Inheritance of Resistance to Four Physiologic Races of Phytophthora megasperma var. sojae

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ABSTRACT

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The F_2 populations and F_3 progenies from 10 soybean crosses were tested with physiologic races 1, 2, 3, and 4 of *Phytophthora megasperma* var. *sojae*. The soybean cultivars and plant introductions, Harosoy (susceptible to races 1, 2, 3, and 4), Mukden (resistant to races 1 and 2; susceptible to races 3 and 4), P.I. 54615-1 (resistant to races 1, 2, and 3; susceptible to race 4), P.I. 84637 (resistant to races 1, 3, and 4; susceptible to race 2), and P.I. 86972-1 (resistant to races 1, 2, 3, and 4) were selected as parents based on their reaction to the four races of the pathogen and each one was crossed to the other four. The data indicate that the resistance of Mukden, P.I. 54615-1, and P.I. 84637 is controlled by a different single dominant allele in each located at the same locus. To differentiate these alleles it is suggested that the allele in P.I. 54615-1 be designated Rps^c and the allele in P.I. 84637 be changed from $rps_1{}^2$ to Rps^b to form the allelomorphic series Rps^a, Rps^b, Rps^c, and *rps*, represented by Mukden, P.I. 84637, P.I. 54615-1, and Harosoy, respectively. The data further indicate that the resistance of P.I. 86972-1 is controlled by a single dominant allele located at a different locus. It is suggested that this allele provisionally be designated *Rps*3.

Additional key words: soybean disease.

Inheritance of resistance to Phytophthora root rot of soybeans [*Glycine max* (L.) Merrill] which is incited by *Phytophthora megasperma* Drechs. var. *sojae* A. A. Hildeb. was investigated first in 1957 (2) and found to be controlled by a single dominant gene in several soybean cultivars, including Mukden.

Physiologic race 2 was reported from Mississippi (9) after an isolate obtained from field-infected plants of experimental soybean strain D60-9647 was pathogenic in greenhouse tests on this and four other lines that had been resistant to previous isolates. Other lines resistant to race 1 were resistant to race 2 and lines susceptible to race 1 were also susceptible to race 2. Inheritance studies established that the resistance in cultivar Semmes to races 1 and 2 was controlled by the single dominant gene *Rps* which was dominant to the rps^2 gene in D60-9647, and that rps^2 was dominant to the *rps* gene in susceptible lines (4). The resistance in Semmes traces to the cultivar Arksoy. Race 3 was reported from Ohio (10) based on isolates with the ability to infect cultivars with the Mukden-type resistance. Soybean lines with the Arksoy-type and D60-9647-type resistances were resistant to this race. Race 4 was reported from Kansas in 1974 (11). Lines with the Mukden-type and Arksoy-type resistances were susceptible to this race and lines with the D60-9647-type resistance were resistant. Tests conducted in Indiana (1) identified Altona and 94 other lines that were resistant to races 1, 2, 3, and 4. These tests also identified 23 lines with the Mukden-type resistance, 34 lines with the Arksoy-type resistance, and 27 lines with the D60-9647-type resistance.

Tests with the cultivar CNS crossed with a cultivar with the Arksoy-type resistance and D60-9647 established that the resistance in CNS to root inoculation with races 1 and 2 was controlled by a single independent dominant gene located at a locus other than the locus of *Rps* and rps^2. This gene was designated Rps_2 (5). Plants with the Rps_2 gene are resistant when grown in a liquid culture of the fungus, but give a variable reaction when mycelium of the fungus is inserted into the hypocotyl.

The reaction of cultivars with the Mukden-, Arksoy-, D60-9647-, and Altona-type resistances to races 1, 2, 3, and 4 is not adequately explained by the allelomorphic series Rps_1, $rps_1{}^2$, and rps_1. Both the Mukden-type and the Arksoy-type resistances have been attributed to the Rps_1 gene because only race 1 was used in studying the Mukden-type resistance and only races 1 and 2 were used in studying the Arksoy-type resistance. The resistance in these two cultivars cannot be controlled by the same gene since they differ in their reactions to race 3. The $rps_1{}^2$ gene in D60-9647 was recessive to Rps_1, when tested with race 2 but $rps_1{}^2$ conveys resistance to race 3 to which Mukden is susceptible and to race 4 to which both Mukden and Arksoy are susceptible. Identification of races 3 and 4 has made it possible to demonstrate these differences and has provided the incentive and materials for additional studies on the inheritance of resistance in soybeans to *P. megasperma* var. *sojae*.

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MATERIALS AND METHODS

The soybean cultivars and plant introductions Harosoy, Mukden, P.I. 54615-1, P.I. 84637, and P.I. 86972-1 were selected as parents based on their reaction to physiologic races of the pathogen, maturity, agronomic type, and presence of recessive and dominant markers for flower and pubescence colors. Harosoy was selected as the universally susceptible parent, Mukden was selected to represent the Mukden-type resistance (resistant to races 1 and 2; susceptible to races 3 and 4), P.I. 54615-1 was selected to represent the Arksoy-type resistance (resistant to races 1, 2, and 3; susceptible to race 4), P.I. 84637 was selected to represent the D60-9647-type of resistance (resistant to races 1, 3, and 4; susceptible to race 2), and P.I. 86972-1 was selected to represent the Altona-type of resistance (resistant to races 1, 2, 3, and 4). The five parents were each crossed to the other four to produce 10 hybrid populations.

Inoculum was prepared by growing the isolates of the respective races on oatmeal agar in petri dishes for 2-3 wk at 24 C. A single isolate of races 1, 3, and 4 from Indiana and an isolate of race 2 from Mississippi were used. Inoculations were made by the hypocotyl method (6). Ten-day-old seedlings of the F_2 and F_3 generations and appropriate parental checks were inoculated with each race and incubated in the greenhouse at 24-27 C. Six days after inoculation the seedlings were classified as resistant (no external symptoms) or susceptible (dead). Approximately 200 F_2 seedlings of each cross were tested with each race and approximately 12 F_3 seedlings from 100 F_2 plants from each cross were tested to verify the segregations obtained in the F_2 populations and to confirm the location of alleles for resistance. The progeny of only 25 F_2 plants were evaluated if no segregation occurred in the F_2 population.

Data from the F_2 and F_3 generations were analyzed by the χ^2 (chi-square) test for goodness of fit (8).

RESULTS

The F_2 populations from the crosses of Harosoy with Mukden, P.I. 54615-1, P.I. 84637, and P.I. 86972-1 each segregated in a ratio of 3 resistant: 1 susceptible to those races to which the parent other than Harosoy was resistant (Table 1). To those races to which both parents were susceptible, the F_2 populations were uniformly susceptible except for a few apparent escapes with races 3 and 4 in the Mukden × Harosoy cross (Table 1). The F_2 plants from these four crosses, as tested by their F_3 progenies, segregated in a ratio of 1 homozygous resistant: 2 segregating: 1 homozygous susceptible to those races to which the one parent was resistant (Table 2). This verified the F_2 segregation. The F_3 progenies that were all resistant, segregating, or all susceptible to race 1 had the same reaction to the other races to which the parent other than Harosoy was resistant. All F_3 progenies were susceptible to those races to which both parents were susceptible. Apparently resistance in Mukden to races 1 and 2; in P.I. 54615-1 to races 1, 2, and 3; in P.I. 84637 to races 1, 3, and 4; and in P.I. 86972-1 to races 1, 2, 3, and 4 is controlled by a single dominant allele in each. Probabilities for χ^2 goodness of fit were greater than $P = 0.05$ in all cases.

The F_2 populations from intercrossing Mukden, P.I. 54615-1, and P.I. 84637 were resistant to those races to which both parents were resistant, were susceptible to the race to which both parents were susceptible, and segregated in a ratio of 3 resistant: 1 susceptible for those races to which only one parent was resistant (Table 1). The F_2 plants of these crosses, as tested by their F_3 progenies, were homozygous-resistant to those races to which both parents were resistant, were homozygous-susceptible to the race to which both parents were susceptible, and segregated in a ratio of 1 homozygous-resistant: 2 segregating: 1 homozygous-susceptible to those races to which only one parent was resistant (Table 2). The F_3 data verify the segregation in the F_2 populations. Probabilities for χ^2 goodness of fit in all cases were greater than $P = 0.05$.

For the cross of P.I. 54615-1 × P.I. 84637, F_3 progenies that were all resistant to race 2 were all susceptible to race 4, and F_3 progenies that were all susceptible to race 2 were all resistant to race 4. The F_3 progenies that segregated for race 2 also segregated for race 4.

For the cross of Mukden × P.I. 84637, F_3 progenies that were all resistant or all susceptible to race 2 were all susceptible or all resistant, respectively, to races 3 and 4. The F_3 progenies that segregated for race 2 also segregated for races 3 and 4.

The results indicate that the single dominant alleles for resistance in Mukden, P.I. 54615-1, and P.I. 84637 are located at the same locus and form an allelomorphic series.

The F_2 populations from crosses of P.I. 86972-1 with Mukden, P.I. 54615-1, and P.I. 84637 each segregated in a ratio of 15 resistant: 1 susceptible to those races to which both parents were resistant; and segregated in a ratio of 3 resistant: 1 susceptible to those races to which only P.I. 86972-1 was resistant (Table 1). The F_2 plants of these crosses, as tested by their F_3 progenies, segregated in a ratio of 7 homozygous-resistant: 8 segregating: 1 homozygous-susceptible to those races to which both parents were resistant; and segregated in a ratio of 1 homozygous-resistant: 2 segregating: 1 homozygous-susceptible to those races to which only P.I. 86972-1 was resistant (Table 2). The breeding behavior of the F_3 progenies verified the F_2 segregation ratio of 15 resistant: 1 susceptible when both parents were resistant, indicating the independent segregation of two dominant genes, and 3 resistant: 1 susceptible when only P.I. 86972-1 was resistant, indicating a single dominant gene for resistance in P.I. 86972-1. Probabilities for χ^2 goodness of fit in all cases were greater than $P = 0.05$. The F_3 progenies that were all resistant to race 1 were all resistant to the other races to which the parent other than P.I. 86972-1 was resistant and were all resistant, segregating, or all susceptible to the races to which this parent was susceptible. The F_3 progenies that were segregating to race 1 also were segregating to those races to which the parent other than P.I. 86972-1 was resistant and were segregating or all susceptible to the races to which this parent was susceptible. The F_3 progenies that were all susceptible to race 1 also were all susceptible to races 2, 3, and 4. These results further substantiate the hypothesis that Mukden has a dominant gene for resistance to races 1 and 2; P.I. 54615-1 has a dominant gene for resistance to races 1, 2, and 3; and P.I. 84637 has a dominant gene for

resistance to races 1, 3, and 4. Line P.I. 86972-1 has a dominant gene for resistance to races 1, 2, 3, and 4 which segregates independently of the genes present in Mukden, P.I. 84637, and P.I. 54615-1 and must be located at a different locus.

There were a few minor discrepancies in the F_3 data in the crosses of Mukden × Harosoy, Mukden × P.I. 84637, and P.I. 54615-1 × P.I. 84637 (Table 2). These apparently were due to the inability to detect any of the susceptible progenies from a segregating F_2 plant because of insufficient numbers.

DISCUSSION

The F_2 data, verified by the breeding behavior of the F_3 progenies, show that Mukden, P.I. 54615-1, P.I. 84637, and P.I. 86972-1 each have a single dominant allele for resistance to those races to which each is resistant. The alleles in Mukden, P.I. 54615-1, and P.I. 84637 form an allelomorphic series at one locus while the allele in P.I. 86972-1 is located at a different locus and segregates independently.

The dominant allele for resistance in both Mukden and

TABLE 1. Segregation of the F_2 populations of 10 soybean crosses to physiologic races 1, 2, 3, and 4 of *Phytophthora megasperma* var. *sojae*

Parentage	Race	No. of plants[a]		χ^2 probability	
		Res.	Susc.	3:1 ratio	15:1 ratio
Mukden × Harosoy	1	138	41	.70-.50	
	2	140	43	.70-.50	
	3	13	158		
	4	4	163		
Harosoy × P.I. 84637	1	137	54	.30-.20	
	2	0	203		
	3	136	41	.70-.50	
	4	131	54	.20-.10	
Harosoy × P.I. 54615-1	1	148	44	.70-.50	
	2	139	52	.50-.30	
	3	149	48	.90-.80	
	4	0	194		
Harosoy × P.I. 86972-1	1	157	49	.70-.50	
	2	155	64	.20-.10	
	3	150	36	.10-.05	
	4	163	52	.80-.70	
Mukden × P.I. 54615-1	1	172	0		
	2	200	0		
	3	117	44	.50-.30	
	4	0	182		
P.I. 54615-1 × P.I. 84637	1	168	0		
	2	128	45	.80-.70	
	3	150	0		
	4	103	32	.80-.70	
Mukden × P.I. 84637	1	106	1		
	2	70	31	.20-.10	
	3	87	26	.70-.50	
	4	119	44	.70-.50	
P.I. 86972-1 × P.I. 54615-1	1	190	10		.50-.30
	2	183	11		.80-.70
	3	169	14		.50-.30
	4	130	39	.70-.50	
P.I. 86972-1 × P.I. 84637	1	175	6		.20-.10
	2	127	50	.50-.30	
	3	173	12		.90-.80
	4	176	8		.30-.20
Mukden × P.I. 86972-1	1	170	13		.70-.50
	2	164	17		.10-.05
	3	153	49	.90-.80	
	4	146	46	.70-.50	

[a]Abbreviations: Res. = resistant; Susc. = susceptible.

Arksoy was previously assigned the symbol Rps_1 and the allele in D60-9647 the symbol rps_1^2. These assignments were based on results from testing Mukden with race 1 and D60-9647 and a cultivar with the Arksoy-type resistance with races 1 and 2 of the pathogen. The symbol rps_1^2 was assigned to signify the recessive nature of the allele in D60-9647 for race 2 in comparison with the dominant allele Rps_1 for resistance to races 1 and 2 in a cultivar with the Arksoy-type resistance. The results from our crosses indicate that the allele in P.I. 84637 (D60-9647-type) is recessive to the allele in Mukden and the allele in P.I. 54615-1 (Arksoy-type) for race 2, but is dominant to the allele in Mukden for races 3 and 4 and also to the allele in P.I. 54615-1 for race 4. To denote the dominant nature of the allele in P.I. 84637 to races 3 and 4 it is suggested that the symbol be changed from rps_1^2 to Rps^b. The soybean genetics committee has recommended the use of lower-case letters rather than numbers as superscripts to denote different alleles at the same locus.

The dominant allele for resistance to races 1 and 2 in the cultivar with Arksoy-type resistance was designated Rps_1. This is the same symbol given to the allele for resistance to

TABLE 2. Breeding behavior of the F_3 progenies from F_2 plants of 10 soybean crosses to physiologic races 1, 2, 3, and 4 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
Mukden × Harosoy	1	24	55	21	.70-.50	
	2	25	54	21	.70-.50	
	3	0	0	25		
	4	0	0	25		
Harosoy × P.I. 84637	1	17	52	31	.20-.10	
	2	0	0	100		
	3	17	52	31	.20-.10	
	4	17	52	31	.20-.10	
Harosoy × P.I. 54615-1	1	27	56	17	.20-.10	
	2	27	56	17	.20-.10	
	3	27	56	17	.20-.10	
	4	0	0	25		
Harosoy × P.I. 86972-1	1	24	51	25	.98-.95	
	2	24	51	25	.98-.95	
	3	24	51	25	.98-.95	
	4	24	51	25	.98-.95	
Mukden × P.I. 54615-1	1	100	0	0		
	2	100	0	0		
	3	19	55	26	.50-.30	
	4	0	0	25		
P.I. 54615-1 × P.I. 84637	1	100	0	0		
	2	29	50	21	.70-.50	
	3	25	0	0		
	4	21	51	28	.70-.50	
Mukden × P.I. 84637	1	100	0	0		
	2	26	47	27	.90-.80	
	3	28	48	24	.80-.70	
	4	28	48	24	.80-.70	
P.I. 86972-1 × P.I. 54615-1	1	54	42	4		.20-.10
	2	54	42	4		.20-.10
	3	54	42	4		.20-.10
	4	31	47	22	.50-.30	
P.I. 86972-1 × P.I. 84637	1	49	44	7		.50-.30
	2	29	55	16	.20-.10	
	3	50	43	7		.50-.30
	4	50	43	7		.50-.30
Mukden × P.I. 86972-1	1	45	50	5		.90-.80
	2	45	50	5		.90-.80
	3	23	59	18	.20-.10	
	4	23	59	18	.20-.10	

[a]Abbreviations: Res. = resistant in F_3; Seg. = segregating in F_3; Susc. = susceptible in F_3.

race 1 in Mukden. However, Mukden is susceptible to race 3, and P.I. 54615-1 (Arksoy-type) is resistant to race 3. To differentiate the dominant allele for resistance in the Arksoy-type from the allele for resistance in the Mukden-type we propose the symbol *Rps*^{c} be assigned to this allele. This extends the allelomorphic series to *Rps*^{a}, *Rps*^{b}, *Rps*^{c}, and *rps* represented by Mukden, P.I. 84637 (D60-9647-type), P.I. 54615-1 (Arksoy-type), and Harosoy, respectively.

Line P.I. 86972-1 was selected to represent the Altona-type of resistance (resistant to races 1, 2, 3, and 4). Subsequent identification of races 5-9 (3, 7) has shown that P.I. 86972-1 and Altona are not identical in their reactions to all races. Our tests have shown that P.I. 86972-1 is resistant to races 5, 8, and 9, and that Altona is susceptible to races 5-9. For this reason, the resistance conferred by the dominant allele in P.I. 86972-1 will be referred to as the P.I. 86972-1-type of resistance. The results from these crosses clearly show that the dominant allele for resistance in P.I. 86972-1 is not located at the locus of the *Rps* allelomorphic series. We propose that the symbol *Rps*3 be provisionally assigned to the dominant allele for resistance to races 1, 2, 3, and 4 in P.I. 86972-1. There is no evidence that *Rps*3 and *Rps*2 (CNS-type resistance to root inoculation) are not located at the same locus, but this would be difficult to determine by hypocotyl inoculation because of the variable reaction of *Rps*2 to this method of inoculation.

There are now five known dominant alleles for resistance to *P. megasperma* var. *sojae*; three of which are located at the same locus. These are *Rps*^{a} (Mukden-type) allele for resistance to races 1 and 2; *Rps*^{b} (D60-9647-type) allele for resistance to races 1, 3, and 4; *Rps*^{c} (Arksoy-type) allele for resistance to races 1, 2, and 3; *Rps*2 (CNS-type) allele for resistance to races 1 and 2 to root inoculation; and *Rps*3 (P.I. 86972-1-type) allele for resistance to races 1, 2, 3, and 4.

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