Races of *Phytophthora sojae* and Their Virulences on Soybean Cultivars in Heilongjiang, China

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ABSTRACT

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Phytophthora root and stem rot, caused by *Phytophthora sojae*, is an economically important disease of soybean (*Glycine max*) in Heilongjiang Province, China. The objectives of this research were to determine the race profile of *P. sojae* in Heilongjiang and evaluate soybean cultivars for reactions to the pathogen races. A total of 96 single-zoospore *P. sojae* isolates were obtained from soil samples collected from 35 soybean fields in 18 counties in Heilongjiang from 2005 to 2007. Eight races of *P. sojae*, including races 1, 3, 4, 5, 9, 13, 44, and 54, were identified on a set of eight differentials, each containing a single resistance *Rps* gene, from 80 of the 96 isolates. Races 1 and 3 were predominant races, comprising 58 and 14 isolates, and representing 60 and 7% of the pathogen population, respectively. Races 4, 5, 44, and 54 were identified for the first time in Heilongjiang, and each was represented by two to three isolates only. Sixty-two soybean cultivars commonly grown in Heilongjiang Province were evaluated for their resistance to the eight *P. sojae* races identified using the hypocotyl inoculation technique. Based on the percentage of plant mortality rated 5 days after inoculation, 44 cultivars were resistant (<30% mortality) to at least one race. These cultivars may be used as sources of resistance in soybean breeding programs.

Phytophthora root and stem rot, caused by *Phytophthora sojae* Kaufmann & Gerdemann, is a destructive disease of soybean (*Glycine max* (L.) Merr.) worldwide (8,31). The disease was first observed in Indiana in 1948 and Ohio in 1951 in the United States, and the causal agent was described in 1955 (14). Phytophthora root and stem rot reduces soybean yield by 10 to 40% (2), and severe infection can result in a total yield loss. China is the third largest soybean producing country in the world, following the United States and Brazil. *P. sojae* was not found in China until 1991, when Shen and Su (28) isolated the pathogen for the first time in Heilongjiang Province where most of the soybean are grown in China. Since then, the disease has become widespread in Heilongjiang, and the annual infected

area is estimated at over 150,000 ha (11,20,32).

The pathogenic variation of *P. sojae* was first reported in 1955 (14). To date, there have been at least 55 races identified based on their reactions on a set of 8 or 13 differentials, each containing a single resistance gene (10,13,17,23). Although new races of *P. sojae* may appear with the release of resistant cultivars, the use of genetic resistance still remains the most effective strategy to reduce losses caused by the pathogen (6). A total of 14 single dominant genes (*Rps*) at eight genomic loci conferring resistance to specific races of *P. sojae*, including *Rps1a*, *Rps1b*, *Rps1c*, *Rps1d*, *Rps1k*, *Rps2*, *Rps3a*, *Rps3b*, *Rps3c*, *Rps4*, *Rps5*, *Rps6*, *Rps7*, and *Rps8*, have been reported in the world (1,3,16).

Monitoring the racial composition and dynamics of the pathogen population is a key component of resistance breeding programs to Phytophthora root and stem rot. Race 1 was the first *P. sojae* race identified in Heilongjiang in 1999 (22). Since then, races 3, 9, 11, 13, 17, 21, and 24 have also been reported (20,21,33,36). These races were identified from the pathogen collected in isolated fields in a few coun-

ties in Heilongjiang. There has been no extensive research on race profile and dynamics of the pathogen population in Heilongjiang, resulting in a lack of information needed by the regional resistance breeding programs. The objectives of this research were to collect and characterize *P. sojae* isolates from soybean fields across Heilongjiang Province, and to evaluate soybean cultivars commonly grown in the province for their resistance to the various races.

MATERIALS AND METHODS

Field sampling. Soil samples were collected from 10 fields in 7 counties in 2005, 16 fields in 12 counties in 2006, and 9 fields in 7 counties in 2007. The 18 counties where the 35 samples were collected are shown in Figure 1. Fields were selected for sampling based on the presence of Phytophthora root and stem rot symptoms. In each field, a bulk sample of approximately 2 kg of soil was collected from at least five random sites, and soil was taken to a depth of 15 cm from the rhizosphere of severely affected plants using a hand trowel. The soil samples were air-dried and stored at 3°C before being used for pathogen isolation.

Isolation of *P. sojae*. The re-activation of *P. sojae* in the soil samples was conducted using the baiting method described by Canaday and Schmitthenner (4) and the isolation of the fungus using the soybean seedling bioassay procedure described by Schmitthenner and Bhat (26). Each soil sample was ground to fine particles and placed in vinyl pots (10 cm diameter). The potted soil was flooded for 24 h and then allowed to dry slowly in the dark at room temperature until the soil began to pull away from the sides of the pots. To induce oospore germination, pots were placed in plastic bags for approximately 2 weeks until planting. Ten seeds of soybean cultivar Williams (*rpsrps*), susceptible to all known *P. sojae* races, were placed on the surface of the potted soil and covered with wet coarse vermiculite. Pots were then placed in clear plastic bags in the growth chamber operated at 25°C day and 20°C

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night with a 16-h photoperiod at a light intensity of $335 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Three days after planting, when primary roots were about 5 cm long, the pots were removed from the bags, flooded again for 24 h, and returned to the growth chamber. Affected plants showing prominent lesions or collapse of hypocotyls were identified and used for pathogen isolation within 10 days after planting.

To isolate the pathogen, sections (1 cm) cut from the margin of lesions on hypocotyls were surface-disinfested in 0.25% sodium hypochlorite solution for 3 min, and in 70% ethanol for 10 s, then washed in sterilized distilled water, dried with a sterile paper towel, and placed on the semiselective PBNIC medium (26), containing Terrachlor (99% pentachloronitrobenzene) at 0.04 g/liter, Benlate (50% benomyl) at 0.01 g/liter, neomycin sulfate at 0.10 g/liter, Rovral (50% iprodione) at 0.04 g/liter, and chloramphenicol at 0.10 g/liter in a V8 juice agar base. Hyphae tips of *P. sojae* that grew out of the infected tissues were cut 3 days after plating and transferred to the PBNIC medium for further purification and identification. *P. sojae* was identified by microscopic examination using taxonomic keys and illustrated morphological manuals for *Phytophthora* spp. (7,24,30).

Single-zoospore isolates. At least one single-zoospore isolate of *P. sojae* was developed from each soil sample following the procedure of Jackson et al. (13). Fifteen 6-mm agar plugs from the edge of a culture actively growing on V8 juice agar were transferred to Erlenmeyer flasks con-

taining 25 ml of V8 juice broth for 48 h. The V8 juice broth was decanted and the plugs were washed with 25 ml of Chen and Zentmyer's (5) salt solution at pH 7.0 four times at 15-min intervals. The plugs were then incubated in 20 ml of sterile distilled water under cool-white 40 W lights at room temperature for 48 h until zoospores were observed using a stereomicroscope. Zoospore concentrations were estimated using hemacytometer. Through serial dilutions, the concentration of the zoospore suspension was adjusted to approximately 1×10^3 spores/ml and plated onto quarter-strength V8 juice agar medium (agar 5.0 g/liter). Single-zoospore isolates were obtained by transferring a single, germinating zoospore to V8 juice agar. A total of 96 single-zoospore isolates were obtained from the 35 soil samples collected in 18 counties during 2005, 2006, and 2007. Each of those single-spore isolates came from a separate isolate, which came from a separate seedling. Single-zoospore cultures were maintained on V8 juice agar slants, incubated at room temperature for 10 days, covered with 2 ml of sterile deionized water, stored at 15°C, and subcultured if needed every 3 months before virulence characterization tests.

Virulence characterization. A set of eight differentials, each containing a single resistance *Rps* gene, and the universal susceptible Williams (*rps*) were used to test each of the 96 single-zoospore isolates of *P. sojae*. The eight differentials included L75-3735 (*Rps1c*), L75-6141 (*Rps1a*), L77-1863 (*Rps1b*), L83-570 (*Rps3a*), L89-1581 (*Rps6*), L93-3258 (*Rps7*), P.I.103

(*Rps1d*), and Williams 82 (*Rps1k*) (13,27). The seed of the differential set was obtained from T. R. Anderson at Harrow Research Center, Agriculture and Agri-food Canada in 2003 and increased in a glasshouse of the Key Laboratory of Soybean Biology, Chinese Education Ministry in Harbin, Heilongjiang in 2004.

For the virulence characterization tests, the differentials were grown in 12-cm-diameter plastic pots containing a sterilized soil:peat:perlite mixture (1:1:1) with five plants per pot in growth chambers at 25°C day and 20°C night temperature with a 16-h photoperiod at a light intensity of $335 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Plants were watered twice weekly from the bottom of the pot. The potting mixture contained sufficient nutrients to support healthy plant growth during the course of the experiments.

Inoculum was prepared by growing each single-zoospore isolate of *P. sojae* on V8 juice agar in a 9-cm petri dish at 25°C for 7 days. Plants were inoculated using a hypocotyl wound inoculation technique described by Kaufmann and Gerdemann (14) at the first-node stage (V1) (9), which occurred 7 to 9 days after planting. Seedlings were slightly incised with a blade along the hypocotyls, and a weft (10 × 10 mm) of aerial mycelium obtained from the margin of a 7-day-old *P. sojae* culture on V8 juice agar was inserted into the longitudinal wound. After inoculation, the inoculated plants were placed in a mist chamber with 100% relative humidity at 24°C with 12 h light for 3 days, and then returned to the growth chambers.

The differential reaction to each isolate was determined with five plants per pot and four replicate pots for each differential in each experiment. The replicate pots of each differential within an experiment were arranged in a complete randomized design, and the experiment was conducted three times for each isolate and differential interaction. In each experiment, four pots of cultivar Williams (*rps*) that were wounded and inoculated with sterile V8 juice agar were included as checks, indicating possible damage of wounding to plants.

The percentage of dead plants was recorded 5 days after inoculation. If a differential exhibited <30% seedling mortality, the reaction was considered resistant. If a differential exhibited >70% seedling mortality, the reaction was considered susceptible. Seedling mortality from 30 to 70% was considered an intermediate reaction (1,13,34). Isolates that produced either resistant or susceptible responses to individual differential cultivars that were consistent in three repeated experiments were characterized to race. Isolates that produced intermediate reactions to at least one of the eight differentials in at least three consecutive attempts were considered unclassifiable (13,17).

Resistance screening. Sixty-two short-season soybean cultivars (Maturity Groups

Fig. 1. Map of Heilongjiang Province, China showing 18 counties where *Phytophthora sojae* isolates were collected. 1 = Heihe, 2 = Bei'an, 3 = Jiansanjiang, 4 = Jiamusi, 5 = Yi'an, 6 = Qing'an, 7 = Hailun, 8 = Suihua, 9 = Jixian, 10 = Baoqing, 11 = Shuangyashan, 12 = Bayan, 13 = Jixi, 14 = A'cheng, 15 = Yanshou, 16 = Shangzhi, 17 = Shuangcheng, 18 = Ning'an.

I to 000) commonly grown in Heilongjiang Province were evaluated for reactions to the eight *P. sojae* races identified in this study in a greenhouse in 2008. Plants were grown and inoculated using the same methods described above. One isolate from each of the eight races was used for inoculating the plants. The reaction of soybean cultivars to each race was determined with five plants per pot and four replicate pots for each cultivar in each experiment. The pots were arranged in a complete randomized design, and the experiment was conducted twice.

RESULTS

Race identification and distribution.

Of the 22 *P. sojae* isolates obtained in 2005, 19 were classified into 6 races, and 3 had intermediate reactions (Table 1). In 2006, 31 of the 44 isolates were classified into 6 races, and 13 had intermediate reactions. In 2007, all 30 isolates obtained were classified into 6 races. A total of 8 races of *P. sojae* were identified during the 3 years. Of the 8 *P. sojae* races identified, race 1 predominated, comprising 60% of the isolates, followed by race 3 which made up 7% of the isolates. Races 4, 5, 9, 13, 44, and 54 were detected infrequently, each comprised of two to three isolates, representing 2 to 3% of the population. Races 4, 5, 44, and 54 have not been previously reported in Heilongjiang Province. The 16 unclassifiable isolates were grouped into 14 intermediate reaction types (IRT) based on their virulence formulae and assigned IRT1 to IRT14 (Table 1).

Race 1 was found in all 18 counties, while races 5, 44, and 54 were each found in a single county (Table 2). There were four to seven *P. sojae* races and IRT identified in each of Jixi, Jiamusi, Jiansanjiang, and Jixian counties where more severe disease development was observed at the time of sample collection. These four counties were located in the eastern part of the province in Sanjiang Plain, where the typical soil type is low-lying and poorly drained clay soil. The remaining counties each had only one to three races identified.

Cultivar resistance. The percentage of mortality of the 62 soybean cultivars to each of the eight *P. sojae* races ranged from 0 to 100% in both experiments. Based on percentage of plant mortality averaged over the two experiments, 44 cultivars were resistant (<30% mortality) to at least one of the eight races, and the remaining were susceptible (Table 3). Of the resistant cultivars, Hefeng-50 was resistant to five races; Hefeng-45 and Xingkangxian-1 were resistant to four races; Hefeng-42, Hefeng-44, Heihe-32, Heilong-46, Heilong-47, Suinong-8, Suinong-11, and Suinong-19 were resistant to three races; and Dongnong-44, Dongnong-49, Heihe-16, Heilong-40, Nen-14, Suinong-2, Suinong-21, Suinong-23, and

Xingdou-4 were resistant to two races. Intermediate reactions (30 to 70% mortality) were observed in a number of cultivar and race combinations, but none of the 62 cultivars showed an intermediate response to all eight races.

DISCUSSION

This study demonstrates that race 1 is the predominant race of *P. sojae* in Heilongjiang Province. The result is in agreement with earlier reports from China (18,20,33,36). However, four races, including races 11, 17, 21, and 24, reported earlier in Heilongjiang Province were not found in this study. Likewise, four races,

including races 4, 5, 44, and 54, identified in the present study have not been previously reported. The virulence formulae of the eight races identified were closely related. For example, race 1 (*rps1a*, *rps7*), race 3 (*rps1a*, *rps7*), race 13 (*rps6*, *rps7*), and race 54 (*rps1d*, *rps7*) share the same pattern of virulence, differing by only one gene among those races. Similarly, race 4 (*rps1a*, *rps1c*, *rps7*) differs from race 5 (*rps1a*, *rps1c*, *rps6*, *rps7*), race 9 (*rps1a*, *rps6*, *rps7*), and race 44 (*rps1a*, *rps1d*, *rps7*) by only one gene. The results support the remark of several *Phytophthora* researchers that the virulence formulae of races within the same region were similar, usually differ-

Table 1. Eight races and 14 intermediate reaction types (IRT) of *Phytophthora sojae* identified from 96 isolates collected in Heilongjiang Province, China in 2005, 2006, and 2007

Race and IRT	Virulence formula (<i>rps</i>) ^z	Number of isolates			
		2005	2006	2007	Total
1	7	12	22	24	58
3	1a, 7	2	4	1	7
4	1a, 1c, 7	0	1	1	2
5	1a, 1c, 6, 7	1	1	1	3
9	1a, 6, 7	1	0	1	2
13	6, 7	1	0	2	3
44	1a, 1d, 7	2	1	0	3
54	1d, 7	0	2	0	2
IRT1	±1a, 1b, 6, 7	0	1	0	1
IRT2	±1a, 1c, 1d, 1k, 7	0	1	0	1
IRT3	1a, ±1d, 7	1	0	0	1
IRT4	1a, 1c, ±3a, 7	1	0	0	1
IRT5	1b, ±3a, 7	0	2	0	2
IRT6	1c, 1k, ±3a, 7	0	2	0	2
IRT7	1k, ±3a	0	1	0	1
IRT8	±3a, 7	0	1	0	1
IRT9	±3a, 6, 7	1	0	0	1
IRT10	3a, ±7	0	1	0	1
IRT11	±1a, 1b, ±1c, 1d, 1k, 3a, 7	0	1	0	1
IRT12	±1b, 1c, ±3a	0	1	0	1
IRT13	1a, ±1b, 1c, 1d, 1k, ±3a	0	1	0	1
IRT14	±1c, 1d, 6, ±7	0	1	0	1
Total		22	44	30	96

^z ± = intermediate reaction (30 to 70% mortality).

Table 2. Distribution of eight races and 14 intermediate reaction types (IRT) of *Phytophthora sojae* in 18 counties of Heilongjiang Province during 2005 to 2007

Origin	No. of samples	No. of isolates	Race and IRT ^z
Heihe	1	3	Race 1(1), Race9(1), IRT4(1)
Bei'an	1	5	Race 1(4), IRT3(1)
Jiansanjiang	5	16	Race 1(7), Race 13(3), Race 3(3), Race 5(3)
Jiamusi	4	8	Race 1(3), Race 44(3), IRT8(1), IRT2(1)
Yi'an	2	4	Race 1(1), Race 3(3)
Qing'an	2	2	Race 1(1), Race 9(1)
Hailun	5	9	Race 1(8), IRT9(1)
Suihua	1	2	Race 1(2)
Jixian	3	13	Race 1(9), Race 54(2), IRT14(1), IRT13(1)
Baoqing	1	1	Race 1(1)
Shuangyashan	1	6	Race 1(4), IRT5(1), IRT10(1)
Bayan	1	1	Race 1(1)
Jixi	2	15	Race 1(8), Race 3(1), Race 4(1), IRT6(2), IRT12(1), IRT1(1), IRT7(1)
A'cheng	1	1	Race 1(1)
Yanshou	2	5	Race 1(3), IRT5(1), IRT11(1)
Shangzhi	1	3	Race 1(2), Race 4(1)
Shuangcheng	1	1	Race 1(1)
Ning'an	1	1	Race 1(1)
Total	35	96	

^z Values in the brackets are numbers of isolates.

ing from one another by virulence on only one *Rps* gene (1,13,15,27,34).

None of the eight races were virulent on *Rps1b*, *Rps1k*, and *Rps3a* genes (Table 1). However, 11 of the 14 IRT were virulent on at least one of the three resistance genes, and IRT13, represented by a single isolate, was virulent on all three resistance genes. In addition, none of the eight *P. sojae* races (1, 3, 9, 11, 13, 17, 21, and 24) reported in Heilongjiang in the previous studies was virulent on *Rps1c* gene, but two of the four new races identified in the present study, races 4 and 5, were able to overcome the *Rps1c* resistance. These results raise concerns on the diversity and dynamics of the *P. sojae* population in Heilongjiang and the likelihood of continued occurrence of new races and IRT possessing virulence on *Rps1c* and *Rps1k*, which are commonly used *Rps* genes in the soybean breeding program (13,19,25).

This study further demonstrates that resistance to all *P. sojae* races is available in

soybean cultivars commonly grown in Heilongjiang Province. Previous efforts in screening soybean germplasm in Heilongjiang for resistance to *P. sojae* had focused on resistance to race 1 or up to two races (20,35,36). This is to our knowledge the first report on the identification of sources of resistance to all eight races for Heilongjiang. Twenty of the 44 resistant cultivars identified in the present study were resistant to more than one race of *P. sojae* (Table 3), and the use of these cultivars in a breeding program will enable the pyramiding of genes in subsequent generations to develop multiple gene resistance for broader effectiveness against the pathogen.

Thirty-three of the 44 cultivars were susceptible to *P. sojae* race 1 but resistant to at least one of the seven remaining races identified (Table 3). These results were unexpected, as race 1 possesses only one virulence gene (*rps7*) and is the least virulent race. If a cultivar is susceptible to race 1, it should have a susceptible interaction

with all of the other races. A possible explanation was that there might be additional virulences in the race 1 isolate used that were not found in the other isolates where there is a resistant reaction. There might also be a possibility that the U.S. differentials do not work for the isolates from Heilongjiang Province.

P. sojae is known for its pathogenic variability (8,25). New races of *P. sojae* can shorten the effective lifespan of a resistant cultivar and may also have virulence against resistance genes that are not currently present in soybean cultivars, rendering these genes ineffective even before the genes are used in a breeding program. However, the use of genetic resistance remains the most effective method of managing *Phytophthora* root and stem rot. In recent years, a number of plant pathologists and breeders have expressed preference for the use of race-non-specific or partial resistance, described as the ability of plants to survive the pathogen infec-

Table 3. List of 44 soybean cultivars with resistance to at least one of the eight races of *Phytophthora sojae* identified in Heilongjiang, China

Cultivar	Plant mortality (%) ^z							
	Race 1	Race 3	Race 4	Race 5	Race 9	Race 13	Race 44	Race 54
Suinong-9	21	90	73	100	56	100	100	100
Heihe-20	100	50	100	100	55	50	100	0
Suinong-18	100	100	75	55	39	90	100	15
Dongnong-42	100	54	100	91	90	100	94	0
Heinong-38	90	95	85	87	91	95	94	0
Heinong-49	100	92	100	100	100	78	100	0
Heihe-9	100	100	61	45	58	95	25	50
Suinong-4	100	100	55	100	91	95	25	61
Dongnong-47	100	88	95	95	75	100	14	45
Hefeng-47	92	94	14	81	54	100	100	83
Hefeng-35	100	92	18	55	61	100	74	82
Heihe-6	100	100	28	95	63	100	97	100
Heinong-37	95	95	15	100	79	95	62	100
Hefeng-41	73	61	100	0	73	73	42	91
Heihe-5	55	100	100	23	95	59	100	63
Heihe-19	100	90	89	24	95	100	90	55
Suinong-16	85	85	55	0	79	95	100	55
Suinong-15	100	85	100	5	62	45	94	75
Dongnong-40	82	0	79	58	56	79	100	95
Hefeng-43	100	95	90	100	75	11	47	55
Heihe-27	100	85	89	84	78	15	100	55
Suinong-20	55	50	95	100	77	0	57	57
Suinong-12	60	55	100	100	50	5	50	55
Suinong-7	57	62	80	100	79	8	90	90
Heihe-16	85	95	1	100	95	100	100	0
Suinong-2	25	10	100	100	58	100	85	90
Suinong-23	45	99	75	100	78	100	22	10
Suinong-21	10	95	100	0	61	63	53	55
Dongnong-49	56	95	5	100	100	0	95	100
Dongnong-44	100	100	23	0	86	61	100	51
Xingdou-4	56	100	47	11	90	56	78	21
Heinong-40	100	95	57	27	55	95	95	0
Nen-14	46	95	100	0	24	56	100	100
Hefeng-44	0	62	100	83	23	55	45	4
Hefeng-42	5	100	100	97	60	100	23	1
Suinong-11	23	95	85	100	100	100	5	0
Heihe-32	0	45	24	60	62	45	100	1
Heinong-46	28	76	20	100	100	45	100	0
Suinong-8	15	75	80	95	90	15	95	23
Suinong-19	45	100	15	20	100	15	100	58
Heinong-47	13	0	90	85	100	55	100	0
Hefeng-45	92	64	12	1	92	21	97	4
Xingkangxian-1	90	100	0	0	85	10	100	7
Hefeng-50	21	20	54	12	91	100	24	22

^z Values are the average of two experiments, 20 plants in four replicate pots of each experiment.

tion without displaying severe disease symptoms or yield loss (3,6,29). Breeding for partial resistance to *Phytophthora* root and stem rot in Heilongjiang is still in the developmental stage (12). Given the fact that new and more virulent races and IRT have been frequently identified during the past several years, cultivars with high levels of partial resistance would be more desirable as sources of resistance for soybean breeding programs dealing with the *P. sojae* population in Heilongjiang.

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