PHYTOPHTHORA MEGASPERMA VAR. SOJAE RACE 4: VARIETAL REACTIONS AND INHERITANCE OF RESISTANCE

by

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INTRODUCTION

A root and stem rot of soybean, *Glycine max* (L.) Merr., caused by a species of *Phytophthora* deBy. was first reported from Ohio by Suhovecky and Schmitthenner (12) in 1951. Since then, it has been reported from many areas of the Midwest and South. Herr (4) identified the causal agent as *Phytophthora cactorum* (Leb. & Cohn.) Schroet. in 1957. In 1958, Kaufmann and Gerdemann (6) described the pathogen as a new species and proposed the name *Phytophthora sojae*. However, in 1959, Hildebrand (5) proposed the trinomial *Phytophthora megasperma* Drechs. var. *sojae* A. A. Hildeb. considering it a variety of that species. This classification is the most widely accepted and will be followed here.

Physiologic specialization was first reported as race 2 from Mississippi by Morgan and Hartwig (7) in 1965. They grouped their isolates into two races based on pathogenicity to selected soybean genotypes. A third race, pathogenically different from races 1 and 2, was reported from Ohio by Schmitthenner (8) in 1972.

Bernard et al. (2) found that resistance to race 1 is controlled by a single dominant gene. Modifier genes which inhibit full expression of the dominant resistance gene in certain crosses have also been reported (10). Resistance to race 2 has been described as part of an allelomorphic series containing three different alleles (3).

Eighteen isolates of *Phytophthora megasperma* var. *sojae (Pms)* were collected from Kansas and Nebraska in 1973. Pathogenicity tests were undertaken to determine if differences existed among these isolates.

METHODS AND MATERIALS

Isolations were made from plants at or near the flowering stage. Pieces of diseased stem were surface sterilized in 0.8% sodium hypochlorite, rinsed in sterile distilled water, and plated on lima bean agar (LBA, Difco, 23 grams/liter). *Pms* was tentatively identified three to five days later by appressant growth and numerous oospores. All cultures were maintained on LBA.

Plant reactions to isolates of the fungus were tested by the hypocotyl inoculation technique of Kaufmann and Gerdemann (6). A small piece of agar with the fungus was placed into a small vertical slit in the hypocotyl and the opening covered with petrolatum. At least eight plants of a soybean line were tested. A soybean line was considered susceptible if the hypocotyl collapsed within 14 days of inoculation. All work was done in the greenhouse at temperatures of 18-27° C.

Reciprocal crosses were made between the cultivar Columbus and the experimental line D60-9647 from Mississippi. The plants were grown in the greenhouse at 18-27° C under a 14 hour photoperiod which was reduced to 12 hours to induce flowering when the plants were six to eight weeks old.

The F_1 seed was planted in an irrigated field at the Ashland Experiment Field near Manhattan. The plants were observed for differences in growth habit and maturity which were the markers for these crosses. D60-9647 has a determinate growth habit and belongs to Maturity Group V or VI. Columbus has an indeterminate growth habit and belongs to Maturity Group IV.

Pods from the F_1 plants were collected late in the season but before maturity, and dried at 43° C for two days. Additional F_2

seed from the crosses D60-9647 X Columbus, D60-9647 X Pomona, Williams X D60-9647, and reciprocal crosses between D60-9647 and Bonus were obtained from C. D. Nickell, Department of Agronomy, Kansas State University, Manhattan. F_2 seeds were planted, 12 per pot in 4½ inch pots, in the greenhouse. The developing plants were inoculated in the hypocotyl with isolate R-ck when the first true leaves had expanded, about 10-16 days after planting.

RESULTS

Pathogenicity tests indicated that four of the isolates were more pathogenic than race 1 or race 2. One isolate from Wayne soybeans in Douglas County, Nebraska fit the pathogenicity decsription for race 3 (8) and was designated R-T. The other three isolates were more pathogenic than any previously decribed races. Two of these isolates were collected in Atchison County, Kansas from Clark 63 and Cutler soybeans in fields about one mile apart on the same farm. These were designated R-ck and R-ct, respectively. The third isolate came from irrigated Calland soybeans in Sedgwick County, Kansas and was designated R-cd. Because isolate R-ct came from the same area as isolate R-ck and the two appeared to be the same, isolate R-ct was dropped from the screening program.

The developing cultures of these isolates were morphologically indistinguishable from a culture of race 1 obtained from B. L. Keeling, Southern Regional Soybean Laboratory, Stoneville, Mississippi.

Within the 51 lines tested against races 1, 2, 3, and isolates R-cd and R-ck, five different reaction groups were recognized (Table 1).

Isolates R-cd and R-ck were alike in pathogenicity and as a group were more pathogenic than races 1, 2, or 3 (7,8). Members of this group are therefore proposed as isolates of a new race 4 (Table 2).

An attempt was made to incorporate resistance to race 4 from the experimental line D60-9647 into the cultivars Bonus, Columbus, Pomona, and Williams, thus providing a means of studying the inheritance of resistance. Bonus, a cultivar that is grown in Kansas, is resistant to races 1 and 2, but susceptible to races 3 and 4. Columbus and Pomona, recently released (1972 and 1974, respectively) soybean cultivars adapted to Kansas, are susceptible to all four races of *Pmg*.

Table 1. Reaction of soybean lines to hypocotyl inoculation of races 1, 2, 3, and isolates R-cd and R-ck of *Phytophthora megasperma* var. *sojae*.

Group A: susceptible to races 1, 2, 3, and isolates R-cd and R-ck.[a]	Group B: susceptible only to race 3 and isolates R-cd and R-ck.	Group C: susceptible only to isolates R-cd and R-ck.	Group D: susceptible only to race 2.	Group E: resistant to races 1, 2, 3, and isolates R-cd and R-ck.
Amsoy	Mitchell	Amsoy 71	Arksoy	D60-9647	Tracy
Bellatti L-263	NK-9210	Beeson	D54-2437	Harrel	
Columbus	SRF-307	Bonus	Lee 68	Nansemond	
Corsoy	SRF-350[b]	Calland	Mack		
Cutler	SRF-425[b]	Clark 63	Pickett 71		
Dare	SRF-450	Cutler 71			
Essex	Seedmakers 1-E	FFR 333			
Forrest[b]	Shawnee	FFR 444			
Hark	TEW2D-313-1	FFR-955318			
K2-70-14	Wabash	K1007[b]			
K2-70-16	Wayne	Oksoy[b]			
K2-70-133	Williams	SRF-200[b]			
Kent	Woodworth[b]	SRF-400			
Pomona	XK 707				
Marshall					

[a] Oksoy segregates against race 1. FFR 444 and FFR-955318 segregate against race 1 and race 2.

[b] Forrest, Oksoy, SRF-200, SRF-425, and Woodworth were not tested against race 2.

Table 2. Reaction of soybean group lines to hypocotyl inoculation with four races of *Phytophthora megasperma* var. *sojae*.

Group	Races[a] 1	2	3	4	Differential variety
A	S[b]	S	S	S	Columbus
B	R[c]	R	S	S	Calland
C	R	R	R	S	Mack
D	R	S	R	R	D60-9647
E	R	R	R	R	Tracy

[a] Race 1 from B. L. Keeling; race 2 from N. T. Keen; race 3 from Nebraska; race 4 from Kansas. [b] Susceptible; hypocotyl collapsed within 14 days of inoculation. [c] Resistant; hypocotyl not collapsed.

The cultivar Williams also performs well in Kansas and has been shown to be field tolerant to race 1 (1), but is susceptible to all four races when inoculated in the greenhouse. D60-9647 is resistant to races 1, 3, and 4, but susceptible to race 2. The breeding experiment was begun before it was realized that the cultivar Tracy is resistant to all four races of *Pms*. However, D60-9647 is a parent of Tracy and Tracy inherits its resistance to race 4 from D60-9647.

The results of inoculation of the F_2 plants with race 4 gave a good fit to a 9:7 ratio except in the D60-9647 X Bonus cross which gave a good fit to a 3:1 ratio (Table 3). Populations of the reciprocal crosses between D60-9647 and Columbus were considered to be too small to obtain valid results.

The low number of susceptible plants in the D60-9647 X Bonus cross indicated that self-pollinated plants of D60-9647 might be present in the population. To test this, all plants resistant to race 4 in the reciprocal crosses involving D60-9647 and Bonus were hypocotyl inoculated with race 2 approximately two weeks after inoculation with race 4. D60-9647 is susceptible, and Bonus is resistant to race 2 and it has been shown that resistance to this race is controlled by a single gene as part of an allelomorphic series (7). If self-pollinated D60-9647 plants were present in the population of the D60-9647 X Bonus cross, then greater than one-fourth of the plants would be susceptible to race 2. Conversely, if self-pollinated Bonus plants were present in the Bonus X D60-9647 cross then fewer than one-fourth of the plants would be susceptible to race 2. Results of these inoculations are shown in Table 4. The results obtained gave a good fit to a 3:1 ratio and thus eliminates the possibility

Table 3. Results of inoculation of F_2 plants with *Phytophthora megasperma* var. *sojae* race 4.

Cross	Plants inoc.	Resist.	Suscep.	Ratio	X^2 a
D60-9647 X Pomona	152	87	65	9:7	.06
	105	61	44	9:7	.15
Williams X D60-9647	64	36	28	9:7	0
	165	81	84	9:7	3.36
Bonus X D60-9647	117	71	46	9:7	.94
Total	603	336	267	9:7	.07
D60-9647 X Bonus	312	235	77	3:1	.02

[a] X^2 value at .05 with 1 DF = 3.84.

Table 4. Inoculation of F_2 plants from reciprocal crosses between Bonus and D60-9647 with *Phytophthora megasperma* var. *sojae* race 2.

Cross	Plants inoc.	Resist.	Suscep.	Ratio	X^2 a
Bonus X D60-9647	72	53	19	3:1	.82
D60-9647 X Bonus	232	170	62	3:1	2.38
Total	304	223	81	3:1	.44

[a] X^2 value at .05 with 1 DF = 3.84.

of self-pollinated plants in the reciprocal crosses involving D60-9647 and Bonus.

DISCUSSION

Race 4 of *Phytophthora megasperma* var. *sojae* is morphologically similar to, but pathogenically different from, *Pms* races 1, 2, and 3. Isolations were made from plants at or near the flowering stage, thus the pathogen is able to attack older plant as well as seedlings. The symptoms produced by race 4 correspond to those produced by the previously described races of *Pms*. Differential cultivars can be used to distinguish each of the four known races of *Pms* (Table 2).

The 9:7 ratios obtained in the crosses D60-9647 X Pomona, Williams X D60-9647, and Bonus X D60-9647 fit a model in which resistance to race 4 would be controlled by two independent dominant genes that are complimentary occuring at loci that are not involved in resistance to races 1 and 2. This can be illustrated as follows using the crosses D60-9647 X Pomona and Bonus X D60-9647.

D60-9647 X Pomona: D60-9647 has been shown to have the $rps_1^2rps_1^2$ allele (7), giving resistance to race 1 and susceptibility to race 2. Pomona has the rps_1rps_1 allele which is recessive to $rps_1^2rps_1^2$ and gives a susceptible reaction to races 1 and 2. Assume for the illustration that AA or Aa in conjuction with rps_1^2___ gives resistance to race 4 and aa gives susceptibility to race 4.

D60-9647 X Pomona

$rps_1^2rps_1^2AA$ X rps_1rps_1aa

F_1 genotype $rps_1^2rps_1Aa$ (F_1 plants were self-pollinated)

F_2 resistant genotypes	F_2 susceptible genotypes
1 $rps_1^2rps_1^2AA$	1 $rps_1^2rps_1^2aa$
2 $rps_1^2rps_1^2Aa$	2 $rps_1^2rps_1aa$
2 $rps_1^2rps_1AA$	1 rps_1rps_1AA
4 $rps_1^2rps_1Aa$	2 rps_1rps_1Aa
	1 rps_1rps_1aa

This gives a theoretical 9:7 ratio.

Bonus X D60-9647: Bonus is resistant to races 1 and 2 and carries the Rps_1Rps_1 allele which is dominant to the $rps_1^2rps_1^2$ allele of D60-9647.

	Bonus	X D60-9647
	Rps_1Rps_1aa	X $rps_1^2rps_1^2AA$
F_1 genotype	$Rps_1rps_1^2Aa$ (F_1 plants were self-pollinated)	
F_2 resistant genotypes		F_2 susceptible genotypes
1 Rps_1Rps_1AA		1 Rps_1Rps_1aa
2 Rps_1Rps_1Aa		2 $Rps_1rps_1^2aa$
2 $Rps_1rps_1^2AA$		1 $rps_1^2rps_1^2aa$
4 $Rps_1rps_1^2Aa$		1 $rps_1^2rps_1^2AA$ *
		2 $rps_1^2rps_1^2Aa$ *

In order to get a theoretical 9:7 ratio in the above example, some of the genotypes that were resistant in the D60-9647 X Pomona cross would have to be placed in the susceptible category in the Bonus X D60-9647 cross as indicated by the asterisk (*). Thus, it seems unlikely that the locus controlling resistance to races 1 and 2 is involved in controlling resistance to race 4.

It is proposed that the genes controlling resistance to race 4 be designated Rps_3rps_3 and Rps_4rps_4. However, further studies are needed before positive identification can be made.

The 3:1 ratio obtained in the D60-9647 cross is difficult to explain. The possibility of self-pollinated D60-9647 plants existing in the population was eliminated by inoculating the population with race 2 and obtaining a good fit to a 3:1 ratio. The possibility of D60-9647 cytoplasm having an effect can be ruled out as D60-9647 was used as a female in the cross with Pomona and a good fit to a 9:7 ratio was obtained with that cross. Germination of the seed was 63%

and it might be possible that germination was higher for seeds that became resistant plants. Another possibility might be that since D60-9647 is an experimental line, some minor genetic differences might exist between plants in the same line. Testing of succeeding generations should give sufficient data to explain the 3:1 ratio obtained in the F_2 generation of the D60-9647 X Bonus cross.

Appendix A. Reaction of soybean lines inoculated with four races of *Phytophthora megasperma* var. *sojae*.

Variety	race 1	race 2	race 3	race 4 isolate R-cd	race 4 isolate R-ck	race 4 isolate R-ct
Amsoy	8/8[a]	10/10	8/8	9/9	10/10	-[b]
Amsoy 71	0/10	0/20	10/10	16/16	12/12	-
Arksoy	0/11	0/18	0/8	55/66	8/9	-
Beeson	0/14	0/11	11/11	15/15	17/17	-
Bellatti L-263	11/11	17/17	11/11	11/11	10/10	-
Bonus	0/9	0/17	9/9	9/9	8/8	-
Calland	0/19	0/16	17/17	14/15	11/11	10/10
Clark 63	0/10	0/15	11/11	15/15	11/11	-
Columbus	23/23	14/14	16/16	18/18	12/12	10/10
Corsoy	8/8	18/18	10/10	9/9	8/8	-
Cutler	8/8	9/9	8/8	9/9	12/12	3/3
Cutler 71	0/11	0/14	10/10	11/11	8/8	-
D54-2437	1/10	0/14	1/10	15/17	8/10	-
D60-9647	0/9	11/11	0/18	2/19	1/17	-
Dare	8/8	7/8	11/11	11/11	11/11	-
Essex	11/11	14/15	11/11	12/12	12/12	-
FFR 333	1/13	0/9	13/13	11/11	11/11	-
FFR 444	7/19[c]	8/15[c]	10/10	11/11	10/10	-
FFR 955318	13/24[c]	7/15[c]	9/9	12/12	12/12	-
Forrest	9/9	-	8/8	7/8	8/8	-
Hark	9/9	17/18	10/10	18/18	10/10	-
Harrel	0/12	10/12	0/12	0/12	0/11	-
K2-70-14	18/18	11/11	8/8	18/18	11/11	-
K2-70-16	17/17	19/19	8/8	20/20	8/8	-
K2-70-133	8/8	9/9	10/10	13/13	11/11	-
Kent	10/10	19/19	21/21	22/22	8/8	-
Lee 68	0/10	0/18	0/8	11/11	8/8	-
Mack	1/33	0/14	0/23	26/26	20/20	12/12
Marshall	11/11	17/17	21/21	22/22	8/8	-
Mitchell	10/10	13/15	9/9	8/8	10/10	-
NK-9210	9/9	15/15	8/8	11/11	9/9	-
Nansemond	0/12	14/14	0/11	1/11	2/11	-
Oksoy	6/13[c]	-	8/8	8/8	10/10	-

Variety	race 1	race 2	race 3	race 4 isolate R-ed	race 4 isolate R-ck	race 4 isolate R-ct
Pickett 71	0/12	0/16	0/24	23/23	8/8	-
Pomona	13/13	15/15	14/14	-	14/14	-
K1007	0/12	0/20	10/10	9/9	9/9	-
SRF-200	0/10	-	12/12	9/9	9/9	-
SRF-307	14/14	17/17	9/9	18/18	10/10	-
SRF-350	10/10	8/9	8/8	10/10	11/11	-
SRF-400	1/26	0/16	24/24	18/18	21/21	-
SRF-425	11/11	-	9/9	15/15	9/9	-
SRF-450	11/11	12/14	8/8	9/9	17/17	-
Seedmakers 1-E	11/11	16/16	9/9	11/11	10/10	-
Shawnee	10/10	16/16	12/12	9/9	12/12	-
TEW2D-313-1	11/11	17/17	11/11	8/8	11/11	-
Tracy	0/10	0/15	0/8	0/10	1/16	-
Wabash	9/10	15/15	12/12	13/13	21/21	-
Wayne	19/19	15/15	22/22	18/18	22/22	-
Williams	10/10	15/15	9/9	9/9	10/10	-
Woodworth	10/10	-	9/9	8/8	9/9	-
XK 707	20/20	14/14	10/10	8/8	17/17	-

[a]number dead/number inoculated, after 14 days; at least eight plants per variety were inoculated. [b]- indicates not tested. [c]mixed population; close to 50% killed.

Appendix B. Methods used in making soybean crosses.

Flowers to be used as females for seed production were emasculated by gently removing the corolla from the flower with a pair of forceps just as the corolla began to emerge from the calyx. Pollen used in the crosses was obtained by gently removing the stamens by their filaments from selected flowers using forceps. Pollen was always selected from flowers in which the corolla had not yet opened. Pollination was achieved by inserting the stamens into the emasculated flower.

A tag labeled with the parents, female X male, was placed around the stem just below the node where the cross was made. Any new flower buds that later appeared at a node where a cross was made were removed. Crosses were made no later than two hours after sunrise and whenever flowers to be used as females were at the proper age and continued until the plants stopped flowering. The plants were allowed to mature and the F_1 seed collected from individual pods.

Appendix C. Attempts to hybridize *Phytophthora megasperma* var. *sojae*.

An attempt was made to hybridize races of *Pms*. Four different combinations were used: race 1 X race 2, race 1 X race 3, race 1 X race 4(isolate R-ck), and race 2 X race 4(isolate R-ck).

The two races were placed on opposite sides of a petri plate containing lima bean agar and were allowed to grow until the colonies met. Five days after the colonies merged, subcultures were made from the overlap area. Each of these subcultures was allowed to grow and then used to inoculate a set of differential cultivars. The criterion for determining that hybridization had occurred would be a pathogenicity pattern unlike that of either parent.

In all cases, the reaction was that of the more virulent parent race; thus no detectable hybridization had occured. Since *Pms* is homothallic and the antheridium and the oogonium are in close proximity it seems unlikely that any sexual outcrossing would occur between races. However, hyphal fusion could occur, but the cultures were not followed close enough to observe this. The inoculum introduced into the plant could have been a mixture of both races with the most virulent one producing the reaction.

Appendix D. Soil infestation with *Phytophthora megasperma* var. *sojae*.

Four different methods of soil infestation with *Pms* were tried in an attempt to find a method that would allow a more natural type infection and at the same time yield results similar to those obtained by artificial hypocotyl inoculation. No controls were used in the experiments as they were preliminary tests.

The first method was based on that of Slusher and Sinclair (9) except that instead of seeding directly into sand, five day-old Columbus seedlings were transplanted into infested sand in four-inch pots and race 4 (isolate R-ck) was used instead of race 1.

In the second method, the inoculum consisted of an entire lima bean agar disc from a 100 mm petri plate completely covered with *Pms* race 4 (isolate R-ck). A four-inch pot was two-thirds filled with soil and the agar disc placed on top of the soil. The agar disc was then covered with one inch of soil. Ten Columbus seeds were placed on the soil and covered with vermiculite.

The inoculum for the third method consisted of an entire lima bean agar disc from a 100 mm perti plate covered with *Pms* race 4 (isolate R-ck) blended in 50 ml of distilled water for 10 seconds and then diluted to 300 ml. Half of this mixture was poured around the base of 11 day-old Columbus seedlings planted in soil in four-inch pots. The other half was poured around the base of 11 day-old D60-9647 seedlings planted in soil in four-inch pots.

For the fourth method, 50 seeds of K2-70-16 soybeans were planted in sand in an eight-inch diameter pot and allowed to grow. The developing plants were inoculated in the hypocotyl with *Pms* race 1 (isolate Pn-2), allowed to die, and the dead plants buried in the upper 1½ inches of sand. This procedure was repeated in the same pot. A third

planting was made and the plants that emerged were allowed to grow.

Sixty seedlings were transplanted into infested sand in the first method and 15 were killed after 10 days.

For the second method, of the 60 seeds planted, 54 seedlings emerged and six of these died after emergence.

The third method was replicated twice with one pot of each variety per replication. None of the 22 Columbus seedlings were killed and all 18 of the D60-9647 seedlings remained healthy after 10 days.

The fourth method gave results most consistent with results obtained by hypocotyl inoculation. After the sand had been infested, 23 of the 50 seedlings from the third planting emerged and all 23 died within 10 days. Germination of healthy seed was 82%.

Based on these four experiments, hypocotyl inoculation is still the best method especially when screening small numbers of seed. The fourth method gave good results, but part of the seed would have to be used to determine the germination percentage and would reduce the number of seeds tested.

Appendix E. Inoculation of soybean with alfalfa pathogen *Phytophthora megasperma* Drechs. and inoculation of alfalfa with soybean pathogen *Phytophthora megasperma* Drechs. var. *sojae* A. A. Hildeb. race 4.

The possibilities that the alfalfa pathogen *Phytophthora megasperma* might attack Columbus soybean and the soybean pathogen *Phytophthora megasperma* var. *sojae* race 4 might attack Kanza alfalfa were explored.

Twelve 13 day-old alfalfa plants and 11 13 day-old soybean plants were inoculated in the hypocotyl with *Pms* race 4 (isolate R-ck). The alfalfa plants showed no reaction 14 days after inoculation, while all the soybean plants were dead.

Nine 12 day-old alfalfa plants and 12 12 day-old soybean plants were inoculated in the hypocotyl with *Phytophthora megasperma* obtained from D. L. Stuteville, Department of Plant Pathology, Kansas State University, Manhattan. Ten days after inoculation, all alfalfa plants were dead. Three alfalfa plants were slit and covered with petrolatum to serve as controls. All three remained healthy. Three soybean plants developed slight necrosis at the point of inoculation; the other nine remained symptomless.

Appendix F. Survey for *Phytophthora megasperma* var. *sojae* in Kansas.

Thirty-three eastern and central Kansas counties were surveyed in 1974 to determine if *Pms* race 4 could be found in areas of the state other than where it was first found in 1973 and to determine the prevelance of other races.

Pieces of plants that appeared as if they might have been killed by *Pms* were surface sterilized and plated on lima bean agar to try to recover the fungus. In addition, slices of infected plant tissue were autoclaved in lactophenol with Sudan IV for 15 minutes to demonstrate oospores; this latter method helped determine the presence of *Pms* in plants that had been dead too long to permit easy recovery of the fungus.

Pms race 4 was recovered from two farms in McPherson County. One isolate was recovered from Clark 63 soybeans in a field that had been continuously planted to soybeans for nine years. The field was irrigated by a center pivot sprinkler system. The second isolate was recovered from Williams soybeans in a field that was furrow irrigated.

Pms race 1 was recovered from Jackson, Johnson, and Riley Counties.

Plants from each of the following 11 counties gave positive stain results for oospores: Anderson, Atchison, Douglas, Franklin, Jackson, Johnson, McPherson, Miami, Osage, Riley, and Sedgwick. It was not possible to determine the race of *Pms* by the staining technique.

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PHYTOPHTHORA MEGASPERMA VAR. SOJAE RACE 4: VARIETAL REACTIONS AND INHERITANCE OF RESISTANCE

by

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Isolates of *Phytophthora megasperma* var. *sojae* found in Kansas in 1973 were pathogenically different than races 1, 2, and 3 of this fungus. These isolates are proposed as isolates of a new race 4. Resistance to race 4 is controlled by two independent dominant genes that are complimentary. These genes occur at loci that are not involved in resistance to races 1 and 2.