Rps$_6$, a Major Gene for Resistance to *Phytophthora megasperma* f. sp. *glycinea* in Soybean

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Supported in part by the Indiana Crop Improvement Association and the American Soybean Association Research Grant ASARP 81543.
Journal Series Paper 9025, Purdue Agricultural Experiment Station.
Accepted for publication 28 July 1982.

ABSTRACT

Athow, K. L., and Laviolette, F. A. 1982. *Rps*$_6$, a major gene for resistance to *Phytophthora megasperma* f. sp. *glycinea* in soybean. Phytopathology 72:1564-1567.

The inheritance of resistance to *Phytophthora megasperma* f. sp. *glycinea* was studied in the F_2 and F_3 generations from crosses of the soybean cultivar Altona with Harosoy, Mukden, Sanga, PI 54615-1, Williams 82, PI 86972-1, and PI 86050. The data indicate that Altona has a single dominant gene for resistance to races 1–4. The symbol *Rps*$_6$ is proposed for this gene. The action of *Rps*$_6$ is similar to that of *Rps*$_4$ except that it conditions susceptibility to race 13, whereas *Rps*$_4$ conditions resistance.

Additional key words: soybean diseases.

Eight major dominant genes for resistance to *Phytophthora megasperma* Drechs. f. sp. *glycinea* Kuan and Erwin (9) (syn. *P. megasperma* Drechs. var. *sojae* Hildeb.) have been reported in soybean (*Glycine max* (L.) Merr.). *Rps*$_1$ from Mukden (4); *Rps*$_1^b$ from D60-9647 (6), PI 84637 (10), or Sanga (data [*unpublished*] from intercrossing Sanga, PI 84637, and D60-9647); *Rps*$_1^c$ from Arskoy (10) or PI 54615-1 (10); and *Rps*$_1^k$ from Kingwa (3) are allelic and equivalent. *Rps*$_2$ was found in the cultivar CNS and in strains derived from root inoculations with races 1 and 2 (8). *Rps*$_3$ was reported in PI 86972-1 (10) and in combination with *Rps*$_1^b$ in the cultivar Tracy (2). In 1980, we reported *Rps*$_4$ in combination with *Rps*$_1^c$ in PI 86050 (1). Furthermore, we showed that *Rps*$_4$ conditioned resistance to races 1–4 and susceptibility to races 5–9 and was similar to the gene in the differential variety Altona, although *Rps*$_4$ was not at the same locus as the allele in Altona. To determine how Altona inherits resistance, 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 PI 86050 (*Rps*$_1^c$ *Rps*$_4$). The results of inoculating the F_2 population and progenies from F_2 plants from each cross with *Phytophthora megasperma* f. sp. *glycinea* races 1–5, 7, and 9 are reported here. *Rps*$_5$ was reported in soybean strain L62-904 while this article was in preparation (5).

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0031-949X/82/12156404/$03.00/0

MATERIALS AND METHODS

The soybean cultivars and plant introductions Harosoy, Mukden, Sanga, PI 54615-1, Williams 82, PI 86972-1, and PI 86050 were selected as parents, based on their known genotype or reaction

to races 1–9 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. Sanga has the gene *Rps*$_1^b$ (*unpublished data*) 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. L24 (now Williams 82) has the gene *Rps*$_1^k$ and is resistant to races 1–9. PI 86972-1 has the gene *Rps*$_3$ and is resistant to all but races 6 and 7. PI 86050 has the genes *Rps*$_1^c$ *Rps*$_4$ and is resistant to all but race 5.

Between 155 and 251 F_2 seedlings from each cross were tested with races 1–5, 7, and 9. Approximately 12 F_3 seedlings from 100 F_2 plants from each cross were tested with these seven races to verify the segregation ratio obtained in the F_2 population. Races 6 and 8 were not used because race 6 is no longer available and race 8 does not differ from race 9 in its reaction to any of the parental strains. Approximately 100 F_2 plants were evaluated if all were expected to be susceptible. The progeny of only 25 F_2 plants were evaluated in the F_3 generation if no segregation occurred in the F_2 population. Different progenies from the same F_2 plants were tested with each race.

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 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 (*rps*) with Altona segregated in a ratio of three resistant to one susceptible to races 1–4, indicating a single dominant gene for resistance to each of these races in Altona (Table 1). The F_2 population from this cross was susceptible to races 5, 7, and 9 as expected because both parents were susceptible to these races.

The F_2 population from the cross Mukden (*Rps*$_1$) with Altona segregated in a ratio of 15 resistant to one susceptible to races 1 and 2 and in a ratio of three resistant to one susceptible to races 3 and 4 (Table 1). These results substantiate the data in the previous cross, which indicated a single dominant gene for resistance to races 1–4 in Altona. They also indicate that *Rps*$_1$ is not allelic to the gene in Altona.

In the cross of Sanga (*Rps*$_1^b$) with Altona, the F_2 population segregated in a ratio of 15 resistant to one susceptible to races 1, 3, and 4 and in a ratio of three resistant to one susceptible to races 2, 5, 7, and 9 (Table 1). These data indicate two nonallelic genes, one from Altona and *Rps*$_1^b$ from Sanga, conditioning resistance to races 1, 3, and 4, but only the gene from Altona giving resistance to race 2, and only *Rps*$_1^b$ conditioning resistance to races 5, 7, and 9.

The F_2 population from the cross of PI 54615-1 (*Rps*$_1^c$) with Altona segregated in a ratio of 15 resistant to one susceptible to races 1–3, to which the gene *Rps*$_1^c$ and the gene in Altona both condition resistance (Table 1). The F_2 population segregated in a ratio of three resistant to one susceptible to race 4, to which only the gene in Altona conditions resistance, and to races 7 and 9, to which only *Rps*$_1^c$ conditions resistance. The entire F_2 population was susceptible to race 5.

In the cross of Williams 82 (*Rps*$_1^k$) with Altona, the F_2 population segregated in a ratio of 15 resistant to one susceptible to races 1–4 and in a ratio of three resistant to one susceptible to races 5, 7, and 9 (Table 1). These data indicate that a gene in Altona conditions resistance to races 1–4 and segregates independently of *Rps*$_1^k$, which gives resistance to races 1–9.

The F_2 population from the cross of PI 86972-1 (*Rps*$_3$) with Altona segregated in a ratio of 15 resistant to one susceptible to races 1–4 had a ratio of three resistant to one susceptible to races 5 and 9, and was susceptible to race 7. These data further substantiate the presence of a single gene for resistance to races 1–4 in Altona, which has equivalence with *Rps*$_3$ but is not at the same locus. *Rps*$_3$ conditions resistance to races 5 and 9 and susceptibility to race 7.

In the cross of PI 86050 (*Rps*$_1^c$ *Rps*$_4$) with Altona, which prompted this study, the F_2 populations segregated in a ratio of 63 resistant to one susceptible to races 1–3, indicating that the genes *Rps*$_1^c$ and *Rps*$_4$ segregate independently of the gene in Altona

TABLE 1. Segregation of F_2 populations from crosses of Altona with Harosoy, Mukden, Sanga, PI 54615-1, PI 86972-1, and PI 86050 to seven physiologic races of *Phytophthora megasperma* f. sp. *glycinea*

Parentage and gene(s)	Race	Number of plants		Ratio[a]	χ^2 probability
		Resistant	Susceptible		
Harosoy (*rps*) × Altona	1	122	51	3:1	0.20–0.10
	2	147	64	3:1	0.10–0.05
	3	148	46	3:1	0.70–0.50
	4	124	56	3:1	0.10–0.05
	5	0	98	S	
	7	0	86	S	
	9	0	85	S	
Mukden (*Rps*$_1$) × Altona	1	160	10	15:1	0.98–0.95
	2	162	14	15:1	0.30–0.20
	3	172	44	3:1	0.80–0.70
	4	137	35	3:1	0.20–0.10
	5	1	81	S	
	7	0	91	S	
	9	0	97	S	
Sanga (*Rps*$_1^b$) × Altona	1	181	11	15:1	0.90–0.80
	2	157	41	3:1	0.20–0.10
	3	176	17	15:1	0.20–0.10
	4	168	15	15:1	0.30–0.20
	5	130	53	3:1	0.30–0.20
	7	140	46	3:1	0.90–0.80
	9	149	39	3:1	0.20–0.10
PI 54615-1 (*Rps*$_1^c$) × Altona	1	146	15	15:1	0.20–0.10
	2	140	15	15:1	0.10–0.05
	3	167	17	15:1	0.10–0.05
	4	131	49	3:1	0.50–0.30
	5	0	100	S	
	7	74	28	3:1	0.70–0.50
	9	69	17	3:1	0.30–0.20
Williams 82 (*Rps*$_1^k$) × Altona	1	213	19	15:1	0.30–0.20
	2	219	17	15:1	0.70–0.50
	3	223	18	15:1	0.50–0.30
	4	229	12	15:1	0.50–0.30
	5	167	57	3:1	0.90–0.80
	7	168	69	3:1	0.20–0.10
	9	163	69	3:1	0.10–0.05
PI 86972-1 (*Rps*$_3$) × Altona	1	164	11	15:1	0.98–0.95
	2	155	16	15:1	0.20–0.10
	3	153	12	15:1	0.70–0.50
	4	164	6	15:1	0.20–0.10
	5	143	34	3:1	0.10–0.05
	7	0	88	S	
	9	118	37	3:1	0.80–0.70
PI 86050 (*Rps*$_1^c$ *Rps*$_4$) × Altona	1	179	3	63:1	0.95–0.90
	2	204	3	63:1	0.90–0.80
	3	224	5	63:1	0.50–0.30
	4	237	17	15:1	0.80–0.70
	5	0	111	S	
	7	170	52	3:1	0.70–0.50
	9	172	44	3:1	0.20–0.10

[a] Ratio = resistant to susceptible.

TABLE 2. Breeding behavior of the progenies from F_2 plants from crosses of Altona with Harosoy, Mukden, Sanga, PI 86972-1, and PI 86050 to seven physiologic races of *Phytophthora megasperma* f. sp. *glycinea*

Parentage	Race	Number of F_2 plants[a]			Ratio[b]	χ^2 probability
		Resistant	Segregating	Susceptible		
Harosoy × Altona	1	18	48	34	1:2:1	0.20–0.10
	2	18	48	34	1:2:1	0.20–0.10
	3	18	48	34	1:2:1	0.20–0.10
	4	18	48	34	1:2:1	0.20–0.10
	5	0	0	25	S	
	7	0	0	25	S	
	9	0	0	25	S	
Mukden × Altona	1	49	48	3	7:8:1	0.50–0.30
	2	49	48	3	7:8:1	0.50–0.30
	3	18	59	23	1:2:1	0.20–0.10
	4	18	58	24	1:2:1	0.20–0.10
	5	0	0	25	S	
	7	0	0	25	S	
	9	0	0	25	S	
Sanga × Altona	1	39	46	15	7:8:1	0.05–0.02
	2	16	55	29	1:2:1	0.20–0.10
	3	34	51	15	7:8:1	0.02–0.01
	4	34	51	15	7:8:1	0.02–0.01
	5	23	52	25	1:2:1	0.90–0.80
	7	23	52	25	1:2:1	0.90–0.80
	9	23	52	25	1:2:1	0.90–0.80
PI 86972-1 × Altona	1	39	55	6	7:8:1	0.50–0.30
	2	39	55	6	7:8:1	0.50–0.30
	3	39	55	6	7:8:1	0.50–0.30
	4	39	55	6	7:8:1	0.50–0.30
	5	21	53	26	1:2:1	0.70–0.50
	7	0	0	25	S	
	9	21	53	26	1:2:1	0.70–0.50
PI 86050 × Altona	1	61	39	0	37:21:1	0.50–0.30
	2	61	39	0	37:21:1	0.50–0.30
	3	61	39	0	37:21:1	0.50–0.30
	4	42	52	6	7:8:1	0.98–0.95
	5	0	0	25	S	
	7	26	54	20	1:2:1	0.50–0.30
	9	26	54	20	1:2:1	0.50–0.30

[a] F_3 seedlings from the same F_2 plants were tested with each race.
[b] Ratio = homozygous resistant:heterozygous:homozygous susceptible.

(Table 1). The F_2 population segregated in a ratio of 15 resistant to one susceptible to race 4 and was completely susceptible to race 5. Rps_1^c conditions susceptibility to both of these races.

The preceding data indicate that Altona contains a gene that conditions resistance to races 1–4 and susceptibility to races 5–9 of *P. megasperma* f. sp. *glycinea*. The gene is equivalent in function to, but is not allelic with, Rps_1, Rps_1^b, Rps_1^c, Rps_1^k, Rps_3, and Rps_4. Rps_2 gives a variable reaction to hypocotyl inoculation, so the relation of Rps_2 to other genes would be difficult to determine by this method. Rps_5 was reported after this work was completed and was shown not to be at the locus of the gene in Altona (5). We propose that the gene for resistance in Altona be designated Rps_6, according to the rules for genetic symbols suggested by the Soybean Genetics Committee.

The F_2 plants from each of the crosses, as tested by their progenies in the F_3 generation (Table 2), verified the segregation ratios reported in Table 1, except for races 1, 3, and 4 in the cross of Sanga with Altona. Each of the three races in this cross had an excess of five susceptible plants. This is not a large discrepancy, but generally the susceptible category is the most accurate because it lacks the possibility of escapes that exists between the resistant and segregating categories when small numbers are involved. The fact that the same number of plants were susceptible to each race indicates that the data are correct and suggests that the 100-plant sample was not sufficiently representative of the F_2 population to fit a ratio of seven homozygous resistant to eight heterozygous to one homozygous susceptible with an excess in the smallest category, although it did fit a ratio of one homozygous resistant to two heterozygous to one homozygous susceptible to races 2, 5, 7, and 9.

Eleven new physiologic races of *P. megasperma* f. sp. *glycinea* were reported (7) while this work was in progress. We have found that Altona and strains with the gene Rps_4 react similarly to races 10–12 and 14–16, but Altona is susceptible to race 13, to which strains with Rps_4 are resistant. Altona is also resistant to races 18–20. Therefore, the gene Rps_6, which originally was thought to control resistance to only races 1–4, also controls resistance to races 10, 12, 14–16, and 18–20. Rps_6 in combination with Rps_1^k, Rps_1^b Rps_3, or Rps_1^c Rps_3 will give resistance to races 1–20.

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