Plant Loss Response of Soybean Cultivars to *Phytophthora megasperma* f. sp. *glycinea* Under Field Conditions

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ABSTRACT

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Soybean cultivars and lines were evaluated on Brookston clay during 1977–1980 for plant loss caused by *Phytophthora megasperma* f. sp. *glycinea*. Races 3, 7, and 9 of the pathogen were predominant in the soil. Hypocotyl inoculations with races 1, 3, 4, 7, and 9 indicated that some cultivars and lines carried race-specific resistance that resulted in low plant loss. Other variability in plant loss among entries was ascribed to tolerance. There was no significant cultivar × year interaction in 2-yr and 4-yr analyses; broad-sense heritabilities from these analyses were 93 and 96%. Selection for tolerance based on low plant loss, followed by backcrossing to include race-specific resistance, should provide effective, long-term disease control.

Root rot caused by *Phytophthora megasperma* Drechs. f. sp. *glycinea* (Hildeb.) Kuan and Erwin (*Pmg*) is the major disease of soybean (*Glycine max* (L.) Merr.) on clay soils of southwestern Ontario. Effective disease control was obtained from 1963 to about 1973 utilizing resistance to *Pmg* race 1 with the Rps_1 gene. With the occurrence of additional races of *Pmg* and a subsequent increase in disease (5), the Phytophthora control program was redirected to identify soybean cultivars and lines with tolerance to root rot under field conditions.

Tolerance is, as defined by Schmitthenner and Walker (9), the ability of susceptible plants to survive infection without showing severe symptom development such as death, stunting, or yield loss. In the field, tolerance is difficult to distinguish from resistance. Therefore, races in the test area should be monitored and all entries being evaluated for tolerance should also be evaluated for resistance/susceptibility to the prevalent races by means of hypocotyl inoculations. Phytophthora rot is not uniform in a field (7); it varies with soil compaction, drainage, etc., thereby making it difficult to evaluate tolerance in terms of yield loss. Furthermore, the need to evaluate cultivars/lines ranging from maturity groups 000 to III would require separate maturity group tests in order to use plant size and yield as criteria.

Plant loss data were obtained from field tests of cultivars and lines grown under conditions favorable for the development of Phytophthora rot during 1977–1980 with Amsoy 71 as a standard check cultivar. This paper reports the phenotypic and environmental variability for plant loss caused by *Pmg* and considers the usefulness of the technique for evaluating tolerance by means of plant loss.

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MATERIALS AND METHODS

Plant loss tests. The area selected for continuous tolerance evaluation consisted of Brookston clay loam, characteristic of disease-prone areas in southwestern Ontario. In addition to the natural infestation of *Pmg*, soil containing races 3, 4, and 6 (5) was spread on the field in the spring of 1976. The field was plowed in the fall of 1976 and disked the next spring to prepare the seedbed. In subsequent years, tillage consisted of disking and leveling. Fertilizer (8-32-16) was applied annually at the rate of 560 kg/ha. Weeds were controlled each year with chloramben applied at 4.5 kg a.i./ha and by hand-hoeing. Up to 30 mm of water was applied by overhead sprinklers during the 2-wk period following each planting to maintain moist soil conditions.

To determine field reaction to *Pmg*, soybean cultivars and lines were planted in three-replicate tests using single-row plots except for a few entries that were in two-row plots bordered with Amsoy 71. Rows were 3.6 m long and spaced at either 50 or 60 cm with 100 seeds planted per row. Tests were planted 30 May 1977, 5 June 1978, 12 June 1979, and 13 June 1980. The number of emerged seedlings was determined 20–30 days after planting; counts included dead or dying seedlings. After 80–100 days from planting, the number of surviving plants was determined by counting those that produced beans. Percentage of plant loss was based on differences in plant counts from emergence to maturity.

In each test there were from 80 to 96 entries, with some of the cultivars and lines being present in the 1977–1978 and 1977–1980 periods, thereby allowing analyses over years. The set for the 2-yr analysis included nine cultivars that were recommended in Ontario in 1977 but not in 1980 (Beechwood, Harlon, Harosoy 63, Harwood, Nairn, Steele, Vansoy, Viking and XK 505), plus Grande, Marion, Vickery, Wayne, Woodworth, and Minnesota line M405 (a parent of OX20-8). The set for the 4-yr analysis included the 22 cultivars recommended in 1980, plus Corsoy 79 and OX20-8. Amsoy 71, Harcor, and OX20-8 were included in both analyses for comparative purposes. Heritabilities in the broad sense were calculated as the amount of the total variation ascribable to cultivars after removing the cultivar × years and error components.

Genetic test. The F_2 of Williams × Wells was planted 23 May 1979, along with the parents, into a field that had been in continuous soybeans since 1973. *Pmg* race 7 was predominant in the soil; Wells and Williams are both susceptible to race 7 with hypocotyl inoculation. The test had 14 replicates of single-row plots with 100 seeds per row. Emergence was slow as a result of heavy rainfall and soil compaction and crusting. Emergence counts were taken 21 June. Diseased plants were recorded and removed from the plots biweekly until maturity.

Yield tests. Two-row plots of Harcor, Harosoy 63, and Vickery grown on the tolerance test site were harvested for yield in 1977–1978. Cultivars including Corsoy 79 and Harcor were planted in the second field 23 May 1980, using eight replicates of four-row plots with 100 seeds per row. Seedling and plant counts were taken on the two center plot rows as described above. Plants in 2 m were harvested from each of the center rows. In addition, results of cultivar tests were available from other substation fields in which there was better management and drainage of the clay soil, resulting in less disease, and from other locations where Phytophthora rot was not a problem on well-drained sand and clay loam. Tests were grouped according to the severity of Phytophthora rot, and variety comparisons were made within each group.

Race isolations. In 1978, races of *Pmg* at the test site were determined. Surface soil collected at random was placed in 20-cm pots in the greenhouse and planted with Harosoy soybeans. After 2 wk, hypocotyls of diseased plants were surface-sterilized and plated on selective medium (6). Thirty isolates of *Pmg* obtained in this manner were characterized by inoculating 15 plants of each differential soybean cultivar (6). Inoculations resulting in a variable reaction were repeated.

Hypocotyl inoculations. Race-specific resistance of the cultivars and lines evaluated for tolerance to *Pmg* under field conditions was determined by hypocotyl inoculation with *Pmg* races 1, 3, 4, 7, and 9. Thirty to forty 10-day-old seedlings were inoculated with each *Pmg* race. Inoculum was produced on dilute lima-bean agar (10 g/L; Difco) or in 20% V-8 juice broth (clarified by filtration) and applied to wounded hypocotyls by syringe or forceps. Pots of inoculated seedlings were covered for 24 hr with plastic bags. The percentage of dead seedlings was determined 4–5 days after inoculation. Cultivars and lines were rated resistant, intermediate, or susceptible in reaction when plant losses were 0–10, 11–89, or 90–100%, respectively.

RESULTS AND DISCUSSION

Plant loss of cultivars and strains evaluated at the tolerance test site differed significantly ($P = 0.01$), ranging from 8 to 91% (Table 1) and 6 to 92% (Table 2). Wayne and Woodworth had 8 and 18% loss, respectively, which agrees with reports that these cultivars, although susceptible to hypocotyl inoculation, show some degree of resistance/tolerance in the field (3,4,9). Slusher and Sinclair (10) have shown infection and oospore formation in the roots of the Wayne cultivar. Although it is not practical to measure the degree of root infection in field plots, it is not likely that cultivars appear tolerant from having escaped infection.

The average loss for 1977, 1978, 1979, and 1980 was 20, 22, 22, and 29%, respectively. There was no cultivar × year interaction in either the 4-yr or the 2-yr analysis, indicating a consistency of cultivar response to the pathogen, even though error variability within individual tests resulted in coefficients of variation ranging from 41 to 52%. Plants were examined frequently during each growing season to verify that those dying had characteristic symptoms of Phytophthora rot. Stem canker caused by *Diaporthe phaseolorum* var. *caulivora* and natural thinning caused by competition within plant rows were observed occasionally.

Some material tested had race-specific resistance as determined from hypocotyl inoculation (Tables 1 and 2). Corsoy 79 and Vickery carry Rps_1^c, and A1564, A2575, A2656, Amsoy 71, Beechwood, Evans, Gesto, Harcor, Harlon, Harosoy 63, Harwood, Olinda, OX20-8, Steele, Viking (heterogeneous), Wells, and XK505 carry Rps_1. Olinda appears to carry an Rps gene, but when inoculated with *Pmg* races 3 and 4 a variable reaction was obtained. Following inoculation, many seedlings with limited infection partially collapsed but then recovered. Maple Presto reacted in a similar manner with races 7 and 9. Inoculation of Viking resulted in 40–60% plant kill, whereas the remainder of plants appeared resistant.

Pmg races 3, 7, and 9 comprised 10, 57, and 33% of the isolates obtained from the test site in 1978. Although *Pmg* races 4 and 6 were added to soil at the site and race 1 was recently isolated in the immediate vicinity, propagules of these races either were present in low numbers or it may not be possible to distinguish race 7 from race 6 with PI 103.091 (6,8). Because race 1 was not prevalent, the Rps_1 gene found in some of the entries should not have influenced the tolerance evaluation. However, with race 4 not being prevalent, the low plant loss exhibited by Corsoy 79 and Vickery was probably the result of resistance to races 3, 7, and 9 rather than tolerance.

Use of our field technique to obtain plant loss data for licensing and recommendation of cultivars having no more plant loss than Amsoy 71 has resulted in a reasonable degree of control of Phytophthora rot in Ontario. The frequency of fields observed with severe disease at midseason was much less with Harcor compared with Harosoy 63 and Harwood (*unpublished*). Seven cultivars recommended to growers in 1977 that had similar or greater plant loss than Amsoy 71 were dropped by 1980. Consequently, 21 soybean cultivars recommended in Ontario in 1980 had significantly less plant loss from Phytophthora rot than the other recommended cultivar Amsoy 71 (Table 2). Although plant loss of recommended cultivars in the tolerance test is fairly high, similar disease severity has seldom been encountered in growers' fields in recent years. Surveys of growers' fields in 1979 and 1980 had less than 5% plant loss as a maximum (1; *unpublished*).

It has been suggested that tolerance is based on a polygenic system of inheritance (9). The genetic test, although conducted under low to moderate disease severity, supports this hypothesis. Williams, which is moderately tolerant (9), had 3% plant loss; Wells, which is moderately susceptible (Table 2), had 16% plant loss. The F_2 of the cross of these two cultivars was intermediate, with a loss of 7%. Quantitative inheritance will make breeding for tolerance more difficult than breeding for race-specific resistance, which involves major genes. However, broad-sense heritability for plant loss was 93% based on the 2-yr analysis in Table 1 and 96% based on the 4-yr analysis in

Table 1. Plant loss of soybean cultivars and lines caused by Phytophthora rot in 1977–1978 field tests and reaction to hypocotyl inoculation

Cultivar/line	Hypocotyl reaction to races[w] 1	3	4	7	9	Plant loss[x] (%)
Vickery	R	R	S	R	R	8 a[y]
Vansoy	S	S	S	S	S	8 a
Wayne	S	S	S	S	S	8 a
Harcor	R	S	S	S	S	16 a
Grande	S	S	S	S	S	17 a
Woodworth	S	S	S	S	S	18 a
Beechwood	R	S	S	S	S	20 a
XK 505	R	S	S	S	S	35 b
Viking	I	S	S	S	S	37 b
Harlon	R	S	S	S	S	43 bc
Harwood	R	S	S	S	S	44 bcd
Amsoy 71	R	S	S	S	S	45 bcd
Harosoy 63	R	S	S	S	S	48 bcd
Marion	S	S	S	S	S	50 bcd
M405	S	S	S	S	S	52 cd
Nairn	R	S	S	S	S	58 de
Steele	R	S	S	S	S	68 e
OX20-8	R	S	S	S	S	91 f
SE						4.6
CV%						31

Source of variation	DF	Mean squares
Years	1	194
Cultivars	17	3,183**[z]
Cultivars × years	17	220
Error	68	128

[w] R (resistant) = 0–10% of plants killed, S (susceptible) = 90–100%, and I (intermediate) = 11–89%.
[x] Evaluated under conditions favorable to the disease in a field infested with *Pmg* races 1, 3, 4, 7, and 9.
[y] Means from a 1980 test in a field predominantly infested with *Pmg* race 7; there was 12% plant loss range test.
[z] ** Indicates $P = 0.01$.

Table 2. Plant loss of soybean cultivars and lines caused by Phytophthora rot in 1977–1980 field tests and reaction to hypocotyl inoculation

Cultivar/line	Hypocotyl reaction to races[v] 1	3	4	7	9	Plant loss[w] (%)
Corsoy 79[x]	R	R	S	R	R	6 a[y]
Premier (B216)	S	S	S	S	S	7 a
Kentland (S1492)	S	S	S	S	S	10 ab
Coles	S	S	S	S	S	12 abc
A1564	R	S	S	S	S	13 abc
A2575	R	S	S	S	S	16 abcd
Maple Presto	R	R	R	I	I	17 bcd
Starbuck	S	S	S	S	S	17 bcd
Olinda	R	I	I	S	S	17 bcd
A2656	R	S	S	S	S	17 bcd
S1346	S	S	S	S	S	17 bcd
Harcor	R	S	S	S	S	17 bcd
Maple Arrow	R	R	R	S	S	18 bcd
Hodgson	S	S	S	S	S	22 cde
Gesto	R	S	S	S	S	22 cde
Evans	R	S	S	S	S	25 def
McCall	S	S	S	S	S	25 def
Dawn	S	S	S	S	S	26 def
Prestidge (B186)	S	S	S	S	S	26 def
Starlite	S	S	S	S	S	28 efg
Wells	R	S	S	S	S	33 fg
Falcon (C260)	S	S	S	S	S	35 g
Amsoy 71	R	S	S	S	S	45 h
OX20-8	R	S	S	S	S	92 i
SE						3.0
CV%						45

Source of variation	DF	Mean squares
Years	3	1,018**[z]
Cultivars	23	3,512**
Cultivars × years	69	131
Error	189	112

[v] R (resistant) = 0–10% of plants killed, S (susceptible) = 90–100%, and I (intermediate) = 11–89%.
[w] Evaluated under conditions favorable to the disease in a field infested with *Pmg* races 1, 3, 4, 7, and 9.
[x] In 1977, Vickery was used; both are backcross-derived Corsoy with Rps_1^c.
[y] Means followed by the same letter do not differ significantly ($P = 0.05$) by Duncan's multiple range test.
[z] ** Indicates $P = 0.01$.

Table 3. Yield of soybean cultivars with different tolerance or race-specific resistance in tests that differed in severity of Phytophthora rot

Cultivar	Resistance gene	Yield (kg/ha)[u] Disease[v] absent	Disease[w] moderate	Disease[x] severe	Disease[y] very severe
Harosoy 63	Rps_1	3,130 a	2,310 a	1,510 a	...
Harcor	Rps_1	3,480 b	3,210 b	2,590 b	2,230 a
Corsoy 79/Vickery[z]	Rps_1^c	...	3,320 b	2,520 b	3,380 b

[u] Means in columns followed by the same letter do not differ significantly ($P = 0.05$) by Duncan's multiple range test.
[v] Means of 10 cultivar tests, Harrow and Ridgetown, 1974–1978.
[w] Means of three cultivar tests, Woodslee, 1976–1978.
[x] Means from tests given in Table 1.
[y] Means from a 1980 test in a field predominantly infested with *Pmg* race 7; there was 12% plant loss in Corsoy 79 and 27% in Harcor.
[z] Both are backcross-derived Corsoy with Rps_1^c.

Table 2. The high heritability values indicate that field screening based on plant loss could be used as a selection technique for improving levels of field tolerance provided that the race-specific resistance of the segregating material and the races of *Pmg* at the test site are known.

Evaluation of tolerance to *Pmg* should involve measurement of yield, but comparison of cultivar yields in relation to severity of root rot indicates that plant loss in the tolerance test was a suitable criterion for estimating relative tolerance. Harcor, which was rated more tolerant than Harosoy 63 based on plant loss in the tolerance test, outyielded Harosoy 63 by increasing amounts as disease severity in tests increased (Table 3). Harcor outyielded Harosoy 63 by 11% in the absence of disease, by 39% under moderate disease conditions, and by 71% in the tolerance test area where disease conditions were severe.

Although varietal tolerance to Phytophthora rot can reduce yield loss, race-specific resistance can provide better prevention of yield loss under conditions of heavy rainfall (Table 3) when compatible races are not prevalent. However, there are disadvantages of using race-specific resistance. The buildup of compatible races results in losses from disease. The Vertifolia effect (11) can occur; for example, OX20-8 was selected for Rps_1 resistance to race 1, but in the presence of compatible races it is extremely susceptible (Tables 1 and 2), requiring high rates of applied fungicide to reduce plant loss to acceptable levels (2). Transgressive segregation, as with OX20-8 (Table 1), makes it possible for a line to be more susceptible than both parents (M405 × Harosoy 63). To avoid releasing new cultivars with resistance specific to races that are prevalent and with inherently high susceptibility to compatible races that may build up, selection for a high degree of tolerance (low plant loss) followed by backcrossing to incorporate race-specific resistance should provide the most effective, long-term disease control.

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