The Relationship Between Rate-Reducing Resistance to *Phytophthora megasperma* f. sp. *glycinea* and Yield of Soybean

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ABSTRACT

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Field studies were performed in 1980 and 1981 to evaluate various measures of rate-reducing resistance as predictors of soybean yield loss due to Phytophthora root and stem rot; to determine the relationship of resistance, plant growth, and yield components; and to explore the relationship between resistance and tolerance in reducing yield losses. Yield loss was best predicted by critical-point models with disease incidence assessed between the V5 and R7 growth stages as the predictor variable. The area under the disease progress curve, its square root, the simple interest infection rate, its square root, and disease severity at growth stage R5 were also adequate predictors of yield loss. Based on metalaxyl-treated controls, Phytophthora root and stem rot reduced plant heights, numbers of nodes, internode length, and top and root dry weights. Reduction in the number of yielding plants per row was the most critical component contributing to yield reduction due to Phytophthora root and stem rot; significant reductions in weight per seed and number of pods per plant were also observed. Cultivars differed substantially in the yield components affected by root and stem rot. Cultivars with higher levels of rate-reducing resistance showed less reduction in plant height, dry weight, and yield components than did more susceptible cultivars. Cultivars showed no differences in levels of disease tolerance, estimated by adjusting mean percent yield reduction due to root and stem rot to a common disease incidence. The results strongly suggest that differences in rate-reducing resistance are responsible for observed cultivar differences in yield loss due to Phytophthora root and stem rot.

The rate of epidemic development of Phytophthora root and stem rot, which is caused by *Phytophthora megasperma* Drechs. f. sp. *glycinea* (Pmg) (6) (syn. *P. megasperma* Drechs. var. *sojae*), may differ widely among soybean cultivars (24,25). In the field, differences among cultivars were expressed in terms of lower percentages of infected and dead plants and were characterized by the apparent ability of some cultivars to restrict and localize the activity of the pathogen in the tissue of the taproot and/or lower stem (25). It was concluded that reduced disease incidence and severity in these cultivars was an expression of rate-reducing resistance (11,24,25). We quantified cultivar resistance in terms of disease incidence, disease severity, area under the disease progress curve (AUDPC), value of the simple interest infection rate (r_s), and the rate of metalaxyl fungicide required to achieve a final disease incidence of 15% (F_{15}) (25).

While estimates of soybean yield loss due to Phytophthora root and stem rot exist (1,9,13–17,20), the quantitative relationship between different measures of disease intensity and percent yield loss (4,7) has not been explored. In addition, it would be of interest to know the relationship of resistance, plant growth, and soybean yield components to better understand how resistance influences yield. Finally, knowledge of the relative contributions of rate-reducing resistance (25) and disease tolerance (10, page 21) to the variation among cultivars in yield reduction due to Pmg would be of value to plant breeders attempting to incorporate these attributes into commercial cultivars.

The objectives of this study, therefore, were to evaluate various measures of rate-reducing resistance as predictors of yield loss due to Pmg; to determine the relationship of resistance, plant growth, and yield components; and to elucidate the relative roles played by resistance and tolerance in soybean response to Pmg.

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MATERIALS AND METHODS

In 1980 and 1981, soybean cultivars were grown in Racine County, WI, in field plots either untreated or treated with the systemic fungicide metalaxyl (Ridomil; Ciba-Geigy Corp., Greensboro, NC 27409) as described previously (25). Cultivars were evaluated for Phytophthora root and stem rot incidence and severity throughout the growing season.

In 1980, estimates of yield were obtained by harvesting the entire 3.4-m row for each treatment with a small-plot thresher. In 1981, data on plant height, dry weight, and vegetative and reproductive growth stage were obtained from 10-plant samples collected from each treatment throughout the season (25). Estimates of yield were obtained by harvesting the inner two 4.6-m-long rows of each four-row treatment plot with a small-plot thresher. Prior to this, symptomatic or dead pod-bearing plants from these rows were marked with 15-cm wooden pot labels and later were harvested and threshed individually with a small single-plant thresher. Total yields and 300-seed weights were determined after harvested soybeans were dried to uniform moisture content (~12%).

Within each replication, percent yield reductions were determined for rows within cultivars and metalaxyl treatments according to the following formula: yield reduction (%) = ([yield from metalaxyl treated rows − yield from untreated rows]/[yield from treated rows]) × 100. Seed weight reductions were calculated similarly.

The following statistical criteria were used to evaluate models of yield loss (2,22,23): r^2, the coefficient of determination, which indicates the proportion of total variation of the dependent variable (percent yield reduction) that is explained by independent variables (measures of resistance); the F-statistic in the analysis of variance, which tests the overall significance of the regression model at a specific probability level; and the standard error of estimate of the dependent variable, which measures the precision of the estimate of the dependent variable (percent yield reduction).

In 1981, yield component data were obtained in several ways. The number of yielding plants per plot was calculated by subtracting the number of dead plants from the total stand and then adding the number of dead plants that contained pods. Seed weight

per yielding plant was obtained by dividing the total yield for the row by the number of yielding plants in the row including dead pod-bearing plants. Weight per seed was obtained by dividing the 300-seed weight for the row by 300. Numbers of pods per plant were assessed by counting the pods on two groups of ten adjacent plants randomly selected from the outer two rows of each four-row plot just prior to harvest. Plant height at maturity, although not a yield component, is an agronomic variable often used to evaluate cultivar performance. We assessed this variable by measuring the number of centimeters from the soil surface to the plant's growing point for the same 20 plants per replication as were used to assess number of pods per plant.

Yield per plant was computed in 1981 for the center 4.6-m row (designated row two) in which dead plants were not removed (25). This calculation was performed for plants grouped as follows: those not showing symptoms, those symptomatic infected but not dead, those that had died but contained pods, symptomatic infected plants and yielding dead plants combined, all yielding plants combined either untreated or treated with metalaxyl, and all plants combined either untreated or treated with metalaxyl.

TABLE 1. Yield of four soybean cultivars grown in 1980 in a field plot naturally infested with *Phytophthora megasperma* f. sp. *glycinea*

	Yield (q/ha) with metalaxyl (kg a.i./ha) at:				
Cultivar	0.0	0.56	1.12	2.24	Reduction[y] (%)
Steele	1.6 a[z]	13.9 a	17.3 a	12.2 a	89.8
Amsoy 71	0.9 a	12.9 a	27.9 b	16.1 a	96.8
Wayne	16.0 b	22.0 b	28.2 b	16.9 a	42.8
Asgrow A2656	15.2 b	15.3 a	27.5 b	18.0 a	42.4
Mean	8.4	16.0	25.2	15.8	67.9

[y] Percent yield reduction is based on the 1.12 kg a.i./ha rate of metalaxyl.
[z] Means within a column followed by the same letter do not differ significantly according to the Bayes least significant difference procedure, $k = 100$. See text for metalaxyl rate trend comparison. Data are means of three replications.

TABLE 2. Mean yields and 300-seed weights for 12 soybean cultivars grown in 1981 in a field plot naturally infested with *Phytophthora megasperma* f. sp. *glycinea*

	Yield (q/ha)[a]			300-seed weight (g)[a]		
Cultivar	Treated[b]	Untreated	Reduction (%)	Treated[b]	Untreated	Reduction (%)
Steele	27.0	15.2	47.9	54.5	38.9	30.9
Harosoy 63	33.1	21.1	35.4	60.0	54.1	9.9
Marshall	35.6	22.4	39.5	62.3	57.8	7.0
Amsoy 71	33.6	24.5	26.1	51.8	47.7	6.8
Wells	33.3	25.9	21.6	50.1	44.9	10.1
Corsoy	30.5	24.6	19.8	49.1	47.4	3.4
Asgrow A2656	38.0	29.1	22.0	52.1	48.1	7.7
Beeson	33.5	30.9	6.4	57.5	56.3	2.0
Asgrow A2575	33.2	32.6	4.0	49.7	46.4	6.2
Century	34.7	29.7	15.3	54.3	50.7	6.6
Wayne	34.2	32.7	2.7	53.0	51.2	3.3
NK S1492	38.4	35.1	6.4	50.1	47.0	6.1
Mean	33.8	27.0	20.5	53.7	49.2	8.4
BLSD	8.3[c]		32.4[e]	9.1[a]		23.2[e]
BLSD	8.2[d]			7.6[c]		

[a] Data are means of ten observations (five replications times two subsample rows per replication).
[b] Metalaxyl applied at planting at the rate of 1.12 kg a.i./ha.
[c] Bayes least significant difference (BLSD) ($k = 100$) between cultivars for the same metalaxyl treatment.
[d] BLSD ($k = 100$) between metalaxyl treatments for the same cultivar.
[e] BLSD ($k = 100$) between cultivars in percent reductions in yield and seed weight.

To determine whether metalaxyl alone had an effect on seed yield and 300-seed weights, the same 12 cultivars were grown at the University of Wisconsin Experimental Farm at Arlington, WI, in a plot area not infested with Pmg. Four-row plots were hand planted on 21 May 1981 in rows 4.6 m long and 76 cm apart. The plots were arranged in a randomized complete block design with five replications per treatment. Metalaxyl in a 15% granular formulation was applied in an 18-cm band over two rows of each four-row plot at the rate of 1.12 kg active ingredient (a.i.) per hectare (ha). This yielded a split-plot experimental design with cultivars as the main plot and metalaxyl treatment as the subplot. Estimates of yield were obtained by harvesting one row of each two-row treatment combination with a small-plot thresher. Yields and 300-seed weights were determined as described above.

Data were analyzed by analysis of variance, simple and multiple linear regression, and analysis of covariance. Mean comparisons were made by using the Bayes least significant difference procedure (18). In 1980, the functional relationship between metalaxyl level and yield response was explored by using mutually orthogonal single-degree-of-freedom contrasts (orthogonal polynomials).

RESULTS

Effect of root and stem rot on soybean yield and yield components. Yields of the four cultivars grown in 1980 are presented in Table 1. Highly significant ($P = 0.01$) yield differences among cultivars and rates of metalaxyl were found, as well as a significant cultivar-rate interaction ($P = 0.05$). Treatment sums of squares for metalaxyl rate and the cultivar-rate interaction were partitioned into linear, quadratic, and lack-of-fit components. The partitioned cultivar-rate interaction for yield showed significant ($P = 0.05$) cultivar-rate (quadratic) and cultivar-rate (lack-of-fit) effects. Thus, a quadratic or higher order equation would best describe the relationship between metalaxyl level and yield, and this relationship differed among individual cultivars.

Mean yields and 300-seed weights for the 12 soybean cultivars grown in 1981 and either untreated or treated with metalaxyl are presented in Table 2. Significant differences in yield and 300-seed weights were observed among cultivars. Yields and 300-seed weights of metalaxyl-treated rows were significantly higher than those of untreated rows for five and one, respectively, of the 12 cultivars. No significant cultivar-metalaxyl interaction was observed for yield or 300-seed weight.

Mean percent yield reduction and 300-seed weight reduction for the cultivars grown in 1981 ranged from 2.7 to 47.9% and from 2.0

TABLE 3. Yield and 300-seed weights for 12 soybean cultivars grown at Arlington, WI in a field plot free from root and stem rot caused by *Phytophthora megasperma* f. sp. *glycinea*

	Yield (q/ha)		300-seed weight (g)	
Cultivar	Treated[a]	Untreated	Treated[a]	Untreated
Steele	19.9	19.8	50.51	49.53
Harosoy 63	15.3	15.7	51.00	49.99
Marshall	19.0	22.3	59.34	60.90
Amsoy 71	19.0	19.8	49.36	50.09
Wells	21.3	21.7	47.85	47.59
Corsoy	22.5	20.6	47.75	45.76
Asgrow A2656	21.2	21.8	49.34	49.82
Beeson	21.3	21.5	50.18	50.10
Asgrow A2575	23.5	25.0	47.14	47.35
Century	19.4	22.9	48.73	51.42
Wayne	16.2	20.7	45.85	45.94
NK S1492	19.0	21.1	48.42	47.66
Mean	19.8	21.1	49.62	49.68
BLSD[b]	8.1		3.3	
BLSD	3.9[c]		ns[d]	

[a] Metalaxyl applied at planting at the rate of 1.12 kg a.i./ha.
[b] Bayes least significant difference (BLSD) ($k = 100$) between cultivars for the same metalaxyl treatment.
[c] BLSD ($k = 100$) between metalaxyl treatments for the same cultivar.
[d] Analysis of variance F-value for cultivars not significant, $P = 0.05$.

to 30.9%, respectively (Table 2). The correlation coefficient between percent yield reduction and percent 300-seed weight reduction for the 12 cultivars was $r = 0.69$, which was significant ($P = 0.05$, 10 df).

No significant differences among cultivars were found in the mean number of symptomatic plants or the mean number of symptomatic and dead plants combined that contributed to yield. Similarly, no significant differences were found among cultivars in the percent of total yield made up of symptomatic plants, dead plants, or both combined. However, cultivars differed significantly ($P = 0.05$) in the mean number of dead plants that contributed to yield. Mean values of this variable ranged from 0 to 3.6 for the 12 cultivars.

At the Arlington location, where the 12 cultivars had been grown in the absence of disease, significant differences ($P = 0.05$) existed among cultivars in yield and 300-seed weight (Table 3). Metalaxyl-treated plants showed significantly lower yield, but not lower 300-seed weights than did untreated plants (Table 3). There was no significant cultivar-metalaxyl interaction for yield or 300-seed weight.

Yield on a per-plant basis was calculated for plant groupings from row two. Untreated cultivars did not differ significantly in yield per plant based on plants grouped as only those with no visible symptoms, only those with visible symptoms, or all yielding plants combined. However, for yield per plant based on all yielding plants combined excluding plants killed before yielding, significant differences were observed between metalaxyl-treated and untreated plots for cultivar Steele (Table 4). Based on all plants combined (including those killed before yielding), significant differences between cultivars were observed (untreated plots). In addition, for four of the 12 cultivars, significant differences were observed between metalaxyl-treated and untreated plots (Table 4).

Relationship of resistance and soybean yield and yield components. Correlation coefficients were calculated between yield contributions of diseased plants of the 12 cultivars and measures of rate-reducing resistance (25). These measures included final disease incidence, disease severity rating at growth stage R5, AUDPC, r_s, and the time between initial symptom expression and plant death (25, Tables 4–6). Significant ($P = 0.05$) or highly significant ($P = 0.01$) correlations were found between the first four measures of resistance mentioned above and the percentage of total yield from symptomatic plants, dead plants, and both combined as well as the mean number of dead plants and both symptomatic and dead plants combined that contributed to yield (values of the correlation coefficient ranged from 0.63 to 0.95). No significant correlations were found between any of these four measures of resistance and the mean number of symptomatic plants that contributed to yield. However, the time between initial symptom expression and plant death showed a highly significant negative correlation with the percent of total yield made up of symptomatic plants ($r = -0.76$).

Table 5 presents yield component data for each cultivar. Significant differences among cultivars and between metalaxyl

TABLE 4. Yield per plant of 12 soybean cultivars grown in 1981 in a field plot naturally infested with *Phytophthora megasperma* f. sp. *glycinea*

	Yield per plant[a] (g)			
	Excluding plants killed before yielding		Including plants killed before yielding	
Cultivar	Treated[b]	Untreated	Treated[b]	Untreated
Steele	18.2	11.2	16.8	7.7
Harosoy 63	16.3	16.0	16.1	9.1
Marshall	15.5	12.7	15.3	9.4
Amsoy 71	13.3	11.4	13.3	8.9
Wells	13.9	14.0	13.6	12.8
Corsoy	13.4	13.0	13.3	10.7
Asgrow A2656	14.8	11.4	14.7	10.2
Beeson	14.0	12.6	13.9	12.0
Asgrow A2575	15.0	15.6	15.0	13.7
Century	15.5	17.8	15.4	16.1
Wayne	16.1	14.4	16.1	14.2
NK S1492	16.4	15.8	16.3	15.6
Mean	15.2	13.9	15.0	11.7
BLSD	ns[c]		4.6[c]	
BLSD	4.5[d]		4.5[d]	

[a] Based on 4.6-m rows in which dead plants were not removed (row two). Data are means of five replications.
[b] Metalaxyl applied at planting at the rate of 1.12 kg a.i./ha.
[c] Bayes least significant difference (BLSD) ($k = 100$) between cultivar means for the same metalaxyl treatment.
[d] BLSD ($k = 100$) between metalaxyl treatment means for the same cultivar.
[e] Analysis of variance F value for cultivars not significant, $P = 0.05$.

TABLE 5. Total yield, weight per seed, number of yielding plants, number of pods per plant, and plant height at maturity[a], for 12 soybean cultivars grown in a field plot naturally infested with *Phytophthora megasperma* f. sp. *glycinea*

	Total yield (q/ha)			Weight per seed (mg)			Yielding plants (no.)			Pods per plant (no.)			Plant height at maturity (cm)		
Cultivar	Treated[b]	Untreated	Reduction (%)	Treated[b]	Untreated	Reduction (%)	Treated[b]	Untreated	Reduction (%)	Treated[b]	Untreated	Decr. (%)	Treated[b]	Untreated	Decr. (%)
Steele	28.4	17.9	37.0	180	135	25.0	60	47	21.7	55.7	44.1	20.8	77.3	68.9	10.9
Harosoy 63	32.3	21.4	33.9	198	179	9.6	71	58	18.3	54.2	36.6	32.5	100.9	87.1	13.7
Marshall	53.6	23.0	35.3	204	193	5.4	80	64	20.0	44.4	37.4	15.8	94.4	76.1	19.4
Amsoy 71	35.1	22.1	36.9	171	157	8.2	92	67	27.2	42.6	42.8	−0.5	98.7	85.7	13.2
Wells	34.3	29.4	14.2	171	151	11.7	88	74	15.9	57.8	47.9	17.1	87.8	79.7	9.2
Corsoy	30.4	22.7	25.5	163	158	3.1	83	59	28.9	46.4	50.1	−8.0	99.9	83.1	16.8
Asgrow A2656	39.3	27.3	30.6	174	158	9.2	92	84	8.7	54.5	44.9	17.6	109.4	90.4	17.4
Beeson	33.6	28.0	16.8	191	188	1.6	85	80	5.9	47.5	43.3	8.8	105.5	97.1	8.0
Asgrow A2575	33.9	34.5	1.6	163	156	4.3	79	78	1.3	54.0	43.9	18.7	93.1	88.3	5.2
Century	33.8	31.9	5.7	180	169	6.1	77	68	11.7	54.2	42.5	21.6	95.6	90.7	5.1
Wayne	35.4	34.8	1.8	177	170	4.0	79	86	−8.9	51.1	48.1	5.9	105.9	104.4	1.4
NK S1492	41.1	34.9	15.0	164	157	4.3	88	78	11.4	62.2	50.6	18.6	89.2	86.7	2.8
Mean	34.4	27.3	20.9	178	164	7.7	81	70	13.5	52.1	44.4	14.1	96.5	86.5	10.3
BLSD[c]	8.9			25			23			ns[e]			13.9		
BLSD[d]	8.7			20			19			12.6			12.2		

[a] Total yield, weight per seed, and number of yielding plants are based on 4.6-m rows in which dead plants were not removed (row two). Data are means of five replications. For number of pods per plant and plant height at maturity, data are means of five replication each consisting of 20-plant subsamples randomly selected from the outer two rows of each four-row plot just prior to harvest; dead plants containing no pods were omitted from the analysis.
[b] Metalaxyl applied at planting at the rate of 1.12 kg a.i./ha.
[c] Bayes least significant difference (BLSD) ($k = 100$) between cultivar means for the same metalaxyl treatment.
[d] BLSD ($k = 100$) between metalaxyl treatment means for the same cultivar.
[e] Analysis of variance F value for cultivars not significant, $P = 0.05$.

treatments were obtained for total yield, weight per seed, and the number of yielding plants per row based only on row two, from which dead plants were not removed during the season. Cultivars did not differ significantly in numbers of pods per plant (excluding dead plants containing no pods). A significant difference in pods per plant between metalaxyl-treated and untreated plots was observed only for cultivar Harosoy 63. When dead plants containing no pods were included in the analysis, cultivars differed significantly in number of pods per plant, $P = 0.10$, and a significant difference between metalaxyl-treated and untreated plots was observed for Steele and Harosoy 63.

Correlation coefficients between percent yield reduction in row two, and reductions in the number of yielding plants per plot, weight per seed, pods per plant, and plant height at maturity, were calculated for each cultivar (Table 6). For eight of the 12 cultivars, percent reduction in number of yielding plants per plot was the component most highly correlated with percent yield reduction, while for three cultivars (Wells, Beeson, and Wayne) percent reduction in weight per seed showed the highest correlation. For cultivar Corsoy, percent reduction in the number of pods per plant showed the highest correlation with percent yield reduction. Averaged over all cultivars, percent reduction in the number of yielding plants per plot was the component most highly correlated with percent yield reduction ($r = 0.70$, 58 df), followed by percent reduction in weight per seed ($r = 0.56$) and percent reduction in pods per plant ($r = 0.39$). These three correlations were highly significant ($P = 0.01$). The only significant correlation between percent yield reduction and percent reduction in plant height at maturity was obtained with cultivar Corsoy; three of the more resistant cultivars had negative correlations between these variables.

TABLE 6. Correlations between percent yield reduction and percent reduction in yield components and mature plant heights for 12 soybean cultivars grown in 1981 in a field plot naturally infested with *Phytophthora megasperma* f. sp. *glycinea*

Cultivar	Correlation coefficient between percent yield reduction and percent reduction in: Weight per seed	Pods per plant (no.)	Yielding plants per plot (no.)	Plant height at maturity (cm)
Steele	0.879*[a]	0.898*	0.969**[b]	0.699
Harosoy 63	0.665	0.549	0.753	0.697
Marshall	0.360	0.407	0.753	0.775
Amsoy 71	0.521	0.477	0.892*	0.481
Wells	0.928*	0.419	0.204	0.067
Corsoy	0.562	0.925*	0.328	0.880*
Asgrow A2656	0.457	0.168	0.704	0.162
Beeson	0.675	−0.051	−0.163	0.721
Asgrow A2575	−0.130	0.271	0.795	−0.621
Century	0.853	0.713	0.890*	−0.231
Wayne	0.638	−0.496	0.490	−0.019
NK S1492	0.613	0.543	0.952*	0.093
Mean	0.585	0.402	0.631	0.309

[a]One asterisk indicates significant correlation, $P = 0.05$, 3 df.
[b]Two asterisks indicate significant correlation, $P = 0.01$, 3 df.

Correlation coefficients were calculated between four measures of rate-reducing resistance (25) and percent reductions in weight per seed, number of pods per plant, number of yielding plants per plot, and plant height at maturity for the 12 cultivars. Correlations between reduction in weight per seed and the four measures of resistance were highly significant, $P = 0.01$ ($r = 0.71, 0.79, 0.71$, and 0.78 for final disease incidence, disease severity at growth stage R5, AUDPC and r_s, respectively). Percent reduction in the number of yielding plants per plot was significantly correlated with final disease incidence, disease severity at growth stage R5, and AUDPC, but not with r_s ($r = 0.68, 0.68, 0.68$, and 0.50, respectively). This same result was true for percent reduction in plant height at maturity ($r = 0.66, 0.67, 0.63$, and 0.44, respectively). Percent reduction in number of pods per plant was not correlated with any of the four measures of resistance.

Effect of root and stem rot on soybean growth. Metalaxyl-treated plots were compared with untreated plots in 1981 to determine which plant growth parameters were most affected by root and stem rot (Table 7, Fig. 1). Untreated plants were significantly taller than metalaxyl-treated plants at 51, 57, and 70 days after planting; the converse was true at 86 and 112 days after planting (Table 7). Fig. 1 A–D presents mean plant heights obtained from sampled plants of the 12 cultivars at seven observation dates in 1981. Significant differences ($P = 0.05$) in plant height were noted among cultivars at 35, 42, and 51 days after planting.

Top dry weights of metalaxyl-treated plants were significantly lower than those of untreated plants at 42 days after planting; the converse was true at 86 days after planting (Table 7). Significant differences among cultivars in top dry weights were observed at 35.

TABLE 7. Plant growth parameters for soybeans grown in 1981 in a field plot naturally infested with *Phytophthora megasperma* f. sp. *glycinea* and untreated or treated with metalaxyl

Days after planting	Top dry weight (g)		Root dry weight (g)		Plant height (cm)		Vegetative stage[b]		Internode length[c] (cm)		Reproductive stage[d]	
	Untreated	Treated[a]	Untreated	Treated[a]	Untreated	Treated[a]	Untreated	Treated[a]	Untreated	Treated[a]	Untreated	Treated[a]
35	0.15[e] (0.13–0.23[f])	0.15 (0.23–0.19)	0.03[e] (0.01–0.04)	0.04* (0.02–0.06)	6.26[e] ...	6.40 ...	...	...	...	...	...	...
42	0.85 (0.71–1.01)	0.76**[g] (0.57–0.90)	0.17 0.12–0.22)	0.17 (0.13–0.20)	13.08	12.68	...	...	...	...	...	...
51	2.54 (2.19–3.14)	2.47 (2.05–3.21)	0.43 (0.34–0.59)	0.44 (0.36–0.50)	22.82 ...	21.28** ...	5.35 (4.70–6.00)	5.00** (4.51–5.62)	4.55 (3.68–6.13)	4.59 (3.63–5.44)	...	...
57	5.51 (4.20–7.61)	5.07 (3.65–6.90)	0.73 (0.64–1.09)	0.76 (0.63–0.89)	36.02 ...	33.33* ...	7.08 (6.12–8.29)	6.65* (5.68–7.56)	5.16 (4.39–5.96)	5.16 (4.60–5.62)	...	...
70	14.11 (11.08–18.69)	12.80 (8.77–18.59)	1.70 (1.49–2.07)	1.83 (1.30–2.20)	65.67 ...	58.70* ...	10.81 (10.12–11.72)	10.20 (9.06–11.20)	6.09 (5.25–6.90)	5.78 (5.17–6.79)	3.42 (2.31–4.26)	3.09* (2.15–3.94)
86	21.95 (16.94–29.19)	24.96*[g] (17.03–37.02)	1.99 (1.29–2.75)	2.25* (1.75–2.93)	82.65 ...	90.52** ...	13.66 (12.06–15.06)	14.04 (13.02–15.68)	6.21 (5.14–7.06)	6.56** (5.83–7.83)	5.07 (4.44–5.79)	5.02 (4.46–5.60)
112	...	...	...	...	86.52 ...	96.47** ...	16.11 (13.58–17.71)	17.26** (15.00–18.84)	5.37	5.66* (4.71–5.95)	... (4.93–6.56)	...

[a]Metalaxyl applied at planting at 1.12 kg a.i./ha.
[b]Number of nodes on the main stem with a fully developed leaf (3).
[c]Internode length = plant height divided by number of nodes.
[d]Based on soybean reproductive stages R1 to R9 (3).
[e]Data are means of 600 observations (12 cultivars times 5 replications times 10 plants).
[f]Values in parentheses represent the range for the 12 cultivars. For plant heights, see Fig. 1.
[g]* = Significant difference between means of untreated and treated plots, $P = 0.05$; ** = $P = 0.01$.

70, and 86 days after planting. A significant cultivar-metalaxyl interaction was noted at 86 days after planting: at that time, treated plants of cultivar Century showed significantly lower top dry weights than untreated plants.

Treated plants had significantly higher root dry weights than untreated plants at 35 and 86 days after planting (Table 7). Significant differences among cultivars in root dry weights were noted at 42 and 86 days after planting.

Metalaxyl-treated plants showed retarded vegetative development (fewer nodes) compared to untreated plants at 51 and 57 days after planting; the converse was true at 112 days after planting (Table 7). Significant cultivar-metalaxyl interactions were observed; treated plants of cultivar Asgrow A2656 had more nodes than did untreated plants at 51 days after planting, while the same was true of Marshall at 51 and 57 days after planting. Significant (P = 0.05) differences in vegetative stage among cultivars were observed at 112 days after planting.

Internode length of treated plants exceeded that of untreated plants at 86 and 112 days after planting (Table 7). Significant cultivar differences in internode length were observed at all sampling dates. A significant cultivar-metalaxyl interaction was observed at 57 days after planting; at that time, untreated plants of Beeson had significantly longer internodes than treated plants.

Untreated plants showed reproductive stages significantly ahead of those of treated plants at 70 days after planting (Table 7). Significant cultivar differences in reproductive growth stage were observed at 70 and 86 days after planting.

Relationship of resistance and soybean growth. Correlation coefficients were calculated between reductions in the various plant growth parameters due to root and stem rot and measures of rate-reducing resistance for the 12 cultivars (25). Reductions in plant height at growth stages R5 and R7 were significantly correlated (P = 0.05, 10 df) with final disease incidence (r = 0.68 and 0.66, respectively), AUDPC (r = 0.65 and 0.63, respectively), and disease severity at growth stage R5 (r = 0.73 and 0.67, respectively), but not with r_s (r = 0.48 and 0.44, respectively). Reduction in top dry weight at the R5 growth stage was significantly correlated (P = 0.05, 10 df) with disease severity rating at growth stage R5 (r = 0.67) and also showed moderate (but nonsignificant, P = 0.05) correlation with final disease incidence, AUDPC, and r_s (r = 0.57, 0.57, and 0.53, respectively). Reduction in root dry weight at growth stage R5 was significantly correlated (P = 0.05, 10 df) with all four measures of resistance (r = 0.67, 0.69, 0.80, and 0.59 for final disease incidence, AUDPC, disease severity at growth stage R5, and r_s, respectively). Reductions in internode lengths and numbers of nodes were not significantly correlated with any of the measures of resistance.

Prediction of yield loss from measures of rate-reducing resistance. For 1980 and 1981 experiments, percent yield reduction was regressed on measures of rate-reducing resistance (25). Critical-point models (4,22), which imply that yield loss can be estimated from disease assessment at one growth stage, were fit to the data. Tables 8 and 9 show these regressions and their associated statistics for the 1980 and 1981 experiments, respectively. In 1980, the best predictors of yield loss were disease incidence at growth stages V7 and R5; in these models, 65.1 and 62.8%, respectively, of the total variation in yield loss was explained by variation in disease incidence (Table 8). Disease incidence at growth stage V1 was the

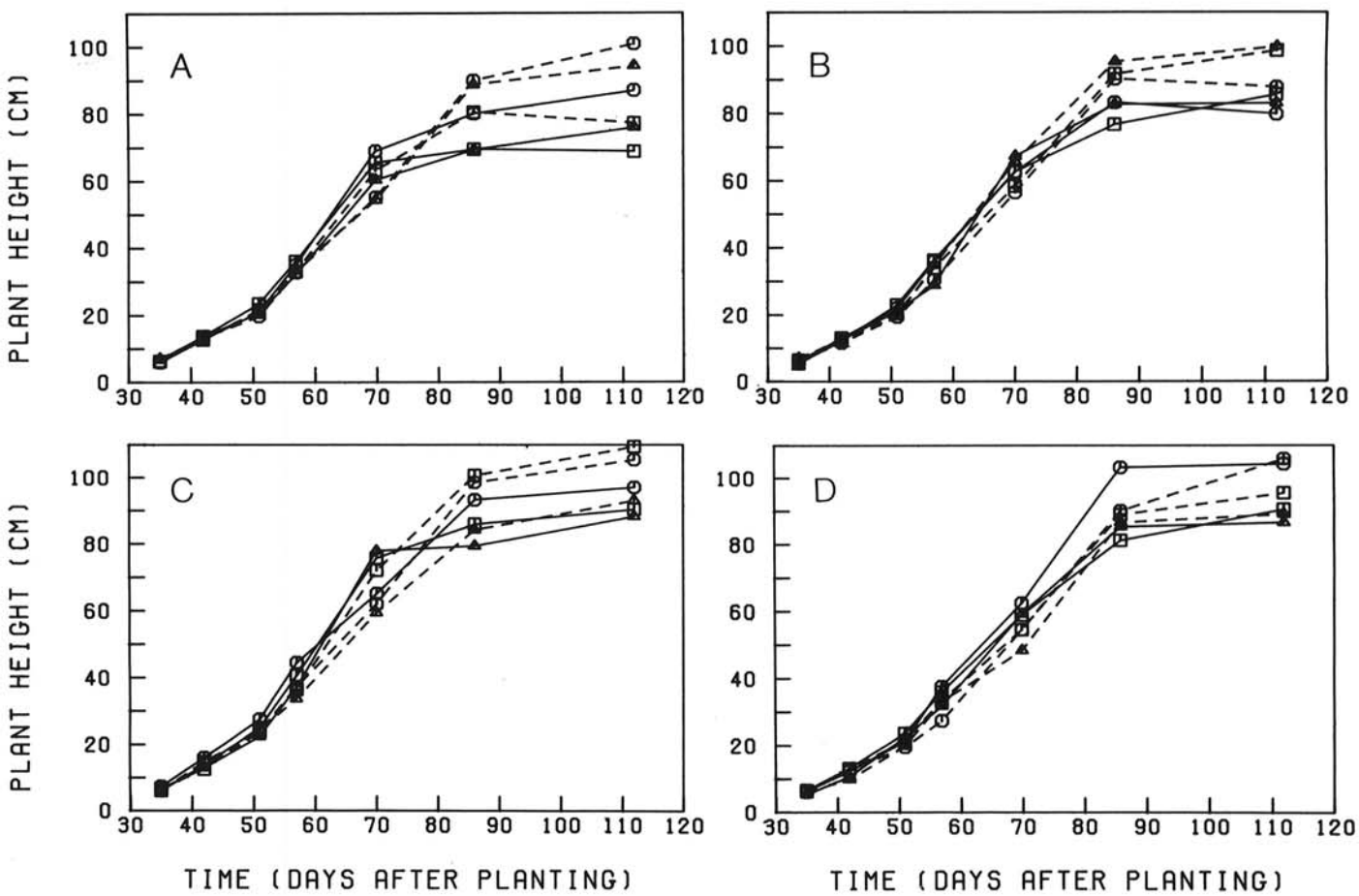

Fig. 1. Plant heights for 12 soybean cultivars either untreated (solid lines) or treated with metalaxyl (dashed lines) at the rate of 1.12 kg active ingredient per hectare and grown in 1981 in a field plot naturally infested with *Phytophthora megasperma* f. sp. *glycinea*. Data are means of 50 observations (five replications times 10 plants per replication). **A,** Squares represent values for cultivar Steele, circles represent those for Harosoy 63, and triangles represent those for Marshall. **B,** Squares represent values for cultivar Amsoy 71, circles represent those for Wells, and triangles represent those for Corsoy. **C,** Squares represent values for cultivar Asgrow A2656, circles represent those for Beeson, and triangles represent those for Asgrow A2575. **D,** Squares represent values for cultivar Century, circles represent those for Wayne, and triangles represent those for Northrup King S1492.

poorest predictor variable, as shown by its nonsignificant F statistic and the low value of r^2, the coefficient of determination. Variables expressing resistance in terms of fungicide equivalency (F_{15} and RF_{15}) were also rather poor predictors of yield loss, although superior to disease incidence at growth stage V1 (Table 8).

TABLE 8. Critical-point models for yield loss caused by Phytophthora root and stem rot of soybean in 1980

Independent[a] variable	Intercept	Regression coefficient	Standard error of dependent variable	F-statistic[b]	r^2 adj. (%)
X1[c]	52.34	0.70	27.22	2.14	9.4
X2	24.73	1.01	16.88	21.55	65.1
X3	21.61	0.98	17.44	19.57	62.8
X4[d]	25.81	1.73	18.54	16.16	58.0
X5	−9.18	16.21	18.36	16.69	58.8
X6[e]	42.52	3,439.20	19.86	12.80	51.8
X7	22.49	582.00	19.33	14.06	54.3
X8[f]	47.72	32.50	24.12	5.46	28.9
X9	89.04	−45.08	23.89	5.75	30.2

[a] Percent yield reduction was the dependent variable in all cases.
[b] The F-value corresponding to independent variable X1 is nonsignificant; those corresponding to independent variables X8 and X9 are significant, $P = 0.05$; all others are significant, $P = 0.01$.
[c] Variables X1 through X3 represent cumulative disease incidence at growth stages V1, V7, and R5, respectively.
[d] Variables X4 and X5 represent the area under the disease progress curve (AUDPC) and its square root, respectively.
[e] Variables X6 and X7 represent the simple interest infection rate (r_s) and its square root, respectively.
[f] Variables X8 and X9 represent the rate of metalaxyl application necessary to reduce final disease incidence to 15% (F_{15}), and the percent reduction relative to Steele in the rate of metalaxyl application necessary to reduce final disease incidence to 15% (RF_{15}).

TABLE 9. Critical-point models for soybean yield loss caused by Phytophthora root and stem rot in 1981

Independent[a] variable	Intercept	Regression coefficient	Standard error of dependent variable	F-statistic[b]	r^2 adj. (%)
X1[c]	10.89	3.74	19.28	49.18	45.0
X2	9.93	2.52	18.66	56.35	48.4
X3	3.67	1.72	15.12	116.31	66.2
X4	2.04	1.43	14.84	122.95	67.4
X5	1.01	1.07	13.07	175.04	74.7
X6	0.30	1.01	12.63	191.56	76.4
X7	−0.54	0.96	12.44	199.44	77.1
X8[d]	13.90	41.64	21.84	25.50	29.3
X9	13.10	15.60	23.25	15.69	19.9
X10	3.20	15.05	18.18	62.44	51.0
X11	19.52	21.50	14.43	133.19	69.1
X12[e]	0.73	1.63	12.99	177.95	75.0
X13	−14.79	12.09	12.87	182.52	75.5
X14[f]	10.54	1,643.70	17.04	79.15	57.0
X15	−4.73	447.70	12.73	187.84	76.0
X16[g]	44.30	−32.47	22.66	13.31	25.5

[a] Percent yield reduction was the dependent variable in all cases. Except for variable X16, all analyses are based on 60 observations; for variables assessed on subsample rows within each replication, mean values over subsamples were used in the analysis to allow consistency with other variables.
[b] All analysis of variance F values are significant, $P = 0.01$.
[c] Variables X1 through X7 represent cumulative disease incidence at growth stages V1, V3, V5, V7, R3, R5, and R7, respectively.
[d] Variables X8 through X11 represent disease severity based on disease classes 0 to 6 at growth stages V5, V7, R3, and R5, respectively.
[e] Variables X12 and X13 represent AUDPC (area under the disease progress curve) and its square root, respectively.
[f] Variables X14 and X15 represent r_s (the simple interest infection rate) and its square root, respectively.
[g] Variable X16 represents the ratio of number of dead plants to total number of diseased plants at the V1 growth stage. Replications containing no diseased plants were omitted from the analysis.

In 1981, disease incidence continually improved as a predictor variable from growth stages V1 through R7 (Table 9). These models explained from 45.0 to 77.1% of the variation in yield loss, with the best model having disease incidence at growth stage R7 as the predictor variable. Disease severity also was an adequate predictor of yield loss, although severities at the R3 and R5 growth stages were much better predictors than severities at the V5 and V7 growth stages.

Time from first symptom expression to plant death was a poor predictor of yield loss, as were ratios of number of dead plants to total number of diseased plants at the V3, V5, V7, R3, R5, and R7 growth stages. None of these predictors explained more than 10% of the total variation in yield loss. Ratio of number of dead plants to total number of diseased plants at the V1 growth stage was a slightly better predictor and explained 25.5% of the variation in yield loss (Table 9).

In both 1980 and 1981, AUDPC and r_s were good predictors of yield loss, and explained from 51.8 to 75.0% of the variation. Models involving the square roots of these variables as predictors resulted in improvements; they explained from 54.3 to 76.0% of the variation in yield loss.

Disease loss estimates may be improved by making more than one disease assessment during an epidemic (4,5,22). Therefore, multiple-point regression models were formulated by combining the independent disease incidence variables in all possible combinations. These were subdivided into two and three growth stage models for the 1980 experiment and into two, three, four, five, six, and seven growth stage models for the 1981 experiment. Adding additional variables to the model resulted in lower values of the F statistic and r^2, and higher standard errors than for the best critical-point models. Thus, none of the models incorporating disease assessments at additional growth stages were superior to the best critical-point models. The same was true for models that incorporated combinations of independent variables representing disease incidence, disease severity, AUDPC, r_s, and the square roots of AUDPC and r_s.

Relationship between resistance and tolerance. For the best prediction equations in 1980 and 1981, regression models involving %YR as the dependent variable and either disease incidence at growth stage V7 (1980) or growth stage R7 (1981) as the independent variable were fit to the data using dummy variables to designate cultivars (2, page 241). Sequential F tests (2, page 101) indicated that slopes did not differ significantly among cultivars ($P = 0.05$). Thus, cultivars sustained similar increments of yield loss for similar increments in disease incidence.

We then tested whether cultivars differed in yield loss when adjusted to a common level of disease incidence (the mean for all cultivars) via analysis of covariance (19, page 411). Mean percent yield reduction for the cultivars was adjusted to provide estimates of what these means would be if disease incidences for all cultivars were equal.

For the 1980 data, the common level of disease incidence to which cultivars were adjusted was 42.8%. The common slope used to adjust means was 0.31 and did not differ significantly from zero, resulting in adjusted means almost identical to the unadjusted means (82.9, 91.9, 50.5, and 46.9% for Steele, Amsoy 71, Asgrow A2656, and Wayne, respectively).

In 1981, mean percent yield reductions (adjusted to a common level of disease incidence at growth stage R7) for the 12 cultivars were: Steele, 14.5; Harosoy 63, 14.7; Marshall, 18.5; Amsoy 71, 13.5; Wells, 14.6; Corsoy, 18.6; Asgrow A2656, 27.7; Beeson, 16.7; Asgrow A2575, 14.2; Century, 29.1; Wayne, 23.4; and NK S1492, 29.0. The grand mean for the group was 19.5%. The common level of disease incidence to which cultivars were adjusted was 20.8%, substantially lower than in 1980 (common slope = 1.22). Adjusted and unadjusted percent yield reduction were not correlated in 1981. Also, adjusted percent yield reduction showed a significant negative correlation ($P = 0.05$, 10 df) with final disease incidence and AUDPC, and a significant positive correlation with time between first symptom expression and plant death ($r = -0.64$, -0.66, and 0.59, respectively).

Although significant cultivar differences in unadjusted percent

yield reduction had been observed in both 1980 (Table 1) and 1981 (Table 2), no such differences were found after adjustment to a common disease incidence ($F = 1.61$ and 1.04 in 1980 and 1981, respectively).

DISCUSSION

Soybean cultivars containing no known race-specific resistance to Pmg differed significantly in yield reduction due to Pmg. This variation among cultivars in yield reduction could largely be accounted for by differences in rate-reducing resistance.

Our results suggest that yield loss can best be predicted by critical-point models with disease incidence assessed between the V5 and R7 growth stages as the predictor variable. In two distinctly different epidemics, the overall relationship between yield loss and disease incidence remained consistent: regression coefficients in the best yield-loss prediction models were close to a value of 1 in both 1980 and 1981, revealing that a 1% increase in disease incidence resulted in a 1% decrease in yield.

The AUDPC and its square root, r_s and its square root, and disease severity at growth stage R5 also were adequate predictors of yield loss, explaining from 52 to 76% of the variation among cultivars in yield reduction due to Pmg. Other workers have found AUDPC to be a good predictor of yield reduction for soybeans affected by Septoria brown spot (8).

Adding disease assessments at additional growth stages to the models resulted in no improvement. This contrasts with the results of other workers who have found multiple-point models to be better predictors of yield losses (5,22).

Although all but one of the critical-point regression models fitted to data from the 1980 and 1981 experiments were highly significant ($P = 0.01$) via the F statistic, Draper and Smith (2, page 93) suggest that for an equation to be regarded as a satisfactory predictor (in the sense that the range of response values predicted by the equation is substantial compared with the standard error of the response), the observed F ratio of (regression mean square)/(residual mean square) should exceed not merely the selected percentage point of the F distribution, but should be at least four times the selected percentage point. In the 1980 experiment, the only equation that fulfilled this criterion ($P = 0.05$) was that having disease incidence at growth stage V7 as the predictor variable. In 1981, all but two of the equations fulfilled this criterion. This indicates a higher degree of precision attained in the 1981 experiment by using more replications.

Our results also show that disease incidence is a more desirable predictor variable than is disease severity. Because we assessed disease severity by examining plants internally, collecting those data was more laborious than collecting disease incidence data; thus, a much smaller sample size was obtained for disease severity estimates. Disease incidence data, being easier to collect and more precise in the prediction of yield loss, should be used in future studies. Also, since we showed disease incidence and disease severity to be highly correlated (25), it may not be necessary for future workers to obtain estimates of both parameters.

The range of yield loss found in this study is comparable to those of other studies (1,9,15,16) in which yields were assessed on near-isogenic soybean lines with and without race-specific resistance. Yield loss estimates based on the use of metalaxyl should be more precise than those based on the use of near-isogenic lines because, to the extent that races capable of overcoming race-specific resistance may have been present, the latter studies may have underestimated yield reduction.

Yield component analysis revealed that reduction in the number of yielding plants per row was the most critical factor contributing to yield reduction due to Phytophthora root and stem rot. This factor was more highly correlated with yield reduction than were reductions in weight per seed or pods per plant. These results indicate that the effect of Pmg on soybean yields results largely from stand depletion due to the killing of plants before they set seed. Teigen and Vorst (21) found that more pods and heavier seed were produced on plants that remained after stands were reduced. This could be responsible for the lack of large differences among cultivars in those yield components.

Cultivars differed substantially, however, with respect to the yield components affected by root and stem rot. All cultivars showed reductions in weight per seed; a similar effect on seed weight has been noted by other workers (12,26) for soybeans affected by Septoria brown spot.

Differences among cultivars in yield per plant were not significant if based only on yielding plants but were significant based on yielding and nonyielding (dead) plants combined. Also, differences were not found in yield per plant when comparing symptomless untreated plants with metalaxyl-treated plants. This reinforces our belief that plant kill is the primary factor reducing yields, but contrasts with the results of Meyer and Sinclair (9) who found reduced yields for plants that did not show visible symptoms. The lack of significant differences among cultivars in yield per plant could be partially due to the variability among plots associated with a nonrandom distribution of inoculum.

Although consistent trends in plant growth reduction due to Pmg were not apparent early in the season, by late season metalaxyl-treated plants had significantly greater plant heights, numbers of nodes, internode lengths, and top and root dry weights than untreated plants. These results agree with those of Meyer and Sinclair (9), who found that root and stem rot reduced plant heights in field tests and root dry weights in greenhouse tests.

Evidence for possible phytotoxicity of metalaxyl to soybeans was provided by the significantly shorter treated plants at the V5, V7, and R3 growth stages, fewer nodes for treated plants of some cultivars at the V5 and V7 stages, significantly shorter internodes for treated plants of cultivar Beeson at the V7 growth stage, and significantly lower top dry weights of treated plants at the V3 growth stage and of Century plants at the R5 growth stage. In addition, either diseased plants show accelerated reproductive development or else metalaxyl retards such development, because differences existed in reproductive stage between treated and untreated plants at the R3 growth stage. Significant differences in yield between metalaxyl-treated and untreated plants in the disease-free Arlington plot also indicate a phytotoxic effect, which was most pronounced for cultivars Wayne, Century, and Marshall.

Our prediction equations showed that significant linear relationships exist between yield loss and measures of rate-reducing resistance. Further analyses revealed significant correlations between levels of resistance and reductions in plant height and dry weight, and between levels of resistance and reductions in the yield components most affected by root and stem rot. Significant correlations between variables, however, do not prove the existence of a cause-and-effect relationship between the variables (2, page 45). Reduced yield losses could have been caused by a third factor, such as disease tolerance (10, page 21) which was also correlated with level of resistance. To show that resistance, rather than tolerance, was responsible for reduced yield losses requires additional evidence which we now present here:

First, we found significant inverse correlations between yield contributions of diseased plants and levels of cultivar resistance. These results suggest that the higher yields seen for resistant cultivars were not largely due to their ability to yield while diseased. Rather, fewer plants of these cultivars became severely diseased. Conversely, the yield of susceptible cultivars consisted, to a greater extent, of contributions made by diseased plants.

Secondly, estimates of tolerance that we calculated by adjusting mean percent yield reduction to a common level of disease incidence revealed no significant cultivar differences. We interpret the lack of a nonzero common slope in 1980 to mean either that tolerance was not expressed at a detectable level (perhaps due to the high relative severity of the epidemic [mean disease incidence 42.8%]) or that the precision for estimating adjusted means was low due to a low number of observations.

In 1981, adjustment to a common level of disease incidence did result in a significant common slope, indicating that adjusted means differed substantially from unadjusted means and that valid estimates of adjusted means were obtained. Such tolerance estimates were not correlated with percent yield reduction and were negatively correlated with measures of rate-reducing resistance, suggesting that the role played by tolerance in reducing yield losses

due to root and stem rot was a minor one.

The above evidence, as well as the positive relationship between resistance, plant growth, and yield, and the fact that resistance is characterized by a pathogen-localization phenomenon (24,25) which would serve to reduce the impact of this disease on yield, leads us to believe that differences in rate-reducing resistance are responsible for the observed cultivar differences in yield loss due to root and stem rot.

Finally, our results illustrate that care must be exercised in choice of a variable to use in assessing resistance. We had considered the time between first above-ground symptom expression and plant death as a measure of resistance (25). However, based on its high correlation with tolerance estimates and lack of correlation with other measures of resistance, it became apparent that this variable more likely represented an additional measure of tolerance. It seems reasonable to assume that once resistance is overcome and above-ground symptoms are noted, a determination of the death rate could accurately represent a measure of tolerance. This observation could be of use to plant breeders seeking to identify tolerance in the field.

Future studies should focus on testing the predictive capacity and usefulness of our yield-loss equations by using data sets collected in other locations and years. Further investigations into the relationship between rate-reducing resistance and tolerance are also needed, as are methods for directly measuring tolerance. The use of such methods combined with those we have outlined (24,25) for identifying and characterizing rate-reducing resistance may allow plant breeders to incorporate both rate-reducing resistance and tolerance into commercially available soybean cultivars.

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