Beneficial Effects of Fungicide Seed Treatments for Soybean Cultivars with Partial Resistance to *Phytophthora sojae*

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ABSTRACT

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Phytophthora sojae is a yield-limiting soybean pathogen in areas where soils remain saturated for long periods of time. *P. sojae* has been successfully managed with single dominant resistance genes (*Rps* genes). The proportion of fields with populations of *P. sojae* capable of causing susceptible interactions with many of the *Rps* genes has increased in number. The fungicides metalaxyl and mefenoxam have been used both as in-furrow and seed treatments to provide protection against damping-off caused by *P. sojae*. To determine the plant age when partial resistance and *Rps* genes are effective against *P. sojae*, we evaluated a greenhouse assay in which soybean seeds were planted and inoculated with a zoospore suspension to compare the disease reaction of soybean seeds and seedlings. Efficacy of different fungicide rates also was evaluated using the cultivar with partial resistance with this inoculation technique. Seeds and seedlings of a cultivar with high levels of partial resistance were susceptible to infection by *P. sojae* while those of a cultivar with an *Rps* gene were resistant. For the cultivar with partial resistance, reductions in percent emergence and the number of damped-off seedlings were significantly higher for plants inoculated at the day of planting compared to inoculations of plants with unifoliates present (5 days after planting). Results also indicate that fungicide seed treatment on cultivars with partial resistance may be beneficial when the environmental conditions that favor *P. sojae* infections occur prior to soybean emergence. This greenhouse assay appears to be useful in examining overall fungicide efficacy; however, it did not detect consistent and quantifiable differences in rates of seed treatment fungicides.

Phytophthora sojae causes damping-off and root and stem rot of soybean in a number of production regions worldwide (22). Saturated soil conditions favor germination and development of oospores and sporangia and infection of soybean roots. The highest economic losses arise as a result of both direct plant loss and the costs of replanting when favorable environmental conditions occur just after planting (15). *P. sojae* has been managed successfully over the years with single gene resistance (*Rps* genes). There are 13 identified single genes for resistance, of which 8 are in allelic series (4,15). The most commonly deployed *Rps* genes to date in commercial soybean cultivars have been *Rps-1a*, *Rps-1c*, *Rps-1k*, *Rps-3a*, *Rps-6*, and *Rps-7*. Fifty-five physiological races of *P. sojae* have been described to date (1,10,23). As a result, in many production regions, popula-

tions of *P. sojae* now exist that have susceptible interactions with soybean cultivars that carry these *Rps* genes, rendering them ineffective (1,10,17,23).

Disease management recommendations from many states increasingly emphasize the use of soybean cultivars with partial resistance (also called rate-reducing resistance, field resistance, or tolerance in the soybean industry; 2,9,11,15,20). Partial resistance in soybean cultivars restricts fungal colonization of plant tissue (11,20) and is effective against all physiological races of the pathogen. Differences in yield among cultivars in *P. sojae*-infested soil have been attributed to the degree of partial resistance present in the cultivar (19,21). Factors which govern partial resistance may or may not be effective at the seed or seedling stage. Schmitthenner (15) stated that "after germination many soybean cultivars quickly develop partial resistance, however, and may not be damaged after the seedling stage". As the number of fields with populations of *P. sojae* capable of causing disease on soybean cultivars with *Rps* genes increases, producers will be forced to rely on cultivars with high levels of partial resistance unless new *Rps* genes are identified. Additional disease management strategies are necessary to ensure minimal yield losses occur when conditions are favorable for severe disease development.

Metalaxyl applied as an in-furrow or seed treatment has reduced plant emergence loss and increased yields of susceptible soybean cultivars when *P. sojae* was present and the environment was conducive to infection (2,7). However, the seed treatments had no effect on yields of partially resistant (tolerant) soybean cultivars in these same studies (2,7). Soybean seed treatment with metalaxyl has significantly increased yields in conservation tillage production systems (6). Despite the beneficial effects of seed treatment on susceptible soybean cultivars, a low percentage of soybean seed planted is treated with metalaxyl or mefenoxam in Ohio and other areas where *P. sojae* is endemic. In addition, recommended labeled rates of fungicide to adequately manage *P. sojae* range from 15.5 to 31.0 g a.i. of metalaxyl per 100 kg of seed (0.75 to 1.5 fl oz/hundred weight) and 7.5 to 15.0 g a.i. of mefenoxam per 100 kg of seed (0.32 to 0.64 fl oz/hundredweight).

Testing for efficacy of fungicide seed treatments in the field has been challenging due to uneven inoculum distribution and dependence on natural environment conditions for development of disease. A greenhouse technique which reliably evaluates the efficacy of seed treatment fungicides that could also differentiate specific rates against *P. sojae* could be useful to pathologists who make recommendations to producers as well as agrochemical companies.

Our objectives in this study were: to determine when partial resistance to *P. sojae* in soybean seeds and seedlings provides some protection compared to single *Rps* gene using greenhouse inoculations, and to determine if a greenhouse inoculation assay could adequately assess the efficacy of a specific fungicide as well as fungicide rates.

MATERIALS AND METHODS

Inoculum production. Zoospores of *P. sojae* (race 7, virulence pathotype 1a, 3a, 4, 5, 6, and 7) were used as inoculum in all greenhouse experiments. Zoospores were produced by salt washing of 2-day-old cultures grown on dilute lima bean extract in 25-ml Erlenmeyer flasks (17). Extracts were decanted and replaced with 25 ml of Chen-Zentmeyer salt solution (pH 7.0) every 15 min for 1 h. After the final salt wash, 25 ml of sterile distilled water was added to flasks, which were then incubated

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in the light overnight. After 16 to 18 h, zoospores were collected, counted with a hemocytometer, and diluted to approximately 1×10^4 zoospores/ml. Later experiments required a greater quantity of zoospores. Zoospores were produced for these experiments by washing 3- to 5-day-old colonies produced on V8 juice agar plates (approximately 40 to 45 plates) similar to the method reported by Ho and Hickman (8).

Greenhouse inoculations. For each greenhouse experiment, 10 soybean seeds were planted in coarse vermiculite (Therm-O-Rock East, New Eagle, PA) in 6.4-cm plastic pots in the greenhouse. Plants were inoculated with a zoospore suspension by placing pots in 470-ml styrofoam cups containing 200 ml of zoospore (1×10^4) suspension for 24 h. Pots were then removed from inoculum and placed on a greenhouse bench in a randomized complete block design of one pot each for each treatment in each experiment, with three replications for plant age evaluations and four replications for seed treatment evaluations. A water control was included in each experiment for each treatment to ensure adequate germination and plant health in this study, but this data was not included in the final statistical analysis. The pots were watered as needed to maintain high moisture levels.

Plant age evaluations. Two soybean cultivars were used in these experiments: Conrad, which has no *Rps* genes and high levels of partial resistance; and Resnik, which has *Rps-1k* and moderate levels of partial resistance to *P. sojae*. To obtain seedlings of different ages for inoculation, pots were planted in a sequence of 0, 2, 3,

4, 5, 6, 7, 10, and 14 days. The *P. sojae* isolate (R7) chosen for these studies causes a resistant reaction when used to inoculate soybean plants with *Rps-1k*. Pots with plants of the soybean cv. Resnik or Conrad

of the different ages were then inoculated on the same day. The number of seedlings with symptoms of Phytophthora damping-off, percent plant emergence, and plant height was recorded after 7 days. Percent

Fig. 1. Inoculation of two soybean cultivars with zoospores of *Phytophthora sojae*. Top, soybean cultivar Conrad with partial resistance; bottom, Resnik with *Rps-1k* resistance. The pots in the picture are (left to right) inoculations at 0, 2, 3, and 5 days after planting and a 3-day-old uninoculated control.

Fig. 2. A, Number of plants with pre- and postemergence damping off, B, seedling height, and C, percent emergence of two soybean cultivars, Conrad (partial resistance) and Resnik (*Rps-1k*), following inoculation of 0-, 2-, 3-, 4-, 5-, 7, 10-, and 14-day-old plants with *Phytophthora sojae* race 7 (vir 1a, 3a, 7) which is incompatible with *Rps-1k* to determine when resistance is effective. Fisher's protected least significant difference (LSD) values ($P \leq 0.05$) are 2.1, 1.9, and 17.9 for Conrad; and not significant, 0.9, and not significant for Resnik for number of damped off seedlings, seedling height, and percent stand, respectively. The variety by age LSD ($P < 0.025$) is 1.05, 1.05, and 9.7 for number of damped off seedlings, seedling height, and percent stand, respectively.

plant emergence refers to the percentage of the number of seeds planted that developed into standing plants without symptoms of damping-off. This study was repeated three times; inoculations took place on 1 February, 23 February, and 29 March 1999.

Seed treatment evaluations. Two fungicides, metalaxyl (Allegiance, Gustafson LLC, Plano TX) and mefenoxam (Apron XL, Novartis Crop Protection, Greensboro, NC), were used at the most commonly applied (Ray Knake, Gustafson LLC, *personal communication*) as well as recommended rates for *Pythium* spp. (metalaxyl and mefenoxam at 4.1 and 3.75 g a.i. per 100 kg of seed, respectively) and *Phytophthora* spp. (metalaxyl at 15.5 and 31.0 g a.i. and mefenoxam at 7.5 and 15.0 g a.i. per 100 kg of seed). Seed (454 g) of the soybean cv. Conrad was treated at each fungicide rate, then used for each experiment. Fungicide was added to water for a final volume of 2.37 ml, mixed thoroughly, and added to the seed in plastic bags. To ensure thorough coverage, seed was shaken and mixed for 15 min until there was no fungicide residue visible on the inside of the bags. Bags were then left open in a

forced air hood at room temperature to allow seed treatment to dry. The seed was stored in a cool, dry place until planted. Plant ages evaluated in this study included 1, 3, 5, and 7 days. Seed treatments in this study included untreated, three rates of metalaxyl, three rates of mefenoxam inoculated with *P. sojae* zoospores, and an untreated, uninoculated control. The number of *Phytophthora* damped-off seedlings, plant emergence, plant height, and whole plant and root fresh weight were recorded after 7 days. Inoculations for this study were on 8 and 28 September 1999.

Statistical analysis. The arcsine square root transformation of the percent emergence was used for statistical analysis. For each study, the experiments were combined and the transformed percent emergence, plant heights, root and top fresh weights, and the number of plants with root rot for each treatment were analyzed by an analysis of variance with the Proc GLM procedure (SAS, Cary, NC). The experiments were then analyzed separately for the seed treatment–plant age study. Fisher's protected least significant difference (LSD) was used to separate the means

of the treatments for both the plant age and the seed treatment studies.

RESULTS

Soybean plant age–resistance. For all three greenhouse experiments, seedlings in all age classes of cv. Conrad developed *Phytophthora* damping-off or root rot in the inoculated pots and no disease developed in the water controls. The amount of disease was limited when the plants were inoculated in the later seedling growth stages; these results are similar to those in other partial resistance assays (17). There was a greater reduction in emergence for plants inoculated 0 to 4 days after planting compared with plants inoculated after 5 to 7 days (Figs. 1 and 2). The combined data analysis of the *P. sojae*-inoculated pots from the three greenhouse experiments indicated that the main effects of greenhouse experiment, cultivar, and plant age were significant ($P < 0.05$) for the number of damped-off seedlings, plant height, and final percent emergence (Table 1). The interactions of greenhouse experiment–cultivar as well as greenhouse experiment–age were not significant for the number of damped-off seedlings and transformed percent emergence, but these interactions were significant for plant height ($P < 0.01$). The cultivar–age interaction was highly significant ($P < 0.001$) for all three measurements. The cultivars representing different types of resistance were significantly different ($P < 0.001$) from each other. Resnik has *Rps-1k*, which has a resistant interaction when inoculated with this race of *P. sojae*. There were more seedlings that damped-off for the partially resistant soybean cv. Conrad (3.2 plants) compared with Resnik with *Rps-1k* (0.3 plants; Fig. 2). The mean percent final emergence for all seedling ages was 66.9% for Conrad (partial resistance) compared to 94.5% for Resnik (*Rps* resistance) for the inoculated pots, whereas the water controls had approximately 95% emergence for both cultivars.

Table 1. Combined analysis of variance for three greenhouse experiments in which the soybean cultivars Resnik (specific gene resistance, *Rps-1k*) and Conrad (partial resistance, *rps*) were inoculated with *Phytophthora sojae* (race 7, vir 1a, 3a, 5, 6, and 7) at 0, 2, 3, 4, 5, 7, 10, and 14 days after planting to determine at what plant age resistance is effective^a

Source	df	Damped-off seedlings (<i>F</i>)	Plant height (<i>F</i>)	Percent emergence (<i>F</i>)
Experiment	2	6.08*	240.01**	6.73*
Rep (Experiment)	6	...	...	...
Cultivar	1	124.13**	141.01**	170.81**
Experiment × cultivar	2	1.48	29.14**	0.10
Age	7	12.96**	84.41**	17.84**
Experiment × age	7	1.35	5.07**	2.02
Cultivar × age	7	11.30**	6.42**	11.79**
Experiment × cultivar × age	7	1.23	0.81	1.44
Error	62	...	...	...

^a *F* = *F* value, * and ** indicate significance at $P \leq 0.05$ and $P \leq 0.01$, respectively. Percent emergence = arcsin (sqrt emergence) adjusted to 1.

Fig. 3. Soybean seedlings of the cultivar Conrad with partial resistance, following inoculation with zoospores of *Phytophthora sojae* at **a** and **d**, 1, **b** and **e**, 5, and **c** and **f**, 7 days after planting with **a**, **b**, **c**, metalaxyl at 0, 4.1, 15.5, and 31.0 g a.i. per 100 kg of seed and **d**, **e**, **f**, mefenoxam at 0, 3.75, 7.5, and 15.0 g a.i. per 100 kg of seed.

The effect of seedling age at inoculation was significantly different for all parameters for the soybean cv. Conrad with partial resistance (Fig. 2). Only seedling height was significantly different among the Resnik treatments, which would be expected when early and late seedling ages are compared. The most striking differences on the effects of inoculation at early plant ages for these two cultivars was the final percent emergence (Fig. 2C). Final percent emergence for soybean cv. Conrad ranged from 38 to 55% emergence, compared with Resnik at 93 to 100% emergence when seedlings were inoculated at 0 to 4 days after planting. There was significantly less seedling emergence for the cv. Conrad when plants were inoculated at seed, 2, 3, 4, or 5 days compared with inoculations at 7, 10, and 14 days (LSD = 13.9, $P \leq 0.05$).

Seed treatment and plant age. Phytophthora root rot developed on seedlings of all plant ages and at all fungicide rates, with the exception of the highest rates of both fungicides (Fig. 3) and the uninoculated, untreated control (*not shown*). The greenhouse experiments were highly significantly different from each other for final percent emergence, plant height, and root weight. The main effect of fungicide seed treatment was significant ($P < 0.001$) for final percent emergence, root weight ($P = 0.012$), plant height ($P < 0.05$), and plant weight ($P < 0.05$). Seedling age at inoculation was only significantly different for plant height ($P = 0.003$; Table 2). There were highly significant interactions ($P < 0.01$) between the experiments and plant age for root weight, plant height, percent germination, and the number of plants with root rot, as well as between experiment by treatments for plant height, top weight, and root weight. The trends from the two experiments were similar; however, due to the significant interactions, the results from one of the greenhouse experiments is presented (Fig. 4). All fungicide seed treatments and the uninoculated, untreated control were significantly different ($P < 0.05$) from the inoculated non-fungicide-

treated control in pairwise comparisons using Fisher's protected LSD for final percent emergence, fresh plant weight, and root weight. Consistent significant differences between the fungicide seed treatments did not occur. The one exception was for the fungicide seed treatment with metalaxyl at 4.1 g a.i. per 100 kg of seed, which was significantly different from the other treatments for root weight and plant weight. Interestingly, the mefenoxam at 7.5 g a.i. per 100 kg of seed was significantly different than the mefenoxam at 15 g a.i. per 100 kg of seed for plant height, but not different than the lower rate of mefenoxam at 3.75 g a.i. per 100 kg of seed in pairwise comparisons (Fig. 4).

DISCUSSION

Seed or in-furrow treatments with metalaxyl have been recommended for management of *P. sojae* in fields where Phytophthora root rot is chronic (7,15,16). Several studies have shown no benefit of seed treatment with metalaxyl for some cultivars (2,6,7). This could be partially explained by our first series of experiments, in which no disease developed on seed or seedlings of a resistant soybean cultivar with an *Rps* gene. However, the soybean cv. Conrad, with a high level of partial resistance, was highly susceptible to infection by *P. sojae* from the day of planting until 5 days after planting. The effect of plant age on susceptibility to *Phytophthora* spp. has been documented previously in other host systems. Young potato plants, 4 to 6 weeks after planting, are more susceptible to *P. infestans* (5,18). Tomatoes developed larger lesions when inoculated with *P. capsici* at 6 to 8 weeks after transplanting, compared with inoculations at 10 and 12 weeks after transplanting (14). Jimenez and Lockwood (9) indicated that the maximum effects of disease are expressed when younger seedlings, 2 to 32 days old, of a susceptible soybean cultivar were inoculated with a *P. sojae* zoospore suspension. The differences between inoculated and uninoculated soybean plants, 16 days of age and older, were not

significantly different at the time the measurements were taken in this study.

Ontogenetically determined resistance (also known as adult plant resistance) is a type of quantitatively inherited resistance that develops during plant maturation (3). For example, adult plant resistance to rust (*Uromyces appendiculatus*) in common bean is expressed as lower disease intensity on the upper plant leaves compared with primary leaves (12). Our studies indicate that the lack of ontogenic resistance expression in seeds and seedlings of soybean cultivars with partial resistance makes them highly susceptible to infection by *P. sojae*. Whether the delay in expression of resistance to *P. sojae* is due to changes in root structure, root age, biochemical changes, or other genetically determined factors has yet to be determined. Once genetic components of partial resistance are identified in soybeans, these types of questions can be answered.

Our data clearly demonstrate the potential benefits of fungicide seed treatment with higher plant emergence, plant height, fresh whole plant weight, and root weight for soybean cultivars with partial resistance to *P. sojae*. This greenhouse assay could be used to evaluate the efficacy of new fungicide materials for *P. sojae*. However, our technique did not consistently separate the effects of fungicide rates, which may be due to a number of reasons. The medium in these pots is coarse vermiculite, which allows for ease of movement of *P. sojae* zoospores. Pfender et al. (13) demonstrated that zoospores moved only 65 and 24 mm in a sandy-loam soil and silt-loam soil, respectively. Soybeans produced in Ohio are planted in diverse soil types; many have 60% clay and are prone to water retention. These heavy soils may have other properties which, combined with heavy spring rains, may warrant the use of higher rates of seed treatment materials than are currently recommended. Metalaxyl applied in-furrow has been shown in field studies (16) to provide longer protection against Phytophthora root rot than when metalaxyl

Table 2. Analysis of variance for percent plant stand, plant height, whole plant weight, and root fresh weight following fungicide seed treatment with metalaxyl (Allegiance) at 4.14, 15.51, and 31.01 g a.i. per 100 kg of seed; mefenoxam (Apron XL) at 3.75, 7.5, and 15.0 g a.i. per 100 kg of seed; and untreated seed for the soybean cultivar Conrad after inoculation of seedlings with a *Phytophthora sojae* zoospore suspension at 0, 3, 5, and 7 days in a greenhouse study^a

Source ^b	df	Percent emergence			Plant height			Plant fresh weight			Root fresh weight		
		MS	F	P	MS	F	P	MS	F	P	MS	F	P
E	1	711.47	12.01	0.013	76.37	33.47	0.001	26.428	3.20	0.124	96.862	152.53	<0.001
R (E)	6	59.23	...	...	2.28	...	...	8.270	...	...	0.635	...	...
T	7	879.76	10.13	<0.001	29.00	4.29	0.048	78.315	6.31	0.020	18.322	7.73	0.012
T × E	6	50.99	0.59	0.740	6.76	...	...	12.411	...	...	2.369	...	...
Age	3	1,094.29	4.80	0.115	1,823.39	72.06	0.003	386.751	5.88	0.089	35.779	1.74	0.330
E × A	3	227.97	...	...	25.30	...	...	65.754	...	...	20.563	...	...
T × A	21	276.51	3.18	<0.001	5.10	1.48	0.201	12.180	2.90	<0.001	2.440	1.37	0.249
T × E × A	18	96.09	1.11	0.349	3.44	...	...	6.099	1.45	0.114	1.775	...	...
Error	174	86.82	...	...	1.88	...	...	4.204	...	...	0.846	...	...

^a Percent emergence = percentage of the number of seeds that developed into plants without symptoms of *P. sojae* damping-off; MS = mean squares.

^b E = experiment, R = rep, T = treatments, A = seedling age of 0, 3, 5, and 7 days after planting for inoculations.

is applied as a seed treatment. In order to adequately evaluate rates of material in a greenhouse, screening technique inoculations of more susceptible soybean cultivars at later growth stages may be necessary.

Our studies suggest that seeds and seedlings with high levels of partial resistance are still vulnerable to attack by *P. sojae* during seed germination until unifoliate are visible. Soybean cultivars with partial resistance that are planted in fields where environmental conditions conducive to

Phytophthora root rot development are likely to exist could benefit from a fungicide seed treatment.

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Fig. 4. Percent emergence, average plant height, and fresh weight of plants and roots of soybean seedlings of partially resistant cv. Conrad, inoculated at 0, 3, 5, and 7 days from one of two greenhouse experiments. Soybean seed was untreated or treated with mefenoxam at 3.75, 7.5, and 15.0 g a.i. per 100 kg of seed or metalaxyl at 4.1, 15.5, and 31.0 g a.i. per 100 kg of seed. Fisher's protected least significant difference (LSD) values ($P \leq 0.05$) among the seed treatments are 8.2, 0.7, 1.4, and 0.4 for percent germination, plant height, whole plant weight, and root fresh weight, respectively. Fisher's protected LSD values ($P \leq 0.05$) for comparisons of plant ages are 6.2, 0.6, 1.0, and 0.3 for percent emergence, plant height, whole plant weight, and root fresh weight, respectively.

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