Genetics

A New Allele at the *Rps*$_3$ Locus for Resistance to *Phytophthora megasperma* f. sp. *glycinea* in Soybean

L. D. Ploper, K. L. Athow, and F. A. Laviolette

Graduate research assistant, professor, and associate professor, respectively, Department of Botany and Plant Pathology, Purdue University, West Lafayette, IN 47907.
Supported in part by the Indiana Crop Improvement Association and the American Soybean Association Research Grant ASARP 81543.
Journal Paper 10,065, Purdue University Agricultural Experiment Station.
Accepted for publication 23 January 1985 (submitted for electronic processing)

ABSTRACT

Ploper, L. D., Athow, K. L., and Laviolette, F. A. 1985. A new allele at the *Rps*$_3$ locus for resistance to *Phytophthora megasperma* f. sp. *glycinea* in soybean. Phytopathology 75:690-694.

The genetics of resistance to *Phytophthora megasperma* f. sp. *glycinea* was studied in soybean (*Glycine max*) PI 172901, which was resistant to races 1 through 16 of the pathogen. PI 172901 was crossed to Harosoy (*rps*), Mukden (*Rps*$_1$), Sanga (*Rps*$_1^b$), Wells II (*Rps*$_1^c$), Williams 82 (*Rps*$_1^k$), PI 86972-1 (*Rps*$_3$), PRX27-108 (*Rps*$_1$ *Rps*$_4$), and Altona (*Rps*$_6$). The F_2 populations and the progenies of F_2 plants from each cross were evaluated for their reaction to physiologic races 1, 2, 3, 4, 5, 7, and 9 of the fungus. The results showed that there were two independent, dominant genes for resistance in PI 172901. One was *Rps*$_1^b$ which gives resistance to races 1, 3, 4, 5, 7, and 9, and susceptibility to race 2. The other gene was an undescribed allele at the *Rps*$_3$ locus which confers resistance to the seven physiologic races included in this study. The symbol *Rps*$_3^b$ was proposed for this gene to indicate a second allele at the *Rps*$_3$ locus and to discriminate it from the gene *Rps*$_3$ which conditions susceptibility to race 7.

Resistance to Phytophthora root rot caused in soybean (*Glycine max* (L.) Merr.) by *Phytophthora megasperma* Drechs. f. sp. *glycinea* Kuan and Erwin (10) (syn. *P. megasperma* Drechs. var. *sojae* Hildeb.) was first reported in 1957 by Bernard et al (5). Since then, nine major dominant genes for resistance to this fungus have been reported. Four of these genes are allelic: *Rps*$_1$ from Mukden (5); *Rps*$_1^b$ from D60-9647 (7), PI 84637 (11) or Sanga; *Rps*$_1^c$ from Arksoy (11), PI 54615-1 (11), or Mack (9); and *Rps*$_1^k$ from Kingwa (4). Genes at other loci are: *Rps*$_2$ from cultivar CNS and derived strains (8); *Rps*$_3$ from PI 86972-1 (11), Tracy (3), and PI 171442 (9); *Rps*$_4$ in combination with *Rps*$_1^c$ from PI 86050 (2), and in combination with *Rps*$_1$ in PRX27-108 (*unpublished*, selection from the cross of Mukden × PI 86050); *Rps*$_5$ from L62-904 (6); and *Rps*$_6$ from Altona (1).

PI 172901 was among seven plant introductions which were found in 1979 to be resistant to the 16 physiologic races known at that time (Athow and Laviolette, *unpublished*). Layton et al (12) have reported on the inheritance of resistance in PI 157409, another of these seven plant introductions. To determine the genetics of resistance in PI 172901, it was crossed to Harosoy (*rps*), Mukden

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked "*advertisement*" in accordance with 18 U.S.C. § 1734 solely to indicate this fact.

(Rps_1), Sanga (Rps_1^b), Wells II (Rps_1^c), Williams 82 (Rps_1^k), PI 86972-1 (Rps_3), PRX27-108 (Rps_1 Rps_4), and Altona (Rps_6). Rps_2 was not included in this study because it was found using root inoculations in a liquid culture solution (8). Rps_5 was not used because it was described after this study was started (6). The results of inoculating the F_2 population and progenies from F_2 plants from each cross with races 1, 2, 3, 4, 5, 7, and 9 of *P. megasperma* f. sp. *glycinea* are reported here.

MATERIALS AND METHODS

The soybean cultivars and plant introductions Harosoy, Mukden, Sanga, Wells II, Williams 82, PI 86972-1, PRX27-108, and Altona were chosen as parents for crosses with PI 172901 based on their genotype or reaction to physiologic races 1 through 9 (Table 1), maturity, and agronomic type. PRX27-108 contains both Rps_1 and Rps_4 and is resistant to races 1, 2, 3, and 4 because Rps_1 conditions resistance to races 1 and 2, and Rps_4 conditions resistance to races 1, 2, 3, and 4, and susceptibility to the other races used. It was originally thought that PRX27-108 had only the gene Rps_4, but this and other studies have shown that it contains both Rps_1 and Rps_4.

F_2 populations, consisting of 160–274 seedlings from each cross, were evaluated in the greenhouse for their reaction to physiologic races 1, 2, 3, 4, 5, 7, and 9. Race 6 was not used because it is no longer available, and race 8 was not used because it would have given the same results as race 9. The F_3 generation was tested to confirm the segregation ratios obtained with the F_2 populations. Approximately 12 F_3 seedlings from the same F_2 plants were evaluated for their reaction to the seven races. The progenies of only 25 F_2 plants were tested in those crosses where the F_2 population was resistant. When segregation ratios of three resistant to one susceptible were obtained in the F_2 generation, the progenies of 60 plants were evaluated. If segregation ratios of 15 resistant to one susceptible or 63 resistant to one susceptible were obtained, the progenies of 100 F_2 plants were evaluated. Progenies from F_2 plants from the cross of PI 172901 with Altona were not evaluated because they were a generation behind the other crosses.

Inoculum of *P. megasperma* f. sp. *glycinea* was prepared by growing isolates of the respective races on oatmeal agar in petri dishes in an unlighted cabinet for 2–3 wk at 22–24 C. The same isolate of each race was used throughout the study. Ten-day-old seedlings were inoculated in the greenhouse by the hypocotyl method, which consists of inserting a 2 × 2-mm piece of mycelium into a longitudinal slit in the hypocotyl and covering the wound with petrolatum to prevent desiccation of the inoculum and host tissue. The inoculated plants were incubated in the greenhouse at 24–27 C. Six days after inoculation the seedlings were classified as resistant (no visible symptoms) or susceptible (dead). Chi-square tests for goodness of fit to hypothesized ratios were used to analyze data from the F_2 and F_3 generations.

RESULTS AND DISCUSSION

In the cross of PI 172901 with Harosoy (*rps*), the F_2 population segregated in a ratio of approximately 15 resistant to one susceptible to races 1, 3, 4, 5, 7, and 9 (Table 2), which indicated that resistance to these races in PI 172901 was controlled by two independent, dominant genes. In the case of race 5, the chi-square value of 3.9027 indicated a significant deviation from the expected ratio, but this deviation was produced by only one excess plant in the susceptible class. Inoculation was repeated on 269 additional F_2 plants with similar results, a chi-square of 4.2530. The F_2 population from this cross segregated in a ratio close to three resistant to one susceptible to race 2, indicating that only one of the two genes in PI 172901 was effective against this race. The chi-square value indicated a significant deviation from the hypothesized ratio caused by a deficit of nine susceptible plants. Another group of 246 F_2 plants were inoculated with race 2 and the results were similar.

The F_2 population from the cross of PI 172901 with Mukden (Rps_1) was uniformly resistant to race 1 (Table 2), which suggested that one of the genes in PI 172901 was allelic to Rps_1 from Mukden. However, this allele at the Rps_1 locus also gave resistance to races 3, 4, 5, 7, and 9 (as shown in this and the previous cross), which indicated that it was not the gene Rps_1 that conditions susceptibility to these races. The F_2 population from this cross segregated in a ratio of 15 resistant to one susceptible to races 2, 3, 4, 5, 7, and 9, indicating the independent assortment of two dominant genes. These results substantiated the results from the cross with Harosoy which indicated a single dominant gene for resistance to race 2, and two genes for resistance to races 1, 3, 4, 5, 7, and 9 in PI 172901.

In the cross of PI 172901 with Sanga (Rps_1^b), the F_2 population was resistant to races 1, 3, 4, 5, 7, and 9 (Table 2), suggesting that one of the genes in PI 172901 was located at the same locus as Rps_1^b. Because both Rps_1^b from Sanga and the allele at the Rps_1 locus in PI 172901 gave resistance to all but race 2, it appeared that they were the same allele. The F_2 population segregated in a ratio of three resistant to one susceptible to race 2, indicating that the other dominant gene in PI 172901 was conditioning resistance because Rps_1^b from Sanga is ineffective for race 2.

The F_2 population from the cross of PI 172901 with Wells II (Rps_1^c) was uniformly resistant to races 1, 3, 7, and 9 (Table 2), which indicated that one of the genes in PI 172901, probably Rps_1^b, was allelic to Rps_1^c from Wells II. It was not Rps_1^c because it conditioned resistance to races 4 and 5 to which Rps_1^c is ineffective. The F_2 population segregated in a ratio of 15 resistant to one susceptible to races 2, 4, and 5, which indicated the presence of two independent, dominant genes. In the case of race 2, one was Rps_1^c from Wells II and the other was the gene in PI 172901 not located at the Rps_1 locus. With races 4 and 5, the two genes from PI 172901 were involved in resistance.

In the cross of PI 172901 with Williams 82 (Rps_1^k), the F_2 population was resistant to races 1, 3, 4, 5, 7, and 9 (Table 2), which suggested that Rps_1^k from Williams 82 was allelic to one of the genes in PI 172901, probably Rps_1^b. The F_2 population segregated in a ratio of 15 resistant to one susceptible to race 2, indicating the independent assortment of Rps_1^k and the gene in PI 172901 not at the Rps_1 locus.

Results from the crosses of PI 172901 with cultivars having alleles at the Rps_1 locus strongly suggested that one of the genes in PI 172901 was Rps_1^b. This gene conditioned resistance to races 1, 3, 4, 5, 7, and 9, and susceptibility to race 2, identical to that conditioned by Rps_1^b.

The F_2 population from the cross of PI 172901 with PI 86972-1 (Rps_3) segregated in a ratio of 15 resistant to one susceptible to race 7 (Table 2). The two genes involved in resistance were from PI 172901 because Rps_3 from PI 86972-1 conditions susceptibility to race 7. The F_2 population was resistant to races 1, 2, 3, 4, 5, and 9, indicating that one of the genes in PI 172901 was located at the same locus as the gene Rps_3 from PI 86972-1. However, they were not the same allele because Rps_3 conveys resistance to races 1, 2, 3, 4, 5, and 9, and susceptibility to race 7, whereas the allele in PI 172901 conditions resistance to all seven races included in this study.

TABLE 1. Cultivars and lines used in crosses with PI 172901 and their gene(s) for resistance and reaction to physiologic races 1 through 9 of *Phytophthora megasperma* f. sp. *glycinea*

Cultivar or line	Gene	Reaction[a] to physiologic race								
		1	2	3	4	5	6	7	8	9
Harosoy	*rps*	S	S	S	S	S	S	S	S	S
Mukden	Rps_1	R	R	S	S	S	S	S	S	S
Sanga	Rps_1^b	R	S	R	R	R	R	R	R	R
Wells II	Rps_1^c	R	R	R	S	S	R	R	R	R
Williams 82	Rps_1^k	R	R	R	R	R	R	R	R	R
PI 86972-1	Rps_3	R	R	R	R	R	S	S	R	R
PRX27-108	Rps_1	R	R	S	S	S	S	S	S	S
	Rps_4	R	R	R	R	S	S	S	S	S
Altona	Rps_6	R	R	R	R	S	S	S	S	S
PI 172901	Rps_1^b Rps_3^b	R	R	R	R	R	R	R	R	R

[a] Abbreviations: R = resistant and S = susceptible.

In the cross of PI 172901 with PRX27-108 (*Rps*$_1$ *Rps*$_4$), the F_2 population was uniformly resistant to race 1 (Table 2), because *Rps*$_1^b$ from PI 172901 is allelic to *Rps*$_1$ from PRX27-108. The F_2 population segregated in a ratio of 15 resistant to one susceptible to races 5, 7, and 9, which indicated two genes for resistance to these races. Both genes were from PI 172901 because *Rps*$_1$ and *Rps*$_4$ from PRX27-108 condition susceptibility to races 5, 7, and 9. The F_2 population segregated in a ratio of 63 resistant to one susceptible to races 2, 3, and 4, which indicated three independent genes for resistance to these races. For race 2, the three genes for resistance

TABLE 2. Segregation of F_2 populations from crosses of PI 172901 with cultivars Harosoy, Mukden, Sanga, Wells II, Williams 82, PI 86972-1, PRX27-108, and Altona to seven physiologic races of *P. megasperma* f. sp. *glycinea*

Parentage and gene	Race	Number of plants[a]			Ratio[b]	χ^2	*P*
		Total	Res.	Susc.			
Harosoy (*rps*) × PI 172901	1	205	199	6	15:1	3.8637	0.05–0.02
16 36	2	211	179	32	3:1	10.8831	<0.01
		246	212	34	3:1	16.3957	<0.01
	3	211	202	9	15:1	1.4183	0.30–0.20
	4	199	180	19	15:1	3.6935	0.10–0.05
	5	222	201	21	15:1	3.9027	0.05–0.02
		269	244	25	15:1	4.2530	0.05–0.02
	7	209	196	13	15:1	0.0003	0.99–0.98
	9	202	193	9	15:1	1.1102	0.30–0.20
Mukden (*Rps*$_1$) × PI 172901	1	255	255	0	R		
	2	258	247	11	15:1	1.7375	0.20–0.10
	3	259	243	16	15:1	0.0023	0.98–0.95
	4	250	228	22	15:1	2.7744	0.10–0.05
	5	267	257	10	15:1	2.8587	0.10–0.05
	7	223	211	12	15:1	0.2873	0.70–0.50
	9	242	224	18	15:1	0.5829	0.50–0.30
Sanga (*Rps*$_1^b$) × PI 172901	1	177	177	0	R		
	2	178	139	39	3:1	0.9064	0.50–0.30
	3	189	189	0	R		
	4	190	190	0	R		
	5	170	169	1	R		
	7	175	175	0	R		
	9	160	160	0	R		
Wells II (*Rps*$_1^c$) × PI 172901	1	258	258	0	R		
	2	271	257	14	15:1	0.5434	0.50–0.30
	3	274	274	0	R		
	4	266	253	13	15:1	0.8431	0.50–0.30
	5	250	237	13	15:1	0.4704	0.50–0.30
	7	272	272	0	R		
	9	268	268	0	R		
Williams 82 (*Rps*$_1^k$) × PI 172901	1	220	220	0	R		
	2	227	217	10	15:1	1.3184	0.30–0.20
	3	219	219	0	R		
	4	218	218	0	R		
	5	215	215	0	R		
	7	239	239	0	R		
	9	239	238	1	R		
PI 86972-1 (*Rps*$_3$) × PI 172901	1	233	233	0	R		
	2	259	258	1	R		
	3	254	254	0	R		
	4	243	242	1	R		
	5	249	249	0	R		
	7	251	228	23	15:1	3.6359	0.10–0.05
	9	232	232	0	R		
PRX27-108 (*Rps*$_1$ *Rps*$_4$) × PI 172901	1	245	245	0	R		
	2	240	236	4	63:1	0.0169	0.90–0.80
	3	250	248	2	63:1	0.9450	0.50–0.30
	4	252	252	0	63:1	4.0000	0.05–0.02
	5	247	219	28	15:1	10.9045	<0.01
		245	215	30	15:1	15.0272	<0.01
	7	243	229	14	15:1	0.0990	0.80–0.70
	9	242	231	11	15:1	1.2000	0.30–0.20
PI 172901 × Altona (*Rps*$_6$)	1	190	188	2	63:1	0.3211	0.70–0.50
	2	122	119	3	15:1	2.9923	0.10–0.05
	3	194	189	5	63:1	1.2990	0.30–0.20
	4	127	125	2	63:1	0.0001	0.99–0.98
	5	185	173	12	15:1	0.0177	0.90–0.80
	7	204	185	19	15:1	3.2680	0.10–0.05
	9	129	124	5	15:1	1.2408	0.30–0.20

[a] Abbreviations: Res = resistant and Susc = susceptible.
[b] Ratio = resistant to susceptible, and R = resistant.

were *Rps*$_1$ and *Rps*$_4$ from PRX27-108, and the allele at the *Rps*$_3$ locus from PI 172901. For races 3 and 4, the genes for resistance were *Rps*$_4$ from PRX27-108 and the two genes from PI 172901. In the case of race 5, the chi-square value indicated a significant deviation from the expected ratio. The inoculation of another sample of the F_2 population with race 5 gave a similar excess of susceptible plants. With race 4, there was a deficit of one susceptible plant which was probably the result of sampling error.

The F_2 population from the cross of PI 172901 with Altona (*Rps*$_6$) segregated in a ratio of 63 resistant to one susceptible to

TABLE 3. Breeding behavior of progenies from F_2 plants from crosses of PI 172901 with Harosoy, Mukden, Sanga, Wells II, Williams 82, PI 86972-1, and PRX27-108 to seven physiologic races of *P. megasperma* f. sp. *glycinea*

Parentage and gene	Race	Number of F_2 plants[a]				Ratio[b]	χ^2	*P*
		Total	Res.	Seg.	Susc.			
Harosoy (*rps*) × PI 172901	1	100	45	47	8	7:8:1	0.7057	0.80–0.70
	2	100	30	48	22	1:2:1	1.4400	0.50–0.30
	3	100	45	47	8	7:8:1	0.7057	0.80–0.70
	4	100	45	47	8	7:8:1	0.7057	0.80–0.70
	5	100	45	47	8	7:8:1	0.7057	0.80–0.70
	7	100	45	47	8	7:8:1	0.7057	0.80–0.70
	9	100	45	47	8	7:8:1	0.7057	0.80–0.70
Mukden (*Rps*$_1$) × PI 172901	1	25	25	0	0	R		
	2	98	67	27	4	7:8:1	24.1895	<0.01
		98†[c]	94		4	15:1	0.7864	0.50–0.30
	3	98	45	48	4	7:8:1	0.3324	0.90–0.80
	4	98	45	48	4	7:8:1	0.3324	0.90–0.80
	5	98	45	48	4	7:8:1	0.3324	0.90–0.80
	7	98	45	48	4	7:8:1	0.3324	0.90–0.80
	9	98	45	48	4	7:8:1	0.3324	0.90–0.80
Sanga (*Rps*$_1^b$) × PI 172901	1	25	25	0	0	R		
	2	60	12	36	12	1:2:1	2.4000	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		
Wells II (*Rps*$_1^c$) × PI 172901	1	25	25	0	0	R		
	2	100	66	30	4	7:8:1	20.1257	<0.01
		100†	96		4	15:1	0.8640	0.50–0.30
	3	25	25	0	0	R		
	4	100	61	35	4	7:8:1	12.1114	<0.01
		100†	96		4	15:1	0.8640	0.50–0.30
	5	100	61	35	4	7:8:1	12.1114	<0.01
		100†	96		4	15:1	0.8640	0.50–0.30
	7	25	25	0	0	R		
	9	25	25	0	0	R		
Williams 82 (*Rps*$_1^k$) × PI 172901	1	25	25	0	0	R		
	2	100	49	43	8	7:8:1	2.1000	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 86972-1 (*Rps*$_3$) × PI 172901	1	100	100	0	0	R		
	2	100	100	0	0	R		
	3	100	100	0	0	R		
	4	99	99	0	0	R		
	5	99	99	0	0	R		
	7	100	44	46	8	7:8:1	0.8114	0.70–0.50
	9	100	100	0	0	R		
PRX27-108 (*Rps*$_1$ *Rps*$_4$) × PI 172901	1	100	100	0	0	R		
	2	100	78	20	2	37:26:1	17.6429	<0.01
		100†	98		2	63:1	0.1244	0.80–0.70
	3	100	71	27	2	37:26:1	7.7003	0.05–0.02
		100†	98		2	63:1	0.1244	0.80–0.70
	4	100	71	27	2	37:26:1	7.7003	0.05–0.02
		100†	98		2	63:1	0.1244	0.80–0.70
	5	100	36	56	8	7:8:1	2.5829	0.30–0.20
	7	100	36	56	8	7:8:1	2.5829	0.30–0.20
	9	100	36	56	8	7:8:1	2.5829	0.30–0.20

[a] Abbreviations: Res = resistant, Seg = segregating, Susc = suceptible.
[b] Ratio = homozygous resistant:heterozygous:homozygous susceptible. R = resistant.
[c] † = combined res and seg categories.

races 1, 3, and 4 (Table 2), indicating the independent assortment of three dominant genes. They were *Rps*$_6$ from Altona and the two genes from PI 172901. The F_2 population segregated in a ratio of 15 resistant to one susceptible to races 2, 5, 7, and 9, indicating two dominant genes for resistance. For race 2 they were *Rps*$_6$ from Altona and the gene in PI 172901 located at the *Rps*$_3$ locus. For races 5, 7, and 9 the two genes from PI 172901 were involved in resistance because *Rps*$_6$ from Altona conditions susceptibility to these races.

The preceding data suggest that there are two independent, dominant genes for resistance in PI 172901. One of them is *Rps*$_1^b$ which gives resistance to races 1, 3, 4, 5, 7, and 9, and susceptibility to race 2. The other gene is an undescribed allele at the *Rps*$_3$ locus which conveys resistance to races 1, 2, 3, 4, 5, 7, and 9. The symbol *Rps*$_3^b$ is suggested for this gene to indicate a second allele at the *Rps*$_3$ locus and to discriminate it from the gene *Rps*$_3$, which conditions susceptibility to race 7.

The breeding behavior of the progenies from the F_2 plants in each cross (Table 3) verified the segregation ratios reported in Table 2. It also helped to substantiate the hypothesized ratios in those few cases where there was not close agreement between expected and observed ratios, such as with races 2 and 5 in the cross with Harosoy, and with races 4 and 5 in the cross with PRX27-108 (Table 2). In some cases, the homozygous resistant and heterozygous categories had to be combined to give acceptable fit to the hypothesized ratios. This was necessary for race 2 in the cross with Mukden; races 2, 4, and 5 in the cross with Wells II; and races 2, 3, and 4 in the cross with PRX27-108. In each case, the deviation was caused by an excess of plants in the homozygous resistant class. This was attributed to the failure to detect the susceptible plants within the segregating families because of the relatively small number of F_3 plants inoculated from each F_2 plant. When the homozygous resistant and heterozygous categories were combined there was satisfactory agreement to the hypothesized ratios (Table 3).

New genes or new alleles at known loci represent new sources of resistance. These genes are likely to differ from the previously reported ones with respect to their reaction to the described physiologic races. This will allow their use either alone or in combination with other genes to give protection against more races of the pathogen.

Rps$_3^b$ confers resistance to races 1, 2, 3, 4, 5, 7, and 9. PI 172901 (*Rps*$_1^b$ *Rps*$_1^b$ *Rps*$_3^b$ *Rps*$_3^b$) is resistant to races 1 through 16, and because *Rps*$_1^b$ confers susceptibility to races 10, 11, 12, and 16, it is evident that *Rps*$_3^b$ conveys resistance to these races. Thus, *Rps*$_3^b$ gives resistance to races 7, 10, and 12 to which *Rps*$_3$ gives susceptibility.

Additional testing is necessary to determine the reaction of gene *Rps*$_3^b$ to races 13, 14, 15, and 17 through 23. F_2 plants with the genotype *rps*$_1$ *rps*$_1$ *Rps*$_3^b$ *Rps*$_3^b$ can be selected from the cross of PI 172901 with Harosoy and used to further characterize the gene *Rps*$_3^b$. This will provide the information needed to determine with which other gene or genes *Rps*$_3^b$ may be combined to provide the desired resistance.

LITERATURE CITED

1. Athow, K. L., and Laviolette, F. A. 1982. *Rps*$_6$, a new major gene for resistance to *Phytophthora megasperma* f. sp. *glycinea*. Phytopathology 72:1564-1567.
2. Athow, K. L., Laviolette, F. A., Mueller, E. H., and Wilcox, J. R. 1980. A new major gene for resistance to *Phytophthora megasperma* var. *sojae*. Phytopathology 70:977-980.
3. Athow, K. L., Laviolette, F. A., and Wilcox, J. R. 1979. Genetics of resistance to physiologic races of *Phytophthora megasperma* var. *sojae* in the soybean cultivar Tracy. Phytopathology 69:641-642.
4. Bernard, R. L., and Cremeens, C. R. 1981. An allele at the *rps*$_1$ locus from the variety Kingwa. Soybean Genetics Newslett. 8:40-42.
5. Bernard, R. L., Smith, P. E., Kaufmann, M. J., and Schmitthenner, A. F. 1957. Inheritance of resistance to Phytophthora root and stem rot in the soybean. Agronomy J. 49:391.
6. Buzzell, R. I., and Anderson, T. R. 1981. Another major gene for resistance to *Phytophthora megasperma* var. *sojae* in soybeans. Soybean Genetics Newslett. 8:30-33.
7. Hartwig, E. E., Keeling, B. L., and Edwards, C. J. Jr. 1968. Inheritance of reaction to Phytophthora rot in the soybean. Crop Sci. 8:634-635.
8. Kilen, T. C., Hartwig, E. E., and Keeling, B. L. 1974. Inheritance of a second major gene for resistance to Phytophthora rot in soybeans. Crop Sci. 14:260-262.
9. Kilen, T. C., and Keeling, B. L. 1981. Genetics of resistance to Phytophthora rot in soybean (*Glycine max*) cultivar PI 171442. Crop Sci. 21:873-875.
10. Kuan, T. L., and Erwin, D. C. 1980. Forma speciales differentiation of *Phytophthora megasperma* isolates from soybean and alfalfa. Phytopathology 70:333-338.
11. Laviolette, F. A., Athow, K. L., Mueller, E. H., and Wilcox, J. R. 1979. Inheritance of resistance to physiologic races 5, 6, 7, 8, and 9 of *Phytophthora megasperma* var. *sojae*. Phytopathology 69:270-271.
12. Layton, A. C., Athow, K. L., and Laviolette, F. A. 1984. Inheritance of resistance to *Phytophthora megasperma* f. sp. *glycinea* in a soybean plant introduction. Plant Dis. 68:1080-1083.