A New Major Gene for Resistance to *Phytophthora megasperma* var. *sojae* in Soybean

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Cooperative investigations of the Purdue Agricultural Experiment Station and AR, SEA, USDA. Supported in part by the Indiana Crop Improvement Association.

Journal Series Paper 7844, Purdue Agricultural Experiment Station.

Accepted for publication 6 April 1980.

ABSTRACT

ATHOW, K. L., F. A. LAVIOLETTE, E. H. MUELLER, and J. R. WILCOX. 1980. A new major gene for resistance to *Phytophthora megasperma* var. *sojae* in soybean. Phytopathology 70:977-980.

The inheritance of resistance to *Phytophthora megasperma* var. *sojae* was studied in the F_2 and F_3 generations from crosses of the soybean plant introduction (PI) 86050 with Harosoy (*rps*$_1$ *rps*$_3$), Mukden (*Rps*$_1$ *rps*$_3$), PI 84637 (*Rps*$_1^b$ *rps*$_3$), PI 54615-1 (*Rps*$_1^c$ *rps*$_3$), PI 86972-1 (*rps*$_1$ *Rps*$_3$), and Altona. The data indicate that PI 86050 has two genes for resistance to races 1, 2, and 3; one gene for resistance to races 4, 6, 7, 8, and 9; and no gene for resistance to race 5. The results show that one of the genes in PI 86050 is *Rps*$_1^c$ which conveys resistance to races 1, 2, 3, 6, 7, 8, and 9. The other gene conveys resistance to races 1, 2, 3, and 4. The symbol *Rps*$_4$ is proposed for this gene. *Rps*$_4$ is not at the same locus as the allele in Altona which also controls resistance to races 1, 2, 3, and 4.

Additional key words: soybean diseases.

We became interested in PI 86050 in 1974 when it was found to be resistant to physiologic races 1, 2, 3, and 4 of *Phytophthora megasperma* Drechs. var. *sojae* Hildb. (1). V. D. Luedders of the University of Missouri previously had crossed PI 86050 with cultivar Williams to utilize the comparatively late flowering of PI 86050 in relation to its maturity to breed for higher insertion of pods on the stem. We evaluated the progenies of 251 F_2 plants from this cross with races 1, 2, 3, and 4. The results (6) indicated two dominant genes conditioning resistance to race 1. There were no clear-cut segregation ratios with races 2, 3, and 4, and no obvious reason for this disparity. In the meantime five additional physiologic races of the fungus were identified (4) and PI 86050 was resistant to all but race 5. In order to re-evaluate the inheritance of resistance of PI 86050, it was crossed to Harosoy (*rps*$_1$ *rps*$_3$), Mukden (*Rps*$_1$ *rps*$_3$), PI 84637 (*Rps*$_1^b$ *rps*$_3$), PI 54615-1 (*Rps*$_1^c$ *rps*$_3$), PI 86972-1 (*rps*$_1$ *Rps*$_3$), and Altona. The results of inoculating the F_2 population and progenies from F_2 plants from each cross with the nine races are reported here.

MATERIALS AND METHODS

The soybean cultivars and plant introductions Harosoy, Mukden, Altona, PI 54615-1, PI 84637, and PI 86972-1 were selected as parents based on their known genotype or reaction to the nine physiologic races of the pathogen. Harosoy was selected as the universally susceptible parent. Mukden has the gene *Rps*$_1$ and is resistant to races 1 and 2. PI 84637 has the gene *Rps*$_1^b$ and is resistant to all but race 2. PI 54615-1 has the gene *Rps*$_1^c$ and is resistant to all but races 4 and 5. PI 86972-1 has the gene *RPS*$_3$ and is resistant to all but races 6 and 7. Altona was included later because it is resistant to races 1, 2, 3, and 4.

Approximately 200 F_2 seedlings from each cross were tested with races 1, 2, 3, 4, 5, 6, 7, 8, and 9. Approximately 12 F_3 seedlings from 100 F_2 plants from each cross were tested with races 1, 2, 3, 4, 5, 7, and 9 to verify the segregation obtained in the F_2 population and to confirm the location of the alleles for resistance. Races 6 and 8 were not used in evaluating the progenies from F_2 plants because of an apparent change in their virulence which resulted in improper reactions on some of the differential check cultivars. Progenies from F_2 plants from the crosses of PI 54615-1 and Altona with PI 86050 were not evaluated because they were a generation behind the other crosses. The progeny of only 25 F_2 plants was evaluated if no segregation occurred in the F_2 population.

Inoculum was prepared by growing the isolates 2–3 wk at 24 C on oatmeal agar in petri plates. The same isolate of each race was used throughout the study. Inoculations were made 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 tissues. Ten-day-old seedlings were inoculated and grown in a greenhouse

0031-949X/80/10097704/$03.00/0

at 24–27 C. 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.

RESULTS AND DISCUSSION

The F_2 population from the cross of Harosoy with PI 86050 segregated in a ratio of 15 resistant:1 susceptible to races 1, 2, and 3 indicating two dominant genes for resistance to each of these races in PI 86050 (Table 1). To races 4, 6, 7, 8, and 9, the F_2 population from this cross segregated in a ratio of 3 resistant:1 susceptible indicating one dominant gene for resistance to each of these races in PI 86050. As expected, the F_2 population was uniformly susceptible to race 5 because both parents were susceptible.

In the cross of Mukden × PI 86050, the F_2 population was uniformly resistant to races 1 and 2 (Table 1). This indicates that one of the two genes for resistance in PI 86050 is allelomorphic to the gene Rps_1 in Mukden which conveys resistance to races 1 and 2. The F_2 population from the cross Mukden × PI 86050 reacted to races 3 through 9 the same as the F_2 population from the cross

TABLE 1. Segregation of F_2 populations from crosses of PI 86050 with Harosoy, Mukden, PI 84637, PI 54615-1, PI 86972-1, and Altona to nine physiologic races of *Phytophthora megasperma* var. *sojae*

Parentage	Race	No. of plants[a]		χ^2 probability		
		Res.	Susc.	3:1 ratio	15:1 ratio	63:1 ratio
Harosoy × PI 86050	1	157	13		.50–.30	
	2	169	10		.80–.70	
	3	190	6		.10–.05	
	4	154	41	.20–.10		
	5	0	178			
	6	71	16	.20–.10		
	7	142	44	.70–.50		
	8	69	25	.80–.70		
	9	113	26	.10–.05		
Mukden × PI 86050	1	202	0			
	2	210	0			
	3	201	7		.10–.05	
	4	180	65	.70–.50		
	5	1	247			
	6	188	59	.70–.50		
	7	371	122	.90–.10		
	8	200	52	.20–.10		
	9	186	55	.50–.30		
PI 84637 × PI 86050	1	201	0			
	2	192	9		.30–.20	
	3	187	0			
	4	173	17		.30–.20	
	5	158	39	.10–.05		
	6	Not tested				
	7	183	0			
	8	Not tested				
	9	179	0			
PI 54615-1 × PI 86050	1	185	0			
	2	202	0			
	3	203	0			
	4	151	47	.70–.50		
	5	0	213			
	6	Not tested				
	7	213	0			
	8	Not tested				
	9	205	0			
PI 86972-1 × PI 86050	1	184	3			.98–.95
	2	182	4			.70–.50
	3	167	3			.90–.80
	4	187	7		.20–.10	
	5	185	60	.90–.80		
	6	172	46	.20–.10		
	7	189	54	.50–.30		
	8	332	16		.30–.20	
	9	242	9		.10–.05	
PI 86050 × Altona	1	179	3			.95–.90
	2	204	3			.90–.80
	3	224	5			.50–.30
	4	237	17		.80–.70	
	5	0	111			
	6	Not tested				
	7	170	52	.70–.50		
	8	Not tested				
	9	172	44	.20–.10		

[a] Res. = resistant, Susc. = susceptible.

Harosoy × PI 86050 because both Mukden and Harosoy are susceptible to these races.

The F_2 population from the cross of PI 84637 × PI 86050 was uniformly resistant to races 1, 3, 7 and 9 (Table 1). This suggests that one of the genes in PI 86050 is at the same locus as the gene $Rps_1{}^b$ in PI 84637 which conveys resistance to all but race 2. It is not identical to $Rps_1{}^b$ as indicated by the 15 resistant:1 susceptible, two gene, segregation ratio to race 2. Furthermore, the ratios of 15 resistant:1 susceptible to race 4, and 3 resistant:1 susceptible to race 5 strongly implicates the gene $Rps_1{}^c$ which conditions susceptibility in the host to these two races.

The F_2 population from the cross of PI 54615-1 × PI 86050 was uniformly resistant to races 1, 2, 3, 7, and 9 (Table 1) indicating that one of the genes in PI 86050 is located at the same locus as $Rps_1{}^c$ which conveys resistance in PI 54615-1 to all except races 4 and 5. The monogenic segregation ratio of 3 resistant:1 susceptible to race 4, and the uniformly susceptible reaction of the F_2 population to race 5 not only proves that $Rps_1{}^c$ is one of the genes for resistance in PI 86050 but this and the results from the crosses with Harosoy, Mukden, and PI 84637 indicate that the other gene controls resistance to only races 1, 2, 3, and 4. The symbol Rps_4 is proposed for this gene.

The F_2 population from the cross of PI 86972-1 × PI 86050 segregated in a ratio of 63 resistant:1 susceptible to races 1, 2, and 3 (Table 1) indicating the independent segregation of three dominant genes. The F_2 population segregated in a ratio of 15 resistant:1 susceptible to races 4, 8, and 9; and a ratio of 3 resistant:1 susceptible to races 5, 6, and 7. These results indicate that the genes $Rps_1{}^c$, Rps_3, and Rps_4 are involved with races 1, 2, and 3. Rps_3 and Rps_4 are involved with race 4, whereas $Rps_1{}^c$ and Rps_3 are involved with races 8 and 9. Only Rps_3 controls resistance to race 5, and only $Rps_1{}^c$ controls resistance to races 6 and 7 in this population.

When it became evident that one of the genes in PI 86050 gave resistance to races 1, 2, 3, and 4, the same reaction as the differential cultivar Altona (4), Altona was crossed with PI 86050. The F_2 population segregated in ratios of 63 resistant:1 susceptible to races 1, 2, and 3; and 15 resistant:1 susceptible to race 4 indicating that the gene for resistance in Altona is not identical to Rps_4 nor is it located at the same locus. As indicated with Rps_3 (7), there is no proof that Rps_4 and/or the gene for resistance in Altona may not be at the Rps_2 locus. Gene Rps_2 was found in the cultivar CNS and derived strains with root inoculation with races 1 and 2 (3). CNS gives a variable reaction to hypocotyl inoculation and the relation of Rps_2 to other genes would be difficult to determine by this method.

The F_2 plants from the cross of Harosoy × PI 86050, as tested by their progenies in the F_3 generation, segregated in a ratio of 7 homozygous-resistant:8 segregating:1 homozygous-susceptible to races 1, 2, and 3 (Table 2) to verify the independent segregation of two dominant genes to these races. The F_2 plants segregated in a ratio of 1 homozygous-resistant:2 segregating:1 homozygous-susceptible to races 4, 7, and 9 substantiating the monogenic resistance of PI 86050 to these races. F_2 plants that were uniformly resistant to races 7 and 9 also were uniformly resistant to races 1, 2, and 3 but were resistant, susceptible or segregating to race 4. F_2 plants that were uniformly susceptible to races 7 and 9 were

TABLE 2. Breeding behavior of the progenies from F_2 plants from crosses of PI 86050 with Harosoy, Mukden, PI 84637, and PI 86972-1 to nine physiologic races of *Phytophthora megasperma* var. *sojae*

Parentage	Race	No. of F_2 plants[a]			χ^2 probability		
		Res.	Seg.	Susc.	1:2:1 ratio	7:8:1 ratio	37:26:1 ratio
Harosoy × PI 86050	1	36	59	5		0.50–0.30	
	2	37	58	5		0.50–0.30	
	3	37	58	5		0.50–0.30	
	4	17	49	34	0.20–0.10		
	5	0	0	100			
	6	Not tested					
	7	22	54	24	0.90–0.80		
	8	Not tested					
	9	22	54	24	0.90–0.80		
Mukden × PI 86050	1	25	0	0			
	2	25	0	0			
	3	41	53	6		0.95–0.90	
	4	19	61	20	0.20–0.10		
	5	0	0	25			
	6	Not tested					
	7	27	42	31	0.50–0.30		
	8	Not tested					
	9	27	42	31	0.50–0.30		
PI 84637 × PI 86050	1	25	0	0			
	2	40	57	3		0.50–0.30	
	3	25	0	0			
	4	42	46	12		0.20–0.10	
	5	21	48	31	0.70–0.50		
	6	Not tested					
	7	25	0	0			
	8	Not tested					
	9	25	0	0			
PI 86972-1 × PI 86050	1	64	33	3			0.30–0.20
	2	64	33	3			0.30–0.20
	3	64	33	3			0.30–0.20
	4	38	53	9		0.50–0.30	
	5	23	56	21	0.50–0.30		
	6	Not tested					
	7	28	50	22	0.70–0.50		
	8	Not tested					
	9	49	44	7		0.70–0.50	

[a] Res. = resistant; Seg. = segregating; Susc. = susceptible. F_3 seedlings from the same F_2 plants were tested with each race.

resistant, segregating or susceptible to races 1, 2, 3, and 4. F_2 plants that were uniformly resistant to race 4 also were uniformly resistant to races 1, 2, and 3; and resistant, segregating, or susceptible to races 7 and 9. F_2 plants that were uniformly susceptible to race 4 were resistant, segregating, or susceptible to races 1, 2, 3, 7, and 9. Progenies of these F_2 plants were uniformly susceptible to race 5. The data show that there are two genes for resistance in PI 86050 with equal dominance and independent segregation. One of the genes controls resistance to races 1, 2, 3, 7, and 9. Based on the F_2 data in Table 1 for races 6 and 8, it is apparent that the latter gene is $Rps_1{}^c$ which was (5) recently described as controlling resistance to races 1, 2, 3, 6, 7, 8, and 9. The other gene in PI 86050, Rps_4, controls resistance to races 1, 2, 3, and 4.

The F_2 plants from the cross of Mukden × PI 86050 as tested by their progenies in the F_3, were all uniformly resistant to races 1 and 2, indicating that at least one of the genes for resistance in PI 86050 was at the same locus as Rps_1, which gives resistance to races 1 and 2 in Mukden (7). F_2 plants that were uniformly susceptible to races 7 and 9 were resistant, susceptible, or segregating to races 1, 2, 3, and 4. F_2 plants that were uniformly susceptible to race 4 were resistant, susceptible, or segregating to races 1, 2, 3, 7, and 9. These data indicate that the gene controlling resistance to race 4 is independent of the gene controlling resistance to races 7 and 9, but both genes control resistance to races 1, 2, and 3.

The F_2 plants from the cross of PI 84637 × PI 86050, as tested by their progenies, were uniformly resistant to races 1, 3, 7, and 9 indicating that at least one of the genes for resistance in PI 86050 was at the locus of $Rps_1{}^b$ which gives resistance to races 1, 3, 4, 5, 6, 7, 8, and 9 in PI 84637 (5). The F_2 plants segregated in a ratio of 1 homozygous-resistant:2 segregating:1 homozygous-susceptible to race 5 when only $Rps_1{}^b$ was operative. The F_2 plants segregated in a ratio of 7 homozygous-resistant:8 segregating:1 homozygous-susceptible to race 2 when genes $Rps_1{}^c$ and Rps_4 were involved and to race 4 when genes $Rps_1{}^b$ and Rps_4 were involved.

The F_2 plants in the cross of PI 86972-1 × PI 86050, as tested by their progenies segregated in a ratio of 37 homozygous-resistant:26 segregating:1 homozygous-susceptible to races 1, 2, and 3, which verified the three-gene segregation ($Rps_1{}^c$, Rps_3, and Rps_4) for these races. The F_2 plants segregated in a ratio of 7 homozygous-resistant:8 segregating:1 homozygous-susceptible to races 4 and 9 indicating two genes for resistance to these races. Individual F_2 plants did not all react the same to races 4 and 9 indicating that different genes were involved with the resistance to race 4 (Rps_3, Rps_4) and race 9 ($Rps_1{}^c$, Rps_3). The F_2 plants segregated in a ratio of 1 homozygous-resistant:2 segregating:1 homozygous-susceptible to races 5 and 7 confirming the monogenic resistance in this cross to these two races. F_2 plants that were uniformly resistant or uniformly susceptible to either race 5 or 7 could be resistant, segregating, or susceptible to the other race indicating that the same gene did not control resistance to races 5 and 7 in this cross. This is further proof that Rps_3 controls resistance to race 5 as well as resistance to races 1, 2, 3, 4, 8, and 9; and $Rps_1{}^c$ controls resistance to race 7 as well as races 1, 2, 3, 6, 8, and 9. F_2 plants with the genotype rps_1, rps_3, Rps_4 were selected by the uniformly resistant reaction of their progenies to races 1, 2, 3, and 4, and the uniformly susceptible reaction to races 5 and 7.

The lines with only gene Rps_4 for resistance may be of some value in genetic studies but are of limited value for developing resistant cultivars. Lines with genotype $Rps_1{}^b$ rps_3 Rps_4 selected from the cross of PI 84637 × PI 86050 for their resistance to the nine races should be useful in breeding for resistance along with the lines with genotype $Rps_1{}^b$ Rps_3 and $Rps_1{}^c$ Rps_3 previously reported (5). Presently, it is not possible to determine directly the presence of Rps_4 in combination with these genotypes. This is the second instance in which resistance to multiple races of *P. megasperma* var. *sojae* in a soybean cultivar is controlled by two genes. The cultivar Tracy with resistance to races 1 through 9 was shown to have genotype $Rps_1{}^b$ Rps_3 (2).

LITERATURE CITED

1. ATHOW, K. L., F. A. LAVIOLETTE, and T. S. ABNEY. 1974. Reaction of soybean germplasm strains to four physiologic races of *Phytophthora megasperma* var. *sojae*. Plant Dis. Rep. 58:789-792.
2. ATHOW, K. L., F. A. LAVIOLETTE, and J. R. WILCOX. 1979. The genetics of resistance to physiologic races of *Phytophthora megasperma* var. *sojae* in the soybean cultivar Tracy. Phytopathology 69:641-642.
3. KILEN, T. C., E. E. HARTWIG, and B. L. KEELING. 1974. Inheritance of a second major gene for resistance to Phytophthora rot in soybean. Crop Sci. 14:260-262.
4. LAVIOLETTE, F. A., and K. L. ATHOW. 1977. Three new physiologic races of *Phytophthora megasperma* var. *sojae*. Phytopathology 67:267-268.
5. LAVIOLETTE, F. A., and K. L. ATHOW, E. H. MUELLER, and J. R. WILCOX. 1979. Inheritance of resistance in soybeans to physiologic races 5, 6, 7, 8, and 9 of *Phytophthora megasperma* var. *sojae*. Phytopathology 69:270-271.
6. LUEDDERS, V. D., K. L. ATHOW, and F. A. LAVIOLETTE. 1974. Genetics of the soybean-Phytophthora association. Agron. Abstr. p. 57.
7. MUELLER, E. H., K. L. ATHOW, and F. A. LAVIOLETTE. 1978. Inheritance of resistance to four physiologic races of *Phytophthora megasperma* var. *sojae*. Phytopathology 68:1318-1322.