Plant Losses and Yield Responses to Monoculture of Soybean Cultivars Susceptible, Tolerant, and Resistant to *Phytophthora megasperma* f. sp. *glycinea*

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ABSTRACT

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Three soybean cultivars differing in reactions to *Phytophthora megasperma* f. sp. *glycinea* (*P. m. glycinea*) were grown on the same plots for five consecutive years to study the effect of monoculture on the severity of disease. Average emergence, plant losses, and yields differed significantly among soybean cultivars susceptible, tolerant, and resistant to *P. m. glycinea*. The resistant cultivar sustained significantly less plant loss and higher yield than the tolerant and susceptible cultivars. Interplanting the monocultured plots with all three cultivars during the sixth year of the experiment resulted in severe disease of the susceptible cultivar on plots previously planted with susceptible and tolerant cultivars and moderate disease on plots planted with the resistant cultivar. Plant losses of the tolerant cultivar were similar in plots previously planted with susceptible and tolerant cultivars and less in plots planted with the resistant cultivar. Plant losses of the resistant cultivar were similar on all plots regardless of previous cultivar. Oospore numbers in roots of soybean seedlings grown hydroponically in the laboratory were greater in the tolerant cultivar than in the susceptible cultivar. Oospore numbers in roots of the resistant cultivar inoculated with an incompatible race of *P. m. glycinea* were low. Disease severity can be similar after monoculture of tolerant and susceptible soybean cultivars, and this may result from similar increases in soilborne inoculum with repeated cropping.

Recent efforts to control root rot of soybean (*Glycine max* (L.) Merr.) caused by *Phytophthora megasperma* f. sp. *glycinea* Kuan & Erwin (*P. m. glycinea*) have been directed toward identifying disease tolerance (4,20), rate-reducing resistance (19), or resistance (2). Tolerance to *P. m. glycinea* is the ability of susceptible plants to survive infection without developing severe symptoms such as stunting or death and without incurring yield loss (12). It is a qualitatively inherited trait conditioning compatibility to all races of *P. m. glycinea* (4,12). Although cultivars with tolerance and/or resistance are available, few studies report the effects of these cultivars on the severity of disease when grown annually on the same area over an extended period. The long-term effect of cultivar monoculture on the severity of disease may influence the effectiveness of tolerance and resistance in disease control programs.

Few field studies concerning the effect of soybean monoculture on the incidence of Phytophthora root rot and yield of soybean have been published. Less stand and yield loss occurred when the resistant cultivar Blackhawk was rotated with corn than occurred in monocropped plots, which suggests inoculum levels increased under a system of monoculture (13). Recently, Schmitthenner and Van Doren (14) observed that multiple race resistance and tolerance contributed 24 and 25%, respectively, to yield increase over low tolerance during the fifth year of an integrated control experiment.

It is probable that concentration of soilborne inoculum and presence of compatible races of *P. m. glycinea* are the most important factors affecting plant losses and yields of soybean cultivars that differ in responses to this pathogen. Results of laboratory studies (10,11) have demonstrated that disease incidence of root rot caused by *P. m. glycinea* increased directly with inoculum density of oospores. One factor that may influence inoculum levels in field soil is the effect of host reaction on reproduction of *P. m. glycinea* in roots.

In laboratory and greenhouse studies, growth and reproduction of *P. m. glycinea* in roots of susceptible, tolerant, and resistant soybean cultivars have been observed. In pots filled with sand and inoculated with *P. m. glycinea*, the percentage of roots infected with *P. m. glycinea* was equal for susceptible Amsoy (43%) and tolerant Wayne (40%), but only 1% of roots from resistant Amsoy 71 contained oospores (17). Less hyphal extension occurred and fewer oospores developed in roots of resistant Harosoy 63 than in roots of susceptible Harosoy after inoculation with *P. m. glycinea* race 1 (3), and oospores have been observed to develop in equal numbers in taproots regardless of tolerance rating (8).

These studies were conducted to determine the effects of monoculture on emergence, plant loss, and yield of cultivars differing in reactions to *P. m. glycinea* and to determine the effect of host reaction on reproduction of *P. m. glycinea* in seedling roots in vitro.

MATERIALS AND METHODS

Field experiments. The monoculture experiment was conducted from 1979 to 1984 on Brookston clay loam at Woodslee in southwestern Ontario. Tillage on the plots consisted of spring disking to prepare a seed bed. Fertilizer (8-32-16) was applied annually at 560 kg/ha. Chloramben was applied pre-emergence at 4.5 kg a.i./ha to control weeds. Cultivars were selected to provide a range of responses to *P. m. glycinea* races 3, 7, and 9, found commonly in Ontario (1), and consisted of Harosoy (susceptible), Coles (tolerant), and Corsoy 79 (resistant). Plant loss data from field trials are unavailable for Harosoy, but plant loss would be similar to that of Harosoy 63 (Rps_1^a) in the presence of compatible races of *P. m. glycinea*. In a field with severe disease caused by compatible races of *P. m. glycinea*, the plant loss of Harosoy 63 is 48% and plant loss of Coles is 13% (4).

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Plant loss of Corsoy 79 (Rps_1^c) is 6% when propagules of *P. m. glycinea* races 4 and 5 are present at a low frequency in soil (4). The cultivar Vickery was used in 1979 rather than Corsoy 79. The two cultivars are backcross-derived Corsoy with the Rps_1^c gene for resistance to prevalent races in Ontario, and they respond similarly in tolerance screening trials (4).

Cultivars were planted with a tractor-mounted soybean planter in 16-m^2 blocks in rows 60 cm wide at a rate of 13 seeds per meter. Treatments were replicated three times. Emergence, plant loss, and yield were determined from the central portion of each 16-m^2 cultivar block consisting of 10 rows, each 5 m long. Each year, plots were planted in early June. Emergence and final stand counts of plants that produced seed were made at the first-node (V_1) and beginning maturity (R7) growth stages (7), respectively. Plant loss during the growing season was determined from the difference between the total number of plants emerged and final stand counts. Plots were inspected periodically during the growing season to determine if dying plants had symptoms of root rot caused by *P. m. glycinea* (9). Stem sections of dead or dying plants were surface-sterilized for 2 min in 0.5% sodium hypochlorite solution and plated on lima bean agar (Difco) at irregular intervals each year during the 6-yr experiment to confirm the presence of *P. m. glycinea* in plants with symptoms of root rot.

In 1984, the central sample area of each cultivar block was planted with three randomly arranged rows of Harosoy, Coles, and Corsoy 79 as indicators of the effects of 5 yr of continuous cultivar monoculture on emergence, plant loss, and yield of subsequent crops. Rows were planted with 20 seeds per meter. Emergence and stand counts were made at V_1 and R7. Yield was determined from the total 5-m length of three rows of each cultivar on each sample area.

In 1980 and 1981, *P. m. glycinea* was isolated from diseased Harosoy plants with characteristic symptoms of Phytophthora root rot to determine prevalent races of *P. m. glycinea* at the site. Stems were surface-sterilized as described previously, and sections were plated on cornmeal agar (Difco) containing pimaricin at 100 μg/ml. *P. m. glycinea* isolates were cultured on dilute lima bean agar (Difco) (12 g/L H_2O) and injected by syringe into hypocotyls wounded with a dissecting needle of eight differential cultivars: Harosoy, Sanga, Harosoy 63, Mack, Altona, PI 103091, PI 171442, and Tracy (1). Mean rainfall during the growing season at the test site was determined from weather records at Woodslee.

Field results were analyzed as two-factor experiments. In the event of a significant factor interaction, the interaction mean square was used as the demoninator in an *F*-test of the cultivar mean square to eliminate the effect of the interaction in determining significant differences. Unless stated, significant differences were determined at $P = 0.05$.

Laboratory experiments. Six soybean cultivars/lines representing a range in tolerance to root rot caused by *P. m. glycinea* were selected to study oospore production in roots of cultivars differing in reaction of *P. m. glycinea*. In addition to Coles, Corsoy 79, and Harosoy used in the field study, OX20-8, Evans, and Kentland were included to expand the range of tolerance from highly susceptible (OX20-8) to highly tolerant (Kentland) (4). Soybean seeds were surface-disinfested in 0.5% sodium hypochlorite for 5 min, rolled in a moist paper towel, and incubated 4 days at 25 C. Three healthy seedlings at the crook or VE (7) stage of development were transferred to square, narrow-mouth bottles containing 250 ml of Hydro-sol + $CaNO_3$ nutrient solution (W. R. Grace, Fogelsville, PA). Seedlings were supported with a cotton plug allowing immersion of roots but not hypocotyls. Seedlings were grown under continuous fluorescent light (90 $\mu E\ m^{-2}\ s^{-1}$). Nutrient solutions were aerated for 2 hr daily through plastic tubing (1 mm i.d.) by means of a central distributor to supply about 6 L of air per hour to each bottle. After 7 days, roots were inoculated by adding 10 ml of zoospore suspension containing 5×10^3 zoospores per milliliter to each bottle. *P. m. glycinea* race 7, cultured for 1 wk on dilute lima bean agar, was used for all root inoculations. Zoospores were produced by washing cultures five times at 30-min intervals and incubating for 10–12 hr in darkness (6). The volume of nutrient solution was adjusted to 250 ml, and aeration was stopped for 24 hr after the addition of zoospore inoculum.

After 72 hr, plants were removed carefully from the nutrient solution and roots were cut at the zone of color transition, blotted dry, and weighed. Roots were placed in acetone for 12–24 hr followed by immersion in 20% sodium hypochlorite for 72 hr. Treated roots were cut into 5-mm sections and mixed in a Waring Blendor for 45–60 sec in 100 ml of H_2O. Numbers of oospores in two 1-ml samples from each root suspension were counted in a plastic dish with a grid base under a dissecting microscope at ×40. Treatments were replicated four times and experiments were conducted three times.

RESULTS

Field experiments. Based on symptoms on dead or dying plants and infrequent isolation of additional pathogens from diseased plant tissue, *P. m. glycinea* was the predominant pathogen at the test site. Additional pathogens, including *Fusarium* sp., *Macrophomina phaseolina* (Tassi) Goid., and *Diaporthe phaseolorum* (Cke. & Ell.) Sacc. var. *caulivora* Athow & Caldwell were isolated rarely and were not considered to influence plant loss or yield significantly. During the 5 yr of cultivar monoculture, emergence of Harosoy, Coles, and Corsoy 79 differed significantly in 1979 and 1982. In 1979, emergence of Coles was significantly greater than that of Vickery (11.7 and 7.1 plants per meter, respectively). In 1982, emergence of Corsoy 79 was significantly greater than that of Harosoy (11.5 and 8.6 plants per meter, respectively). A long-term trend in emergence was not evident with any cultivar. Average emergence over 5 yr for Harosoy, Coles, and Corsoy 79 was 8.1, 9.5, and 9.6 plants per meter, respectively. Average emergence did not differ significantly.

Plant loss increased gradually in successive years in all cultivar plots (Table 1). In 1979, plant losses did not occur in any cultivar, but in 1983, plant losses in Harosoy, Coles, and Corsoy 79 were 39.2, 16.7, and 5.2%, respectively. Significant differences in plant loss among cultivars occurred in 1982 and 1983. The average rates of increase in plant loss during the 5-yr period for Harosoy, Coles, and Corsoy 79 were 7.8, 4.2, and 1.3% plant loss per year of monoculture, respectively. Plant losses of cultivars differed significantly with years ($F = 4.111$). During 5 yr, average plant loss for Harosoy (19.8%) was significantly greater than for Coles (5.8%) and Corsoy 79 (1.6%) when tested with the interaction mean square.

Yields of the three cultivars varied considerably from year to year (Table 2). In general, yield of Harosoy was lowest and yield of Corsoy 79 was highest in most years. Average yields of Harosoy, Coles, and Corsoy 79 were 1,682, 2,520, and 3,187 kg/ha. When tested with the

Table 1. Effects of continuous cultivation on plant losses of soybean cultivars differing in reactions to *Phytophthora megasperma* f. sp. *glycinea* during 1979–1983

Cultivar	Reaction	Plant loss (%)					
		1979	1980	1981	1982	1983	$\bar{x}$
Harosoy	Susceptible	0	4.3 a[y]	12.8 a	42.5 a	39.2 a	19.8 a
Coles	Tolerant	0	0.4 a	3.1 a	8.8 b	16.7 ab	5.8 b
Corsoy 79	Resistant	0[z]	0 a	0.2 a	2.7 b	5.2 b	1.6 b

[y] Means within a column followed by the same letter do not differ significantly ($P = 0.05$) according to Duncan's multiple range test.
[z] Vickery was used in 1979.

significant interaction mean square ($F = 3.206$, $P = 0.01$), average yields among cultivars differed significantly ($F = 5.706$).

The frequency of *P. m. glycinea* races at the site as determined from 24 isolates from infected stems of Harosoy in 1980 and 1981 were race 1 (12%), race 3 (22%), race 7 (43%), race 9 (8%), and race 13 (15%).

The results of the experiment conducted in 1984 to determine the relative plant losses of cultivars in each cultivar plot after 5 yr of monoculture using three cultivars as indicators suggested that monoculture of Harosoy and Coles increased disease severity of the subsequent crop compared with Corsoy 79. Plant emergence of Harosoy was similar on all plots (Table 3). Plant loss for Harosoy during the season was significantly higher and yield significantly lower in plots formerly planted with Harosoy and Coles than in plots formerly planted with Corsoy 79. Emergence of Coles was significantly greater in Corsoy 79 plots than in Harosoy plots. Plant loss of Coles was significantly higher and yield significantly lower in plots of Harosoy and Coles than in plots of Corsoy 79. Emergence, plant loss, and yield of Corsoy 79 were similar in all plots.

The overall means of plant emergence and loss of the three indicator cultivars did not differ significantly among plots formerly planted with Harosoy, Coles, or Corsoy 79. Overall yields of the three indicator cultivars were significantly lower in plots formerly planted with Harosoy (1,536 kg/ha) and Coles (1,550 kg/ha) than in plots planted with Corsoy 79 (2,134 kg/ha).

Average rainfall determined from weather records at Woodslee during June, July, and August in 1979, 1980, 1981, 1982, 1983, and 1984 was 75, 134, 117, 48, 90, and 55 mm, respectively. There was no correlation ($P = 0.05$) between accumulated annual rainfall over each growing season and the incidence of Phytophthora root rot in any cultivar.

Laboratory experiments. Root infection occurred in all cultivars after inoculation with zoospores of *P. m. glycinea* race 7. Roots were observed with a dissecting microscope before fixation. Oospores occurred near root tips and at the junctions of branch roots. Most oospores were observed in tips of lower roots. In general, differences in the numbers of secondary roots between inoculated and check plants were noted 72 hr after inoculation. Inoculated treatments of tolerant and moderately tolerant cultivars (Coles, Evans, and Kentland) had fewer secondary roots, and roots were pale brown. Few secondary roots were observed on check plants of the extremely susceptible OX20-8, and secondary roots were absent on inoculated plants. Approximately equal numbers of secondary roots of the resistant Corsoy 79 were noted in check and inoculated treatments. Secondary roots in the inoculated treatment appeared shorter than in the check treatment, and a dark brown tip was evident on most secondary roots.

Oospores in root suspensions were single or in groups within root cells and tissues. Contents of oospores were refractile or brown in transmitted light. Empty oogonia or oospores were seldom observed, indicating that the fixation and extraction technique did not damage oospores. Significant differences in numbers of oospores produced in roots were noted among cultivars. Highest numbers of oospores were found in roots of Coles and lowest numbers were found in Corsoy 79 (Table 4). There was no correlation between assigned reaction to *P. m. glycinea* based on percentage plant loss in field trials (4) and numbers of oospores in roots in these experiments.

Table 2. Effects of continuous cultivation on yields of soybean cultivars differing in reactions to *Phytophthora megasperma* f. sp. *glycinea* during 1979–1983

Cultivar	Reaction	Yield (kg/ha)					
		1979	1980	1981	1982	1983	$\bar{x}$
Harosoy	Susceptible	2,393 a[y]	637 a	2,274 a	2,000 a	1,105 a	1,682 a
Coles	Tolerant	2,689 ab	1,844 b	2,795 ab	4,158 ab	1,115 a	2,520 b
Corsoy 79	Resistant	2,880 b[z]	1,478 ab	3,792 b	5,725 b	2,058 b	3,187 c

[y] Means within a column followed by the same letter do not differ significantly ($P = 0.05$) according to Duncan's multiple range test.
[z] Vickery was used in 1979.

Table 3. Emergence, plant losses, and yields of soybean cultivars differing in reactions to *Phytophthora megasperma* f. sp. *glycinea* on plots that had been planted with soybeans for five years

Bioassay cultivar	Reaction	Previous cultivar	Emergence (%)	Plant loss (%)	Yield (kg/ha)
Harosoy	Susceptible	Harosoy	57	57	773
		Coles	63	47	922
		Corsoy 79	63	25	1,709
Coles	Tolerant	Harosoy	60	19	1,770
		Coles	68	15	1,669
		Corsoy 79	76	6	2,328
Corsoy 79	Resistant	Harosoy	69	1	2,064
		Coles	75	1	2,059
		Corsoy 79	76	6	2,365
C.V. (%)			13	37	30
LSD (0.05)			15	8	545

Table 4. Numbers of oospores in roots of soybean cultivars differing in reactions to *Phytophthora megasperma* f. sp. *glycinea* inoculated with zoospores of race 7

Cultivar	Plant loss[y] (%)	Reaction	Oospores/g of wet root
Coles	15	Tolerant	6,273 a[z]
OX20-8	94	Susceptible	3,798 b
Evans	29	Moderately tolerant	3,188 bc
Kentland	6	Tolerant	3,119 bc
Harosoy	48	Susceptible	2,564 c
Corsoy 79	3	Resistant	74 d

[y] Plant loss in a field infested with *P. megasperma* f. sp. *glycinea*.
[z] Means within a column followed by the same letter do not differ significantly ($P = 0.05$) according to Duncan's multiple range test.

DISCUSSION

Monoculture of soybean cultivars resulted in increased plant losses regardless of tolerance or resistance to *P. m. glycinea*. Plant losses increased more rapidly in plots of susceptible Harosoy than in plots of tolerant Coles. The slowest increase in plant loss occurred in plots of resistant Corsoy 79. Average rainfall during the growing season did not appear to influence the severity of plant loss. Plant loss of Harosoy increased each year from 1979 to 1983, but rainfall varied from a maximum of 134 mm in 1980 to a minimum of 48 mm in 1982. In this experiment, monoculture and continuous use of a cultivar were the predominant factors influencing plant loss.

The direct enumeration of inoculum of *P. m. glycinea* in field soils has not been accomplished because of the difficulty in controlling the germination of oospores (5,18) that are produced in infected

soybean tissue under field conditions (16). Oospores are considered to be a primary mechanism of extended survival of *Phytophthora* spp. (21), and under conditions of monoculture, they would probably accumulate in field soil. Disease severity of Harosoy was shown to be directly related to number of oospores in soil in laboratory experiments (11). It is probable that monoculture contributed to increases in numbers of soilborne oospores with consequent increases in plant loss in succeeding years of this field experiment.

If soilborne inoculum is responsible for the observed plant losses, inoculum concentrations were higher in plots of Harosoy than Coles after 5 yr of monoculture as determined by plant loss of the indicator cultivar Harosoy, but concentrations were equal based on plant loss of the indicator cultivar Coles. Although this does not agree completely with in vitro results showing that seedling roots of Coles support higher production of oospores than roots of Harosoy, a number of factors may affect oospore production in the field, such as total root production and secondary infection cycles during the growing season. It is also possible that Coles is a less sensitive indicator because it is more tolerant than Harosoy to *P. m. glycinea* infection. The field results agree with previous observations that equal numbers of oospores can be produced in taproots of susceptible and tolerant cultivars (8). Inoculum concentration, as indicated by plant loss of Harosoy and Coles, was lowest in plots of the resistant cultivar Corsoy 79. The laboratory studies demonstrated that low numbers of oospores of the incompatible race 7 can be produced in roots of Corsoy 79. Similar observations of oospore reproduction in roots of resistant cultivars have been reported (3,8,17).

Plant losses of soybeans increased during 5 yr of monoculture, but there is evidence that this trend will not continue indefinitely. A tolerance screening program conducted in an adjacent field at Woodslee since 1977 (4) has resulted in relatively uniform plant losses in recent years. The mean plant losses of 16 cultivars evaluated from 1979 to 1984 ranged from 16 to 26%, and the correlation between plant losses and years ($r = 0.6151$) was not significant (*unpublished*). Factors that limit inoculum increase in field soils have not been investigated, but the disease can be considered irreversible (15) as long as monoculture continues because of the persistent resting structures produced by *P. m. glycinea*.

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