0	0	R	
9		25	25	0	0	R	
Williams 82 (<i>Rps1^k</i>)									
× PI 157409		1	100	100	0	0	R
	2	100	58	38	4	15:1*	0.8640	0.50-0.30	
	3	25	25	0	0	R	
	4	25	25	0	0	R	
	5	25	25	0	0	R	
	7	25	25	0	0	R	
	9	25	25	0	0	R	
	PI 157409								
	× PI 86972-1 (<i>Rps3</i>)	1	100	54	43	3	37:26:1	1.7128	0.50-0.30
2		100	47	46	7	7:8:1	0.6514	0.80-0.70	
3		100	54	43	3	37:26:1	1.7128	0.50-0.30	
4		100	54	43	3	37:26:1	1.7128	0.50-0.30	
5		100	48	41	11	7:8:1	5.6429	0.10-0.05	
7		100	20	47	33	1:2:1	2.6200	0.30-0.20	
9		100	48	41	11	7:8:1	5.6429	0.10-0.05	
PRX27-108 (<i>Rps4</i>)									
× PI 157409		1	100	100	0	0	R
	2	25	25	0	0	R	
	3	25	25	0	0	R	
	4	25	25	0	0	R	
	5	60	14	27	19	1:2:1	1.4333	0.50-0.30	
	7	60	14	27	19	1:2:1	1.4333	0.50-0.30	
	9	60	14	27	19	1:2:1	1.4333	0.50-0.30	

^a R = resistant, Seg. = segregating, and S = susceptible.

^b Ratio = resistant to susceptible and R = resistant. * = Combined resistant and segregating categories.

categories because of the small number of F₃ seedlings tested from each F₂ plant. When these two categories were grouped together, the result was a satisfactory fit to the expected ratio of 15 homozygous resistant or heterozygous to one homozygous susceptible.

PI 157409 is the first soybean strain in which the genes *Rps*₁^b and *Rps*₄ have been reported. This gene combination is useful because it confers resistance to all the reported races, 1 through 22, of *P. megasperma* f. sp. *glycinea*. F₂ plants with the combination *Rps*₁^b*Rps*₄ can be identified from the cross of PI 157409 with Harosoy by evaluating their progenies to races 2 and 7. Resistance to race 2 indicates the presence of *Rps*₄ and resistance to race 7 indicates the presence of *Rps*₁^b. Other two-gene combinations that can be identified from crosses with PI 157409 are *Rps*₁^b*Rps*₃, which is resistant to races 1 through 9, 11, 13 through 18, 21, and 22, *Rps*₁^b*Rps*₄, which

is resistant to races 1 through 4 and 6 through 21, and *Rps*₃*Rps*₄, which gives resistance to races 1 through 5, 8 through 16, and 18 through 21. Even though these combinations do not give resistance to all 22 races, they do give resistance to the races present in the Midwest and can be combined with other genes for additional resistance.

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