Effects of Soil Compaction on the Incidence of *Phytophthora megasperma* f. sp. *glycinea* in Soybean

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ABSTRACT

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Soil compaction experiments were conducted for 2 years on a poorly drained soil with a natural infestation of *Phytophthora*. Prior to planting, the compaction treatment was imposed on strips selected at random in the plot area by repeatedly driving a tractor over the plots. Soil compaction treatments significantly increased soil bulk density in compacted vs. uncompacted plots in both years. Soil compaction significantly increased the incidence of Phytophthora root rot. The increased disease incidence helped differentiate susceptible from resistant cultivars. This implies that soil compaction could be useful in identification of susceptible soybean lines from breeding programs. Disease incidence and area under the disease progress curve were both found to be good measures of cultivar resistance to *Phytophthora*.

Phytophthora root rot, caused by *Phytophthora megasperma* f. sp. *glycinea* Kuan and Erwin, is one of the most destructive soilborne diseases of soybean (*Glycine max* (L.) Merr.). The disease was first observed in Ohio in 1951 (17) and now occurs in most soybean-producing areas of the U.S. and Canada (9). The pathogen may attack plants in all stages of growth with disease development favored by poorly drained soils and cool wet weather. Symptoms of the disease are preemergent or postemergent damping-off of younger plants, and stunting, wilting, or death of older plants.

Resistance to the pathogen has been identified, and effective disease control has been obtained by incorporating race-specific, major gene resistance into adapted cultivars. Nine major host resistance genes have been identified (12). But the use of resistant cultivars has led to a buildup of compatible races of the organism (16), that now total 24 (10). It has become increasingly difficult to identify new sources of resistance, to study their inheritance, and incorporate one or more genes into adapted cultivars as additional races are identified. Non-race-specific resistance has been postulated to reduce the buildup of one race over another and also to minimize losses from the disease. Several researchers have identified non-race-specific resistance and described several techniques to identify, quantify, and incorporate the resistance into adapted cultivars (2,3,7,15,17–21). Field screening may detect genotypes resistant to colonization or with low levels of resistance that may not be detected by seedling screening techniques.

Soil factors, such as bulk density and compaction, have been shown to affect disease incidence. In soybean fields, Hildebrand (8) and Fulton et al (5) observed increased incidence of *P. m.* f. sp. *glycinea*-infected plants in areas of concentrated implement traffic and soil compaction. Gray and Pope (6) found that subsurface soil compaction increased the severity of Phytophthora root rot in the susceptible cultivar Corsoy. They observed an increase in the number of plants killed by *P. m.* f. sp. *glycinea*, and a seed yield decrease in compacted vs. uncompacted plots.

Incorporation of resistance, whether race-specific or non-race-specific, would be more efficient if a consistent method of field screening was available. Large numbers of soybean lines could be evaluated with less time and labor in naturally infested fields. Since Phytophthora root rot incidence varies greatly with environmental conditions, it is often impossible to differentiate susceptible from resistant genotypes. Any method that could accentuate disease response or make identification of disease reaction less dependent on environmental conditions would be useful in field evaluations.

The objectives of this study were to determine 1) if soil compaction would help distinguish resistant from susceptible genotypes in field screening and 2) if isolines with varying degrees of resistance could be separated.

MATERIALS AND METHODS

Soil compaction experiments were conducted in the field at the Agricultural Engineering Farm, Urbana, IL, on a Drummer silty clay loam soil (fine-silty, mixed, mesic typic haplaquoll) in 1983 and 1984. This soil has poor internal drainage and a natural infestation of *P. m.* f. sp. *glycinea*. The field had been planted to soybeans prior to 1983 and plowed each fall. Weeds were controlled each year with a preplant application of 2.8 kg a.i./ha of metolachlor (2-chloro-*N*-[2-ethyl-6-methylphenyl]-*N*-[2-methoxy-1-methylethyl] acetamide) and with 3.36 kg a.i./ha of chloramben (3-amino-2,5-dichlorobenzoic acid), cultivation, and hand hoeing.

Prior to planting, the compaction treatment was imposed on strips selected at random in the plot area by repeatedly driving a tractor over the plots, offsetting the wheels each time until the strips were evenly compacted. The tractors weighed 6,758 kg in 1983, and 4,536 kg in 1984. Soil moisture at the time of compaction was 23.6 and 23.8% in 1983 and 1984, respectively. A disk-harrow was used to prepare the seedbed.

Soil compaction measurements were made by randomly collecting bulk density samples from each of 24 compacted and uncompacted plots 4 wk after the first planting date using a truck-mounted hydraulic probe. The 5.4 cm (diameter) probe was carefully pushed into the soil, to avoid disturbing the core, to a depth of approximately 20 cm. The soil core was removed, the upper 2.5 cm was discarded, and the next two 5-cm sections were saved for bulk density determination. Each section, representing a known volume of soil, was dried at 100 C for 24 hr and weighed. Bulk density measurements in compacted plots were found to be significantly higher than in uncompacted plots both years. The compaction treatment increased bulk density from 1.13 to 1.28 g cm^{-3} in 1983 and from 1.15 to 1.27 g cm^{-3} in 1984, with LSD values at the 0.05 level of 0.04 and 0.05 for the 2 years, respectively.

Plots with four rows 76 cm apart and 4.6 m in length were planted on 11 and 24 May 1983 and 2 and 31 May 1984 at a seeding rate of 32 seeds per m of row.

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Cultivars planted were of Group II maturity and possessed various levels of *P. m.* f. sp. *glycinea* resistance (Table 1). An entry, Multiline, composed of equal proportions of Corsoy 79, L27, and L28 was planted both years while in 1984, Toku and Voris 295 were excluded. The treatments were replicated three times in a split-plot arrangement of a randomized complete block design in which the compacted or uncompacted treatments were whole plots, and cultivars and planting dates were subplots. Replications were considered random while compaction, cultivars, and planting dates were considered fixed effects.

Data were collected from a 3.1-m section of the center two rows of each plot for plant height, maturity, lodging, seed weight, total number of plants emerged, total number of dead plants, and seed yield. Plant height was measured as height in centimeters of an average plant from the soil surface to the uppermost node. Maturity was recorded as days from 1 January to when 95% of the pods had obtained mature color. Lodging was rated on a scale of 1 (all plants erect) to 5 (all plants prostrate). Seed weight was measured as g/100 seeds. Total number of plants emerged was measured at 14 days after planting in 1983, and at 21 days after planting in 1984. Number of dead plants were identified and removed at 1-wk intervals, and later in the season at 2-wk intervals. Seed yield (kg/ha) was determined by harvesting the center two rows that had been trimmed to 3.1 m prior to maturity. Disease incidence was calculated for each plot by expressing dead plants as a percent of the total number of plants emerged. Area under the disease progress curve (AUDPC) was also calculated to express the amount of disease for the entire season:

$$\sum_{i=1}^{n-1} [(X_{i+1} + X_i)/2][t_{i+1} - t_i]$$

where X_i = cumulative disease incidence at the ith observation, t_i = days after planting, and n = total number of observations. Area under the disease progress curve was analyzed for each planting date separately each year.

Data were analyzed by analysis of variance for each year and combined over years. In the combined analysis, replications were random effects while years, compaction, cultivars, and planting dates were considered fixed effects.

RESULTS AND DISCUSSION

Cultivar effects were highly significant for all variables measured in 1983. Disease incidence and number of dead plants increased with compaction while seed weight and total number of plants emerged decreased (Table 2). Seed yield was not significantly affected by compaction, which differs from the results of Lindemann et al (13) who found a trend toward higher yields in compacted plots in dry years, although not significant, and decreased yield when greater than normal precipitation occurred. Yields in 1983 ranged from 3,487 to 2,258 kg/ha for the cultivars Century and Toku, respectively (Table 3).

Cultivar by compaction interactions were found in 1983 for number of dead plants and disease incidence, but not for the other traits measured. Significant cultivar and compaction effects for seed weight and total plants emerged without a cultivar by compaction interaction indicate that soil compaction affected all cultivars in a similar manner. Disease incidence in 1983 (Table 4) ranged from 0 to 5.9% in uncompacted plots for L27 and Sloan (1) and from 0.1 to 18.9% in compacted plots for Toku and Sloan. Only the susceptible cultivar Sloan had significantly higher disease incidence than the other lines in uncompacted

Table 1. Parentage or source of cultivars grown in 1982

Cultivars	*Phytophthora megasperma* f. sp. *glycinea*	Parentage or source[y]
BSR 201	Unknown	Pride B216 × AX901-40-2
Century	Rps_1	Calland × Bonus
Corsoy	rps_1	Harosoy × Capital
Corsoy 79	$Rps_1{}^c$	Corsoy[6] × Lee 68
L27[z]	$Rps_1{}^k$	Corsoy[8] × Kingwa
L28[z]	$Rps_1{}^c$ Rps_2	Corsoy 79 × [Corsoy[6] × (Harosoy[5] × D54-2437)]
L77-1585[z]	Rps_2	Corsoy[6] × (Harosoy[5] × D54-2437)
Sloan	rps_1	M59-120 × IVR Ex4731
Toku	Unknown	PI 86129
Voris 295	Rps_1	Unknown

[y] Pedigrees of unreleased parental lines: Pride B216 = Corsoy × Wayne, AX901-40-2 = Beeson × (Clark[5] × PI 84946-2), D54-2437 = [Roanoke × (Ogden × CNS)] × (Lincoln × Richland), IVR Ex4731, M59-120 = (1).
[z] R. L. Bernard, *personal communication.*

Table 2. Comparison of traits in compacted and uncompacted plots averaged over planting dates in 1983 and 1984

Traits	1983		1984	
	Uncompacted	Compacted	Uncompacted	Compacted
Seed yield (kg/ha)	3,169 a[x]	3,031 a	3,516 a	2,584 b
Seed weight (g/100)	15.5 a	15.0 b	16.3 a	15.1 b
Plant height (cm)	84 a	80 a	97 a	80 b
Lodging[y] (score)	2.5 a	2.5 a	1.8 a	1.3 b
Total plants emerged (number)	192 a	182 b	159 a	95 b
Dead plants (number)	1.94 a	5.27 b	4.52 a	5.70 a
Disease incidence[z] (%)	1.06 a	3.18 b	2.43 a	5.74 b

[x] Means in the same year followed by different letters are significantly different by LSD 0.05.
[y] Score of 1 (all plants erect) to 5 (all plants prostrate).
[z] Percent of dead plants to total plants emerged.

Table 3. Comparison of cultivars averaged over compaction and planting dates in 1983

Cultivar	Seed yield (kg/ha)	Seed weight (g/100)	Plant height (cm)	Lodging (score)[y]	Total plants emerged (no.)
BSR 201	3,154	15.1	81	2.3	196
Century	3,487	18.6	84	1.6	180
Corsoy	2,814	14.4	74	2.3	192
Corsoy 79	3,260	14.3	84	2.6	193
L27	3,147	14.4	84	3.5	199
L28	3,377	14.2	87	2.9	194
L77-1585	3,208	14.2	80	2.8	189
Multiline	3,305	14.2	86	3.1	199
Sloan	2,884	15.4	83	2.2	164
Toku	2,258	18.0	53	1.8	178
Voris 295	3,203	15.2	109	2.4	177
LSD 0.05[z]	202	0.5	4	0.3	12
Mean	3,100	15.3	82	2.5	187

[y] Score of 1 (all plants erect) to 5 (all plants prostrate).
[z] LSD for within-column comparisons.

plots, while both susceptible cultivars Sloan and Corsoy had significantly higher values in compacted plots.

The AUDPC results (Table 5) were similar to disease incidence in that Sloan was the only cultivar with a significantly higher value than other lines in uncompacted plots in the first planting date. In compacted plots, both Sloan and Corsoy had higher AUDPC values than other lines. The genotype by compaction interaction was not significant in the second planting date. However, when genotype means were averaged over compaction, Sloan and Corsoy were significantly higher than the other lines.

Dead plant counts were made six times for both planting dates in 1983, with the last count occurring 72 and 59 days after planting for the two planting dates, respectively. Cumulative disease incidence at each dead plant determination was analyzed as a split-plot in time. In both planting dates, cumulative disease incidence continued to increase until the last dead plant determination, although it was significantly higher only in the first planting date. Disease incidence and AUDPC were calculated using all six determinations. Differences in disease incidence among the lines that increased throughout the season in compacted plots in the first planting date became apparent after the second dead plant determination. Although differences between resistant and susceptible lines were greatest at the last dead plant determination, it was possible to separate lines on the basis of their disease reaction within 45 days after planting. Tooley and Grau (18) concluded that to identify cultivar differences with rate-reducing resistance to *P. m.* f. sp. *glycinea* in the field, with consideration to ease of data collection, AUDPC and disease incidence assessed between the V7 and R7 growth stages were the variables that best met their criteria. In their study, V7 and R7 occurred at 57 and 112 days after planting, respectively.

Planting date effects were found for seed yield, seed weight, and total plants emerged (Table 6). The lower seed yield and seed weight means of the later planting date is probably a result of drought conditions during June and July, in addition to a shorter growing season in 1983. Emergence of higher total plants at the later planting date is probably due to higher soil temperatures at planting and possibly less preemergence damping-off.

In 1984, cultivar effects were significant

Table 4. Comparison of disease incidence in compacted and uncompacted plots averaged over planting dates in 1983 and 1984

	Disease incidence[x]					
	1983		1984		2-Year means	
Cultivar	Uncompacted (%)	Compacted (%)	Uncompacted (%)	Compacted (%)	Uncompacted (%)	Compacted (%)
BSR 201	0.17	0.85	0.33	3.83	0.25	2.34
Century	1.30	0.82	1.67	11.83	1.48	6.33
Corsoy	2.38	9.53	7.67	13.67	5.03	11.60
Corsoy 79	0.42	0.93	2.00	4.00	1.21	2.47
L27	0.00	0.35	0.33	2.83	0.17	1.59
L28	0.25	0.25	0.83	1.83	0.54	1.04
L77-1585	0.28	0.98	1.17	2.50	0.73	1.74
Multiline	0.57	1.00	0.67	1.50	0.62	1.25
Sloan	5.92	18.95	7.17	9.67	6.54	14.31
Toku	0.27	0.10	...	...	...	...
Voris 295	0.08	1.20	...	...	...	...
LSD 0.05[y]	3.12	3.12	3.89	3.89	2.57	2.57
LSD 0.05[z]	4.42		5.52		2.57	
Mean	1.06	3.18	2.43	5.74	1.84	4.74

[x] Percent of dead plants to total plants emerged.
[y] LSD for within-compaction comparisons.
[z] LSD for within-cultivar comparisons.

Table 5. Comparison of area under the disease progress curve in compacted and uncompacted plots in two planting dates in 1983 and 1984

	Area under the disease progress curve							
	1983				1984			
	Date 1		Date 2		Date 1		Date 2	
Cultivar	Uncompacted	Compacted	Uncompacted	Compacted	Uncompacted	Compacted	Uncompacted	Compacted
BSR 201	0.08	0.09	0.01	0.44	0.70	0.92	0.00	1.32
Century	0.37	0.06	0.25	0.24	1.89	4.16	0.24	2.89
Corsoy	0.46	2.58	0.68	2.69	5.56	3.93	0.17	1.73
Corsoy 79	0.24	0.25	0.07	0.15	2.35	3.14	0.00	0.35
L27	0.00	0.11	0.00	0.08	0.94	3.31	0.14	0.40
L28	0.08	0.00	0.09	0.14	0.89	2.52	0.32	0.29
L77-1585	0.14	0.36	0.07	0.28	1.20	3.66	0.45	0.12
Multiline	0.27	0.83	0.08	0.04	0.72	1.84	0.00	0.30
Sloan	1.76	4.60	2.51	5.80	5.67	9.05	0.40	0.22
Toku	0.17	0.08	0.08	0.00	...	...	...	...
Voris 295	0.09	0.28	0.00	0.13	...	...	...	...
LSD 0.05[y]	1.39	1.39	NS	NS	NS	NS	1.20	1.20
LSD 0.05[z]	1.36		NS		NS		1.66	
Mean	0.33	0.84	0.35	0.91	2.21	3.61	0.19	0.85

[y] LSD for within-compaction comparisons, if the *F*-test was significant at the 0.05 probability level.
[z] LSD for within-cultivar comparisons, if the *F*-test was significant at the 0.05 probability level.

for all traits measured, except plant height. Yields ranged from 3,242 to 2,724 kg/ha for the cultivars Century and Corsoy, respectively (Table 7). Soil compaction effects were also significant for all traits, except number of dead plants. The effects of compaction were more severe in 1984 than in 1983, although the severity is not reflected in the bulk density. Yield, seed weight, plant height, and total plants emerged were greatly reduced by compaction in 1984, while little or no difference was seen in 1983 (Table 2). The mean disease incidence for compacted plots in 1984 was nearly double that of uncompacted plots.

The cultivar by compaction interaction was significant for only disease incidence in 1984. Compaction increased the disease incidence of all lines, with Century and Corsoy increasing significantly higher (Table 4). Sloan and Corsoy had higher disease incidence than other lines in uncompacted plots. These two cultivars and Century were higher than other cultivars in compacted plots. Century, with the Rps_1[a] gene, is resistant to fewer of the identified races of *P. m.* f. sp. *glycinea* than the resistant Corsoy isolines (12). The high disease incidence in Century means races of *P. m.* f. sp. *glycinea* other than races 1 and 2 were colonizing this variety.

The AUDPC (Table 5) means in both dates showed higher values in compacted plots. The second planting date means were much smaller than the first date, which is indicative of the dry conditions that prevented expression of *P. m.* f. sp. *glycinea* susceptibility. A genotype by compaction interaction was found only in the second planting date. When cultivar means were averaged over compaction in the first date, Sloan was the only line significantly higher than other lines.

Dead plant determinations were made seven times in the first planting date and five times in the second date, with the last determination occuring 111 and 82 days after planting, respectively. Analysis of cumulative disease incidence showed significant increases at the last two determinations in each planting date. Differences among soybean lines again became apparent several weeks after planting, although differences were greatest at the last determination. It was possible to separate lines approximately 45 days after planting.

Planting date effects were significant for all variables in 1984 (Table 6). Extremely dry conditions from June to September may have contributed to the magnitude of the differences, especially disease incidence. The increase in plant height in the second date is probably due to warmer weather at emergence, resulting in vigorous plants and rapid plant growth.

The combined analysis of the 1983 and 1984 studies showed significant genotype effects for all traits. Significant compaction effects were also found for all traits. The combined disease incidence means of compacted plots (Table 4) were similar to the single-year analyses because the susceptible cultivars Corsoy and Sloan had higher disease incidence than the other lines. Compaction also increased the disease incidence, which made identification of susceptible lines easier. The lines with high levels of *P. m.* f. sp. *glycinea* resistance, L27, L28, and Multiline, had low levels of disease incidence in the single-year and combined analyses.

Several isolates of *P. m.* f. sp. *glycinea* were recovered from dead plants 1 mo after planting. A set of soybean differentials (16) was used to recover races 1, 3, 8, 9, and two unknown races. Only race 1 was isolated from susceptible cultivars, while the other races were recovered from cultivars with genes resistant to race 1. This may indicate that race 1 is more aggressive or competitive than other races when only susceptible cultivars are available to the pathogen, or that race 1 was most prevalent in this field.

In 1983, heavy rainfall and cold soil temperatures during May produced conditions described by Kaufmann and Gerdemann (9) as being ideal for *P. m.* f. sp. *glycinea* disease development. However, disease incidence in the first planting date, which corresponded to the cool, wet weather, was lower than the first date in 1984. The lower number of plants emerged in the first date compared with the second date in 1983 may indicate higher preemergence damping-off, although this was not confirmed. Another reason for the low disease incidence may be that the pathogen was not actively growing at the time of the first planting date. Eye et al (4) found that the optimum temperatures for mycelial growth and zoospore production were 25 and 20 C, respectively. At 10 C, both mycelial growth and zoospore production were greatly reduced. The soil temperatures in the field may have been low enough to allow the seedlings to escape early kill by *P. m.* f. sp. *glycinea*.

Both soil compaction and *P. m.* f. sp. *glycinea* have been found to affect soybean growth (2,11,13,14), and it was difficult to determine and separate how both affect plant growth and yield in this study. Soil compaction did not significantly affect seed yield or plant height in 1983, while both of these traits were decreased by compaction in 1984 (Table 2). Cultivar by compaction interactions for seed yield and height were not

Table 6. Comparison of traits in two planting dates averaged over compaction in 1983 and 1984

	1983		1984	
Trait	**Date 1**	**Date 2**	**Date 1**	**Date 2**
Seed yield (kg/ha)	3,151 a[x]	3,049 b	3,161 a	2,969 b
Seed weight (g/100)	15.5 a	15.1 b	16.0 a	15.4 b
Plant height (cm)	83 a	82 a	81 a	97 b
Lodging[y] (score)	2.4 a	2.5 a	1.4 a	1.7 b
Total plants emerged (number)	180 a	195 b	134 a	121 b
Dead plants (number)	3.42 a	3.79 a	8.69 a	1.54 b
Disease incidence[z] (%)	2.21 a	2.03 a	6.93 a	1.24 b

[x] Means in the same year followed by different letters are significantly different by LSD 0.05.
[y] Score of 1 (all plants erect) to 5 (all plants prostrate).
[z] Percent of dead plants to total plants emerged.

Table 7. Comparison of cultivars averaged over compaction and planting dates in 1984

					Total plants	
Cultivar	**Yield (kg/ha)**	**Seed weight (g/100)**	**Plant height (cm)**	**Lodging (score)[y]**	**Emerged (no.)**	**Dead plants (no.)**
BSR 201	3,204	15.6	86	1.8	136	2.3
Century	3,242	16.6	87	1.0	122	7.4
Corsoy	2,724	15.3	87	1.4	108	12.1
Corsoy 79	30.27	15.7	92	1.5	127	4.3
L27	3,092	15.7	93	1.7	130	2.1
L28	3,119	15.6	91	1.5	138	2.2
L77-1585	2,966	15.2	87	1.6	130	2.4
Multiline	3,003	15.4	88	1.6	127	1.7
Sloan	3,073	16.1	90	2.0	127	11.6
LSD 0.05[z]	282	0.6	NS	0.3	14	3.4
Mean	3,050	15.7	89	1.6	127	5.1

[y] Score of 1 (all plants erect) to 5 (all plants prostrate).
[z] LSD for within-column comparisons, if the *F*-test was significant at the 0.05 probability level.

significant either year. Consequently, it was not possible to separate the effects of soil compaction from *P. m.* f. sp. *glycinea* by comparing susceptible and resistant isolines.

This study has shown that soil compaction increased the incidence of *P. m.* f. sp. *glycinea* in a naturally infested field. The results imply that soil compaction could be used in field evaluations to identify and eliminate susceptible soybean lines from breeding programs. In 1983, only Sloan had a significantly higher disease incidence than other cultivars in uncompacted plots, while both susceptible cultivars Sloan and Corsoy had higher values in compacted plots. This indicates that soil compaction helped to differentiate susceptible from resistant cultivars when environmental conditions prevented full expression of *P. m.* f. sp. *glycinea* susceptibility. The soil compaction treatment did not help differentiate the isolines with varying degrees of Phytophthora root rot resistance. The isolines L27 and L28, with the highest disease resistance, had lower disease incidence than other resistant isolines, but were not significantly lower.

Disease incidence and AUDPC were both good measures of soybean line resistance to *P. m.* f. sp. *glycinea*. Because disease incidence is somewhat easier to calculate, it may be a better measure of resistance when large numbers of soybean lines are screened. This study also indicates that a time period of from 7 to 9 weeks after planting is sufficient time to separate resistant from susceptible lines.

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