Soybean Yield Losses Due to *Heterodera glycines* in Iowa

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ABSTRACT

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Natural field infestations of *Heterodera glycines* race 3 in Boone (central Iowa) and Hancock (north central) counties were used to investigate the effect of the nematode on soybean growth and seed yields in a 2-yr study. Iron deficiency chlorosis, brown stem rot, and Phytophthora rot cause soybean seed yield losses annually in Iowa and may occur in *H. glycines*-infested fields. Soybean cultivars with known reactions to each disease were chosen, and two plots of each cultivar were planted per replication—one treated with aldicarb for *H. glycines* control, and the other not treated. Cultivar reaction to other diseases had no effect on *H. glycines* final populations or soybean seed yields. Seed yields of *H. glycines*-susceptible cultivars were 5.7-35.8% lower than those of resistant cultivars in all environments and were affected by treatment with aldicarb in 1987 but not in 1986. Artificial infestations of *H. glycines* were established in microplots in a field in Story County (central Iowa) to determine damage thresholds. One resistant and one susceptible cultivar were planted following infestation with 0, 10, 50, 250, or 1,250 eggs per 100 cm^3 of soil. In 1986 and 1987, the *H. glycines* density explained 92 and 54%, respectively, of the reduction in seed yields of the susceptible cultivar. The damage threshold was between 10 and 50 eggs, and yields were reduced 52 and 19% at the highest egg density in 1986 and 1987, respectively.

The soybean cyst nematode, *Heterodera glycines* Ichinohe, has become an important pest of soybean, *Glycine max* (L.) Merr., in the north central region of the United States. The nematode was first found in Iowa in 1978, 24 yr after its first U.S. report from North Carolina (5). Its known distribution in Iowa now includes sites in 53 of 99 counties, primarily in the north central and southeastern parts of the state (G. L. Tylka, *personal communication*). *H. glycines* can cause up to 100% seed yield loss in heavily infested areas within a field, and in general soybean yields are negatively correlated with initial (preplant) densities of the nematode (13). Because *H. glycines* is a relatively recent problem in the north central region of the United States, little is known specifically about its interactions with soybean cultivars adapted to the region, particularly those in maturity groups I-III grown in Iowa. The "typical" symptoms of *H. glycines* infestation (stunting, chlorosis) are not consistently observed in fields with known infestations. Because aboveground and root symptoms of *H. glycines* damage are variable and nonspecific, damage caused by the nematode may be attributed to other factors (5). In Iowa, these are likely to include iron deficiency chlorosis, Phytophthora root and stem rot (caused by *P. megasperma* Drechs. f. sp. *glycinea* T. Kuan & D. C. Erwin), and brown stem rot (caused by *Phialophora gregata* (Allington & Chamberlain) W. Gams). Therefore, this research had two objectives: 1) to describe the interactions between soybean and *H. glycines* as affected by host resistance to the nematode, iron deficiency chlorosis, Phytophthora rot, and brown stem rot; and 2) to establish a damage threshold for *H. glycines* in Iowa soybean fields.

MATERIALS AND METHODS

Natural infestations. Two sites were identified with natural infestations of *H. glycines* race 3 (14) and histories of seed yield losses caused by Phytophthora rot, brown stem rot, and iron deficiency chlorosis. One site ("Hancock") in Hancock County in north central Iowa had a clay loam soil (32% sand, 31% silt, and 37% clay) with a 7.6 pH and 7.6% organic matter. The other site ("Boone") in Boone County on an Iowa State University-owned farm had a clay soil (27% sand, 32% silt, and 41% clay) with a 7.4 pH and 4.6% organic matter. Identical experimental designs and methods, except for the number of replications, were conducted on both sites in 1986 and 1987.

Eight soybean cultivars were chosen to represent a range of reactions to iron deficiency chlorosis, Phytophthora rot, brown stem rot, and *H. glycines* (Table 1). Pride B216 was included only in 1986. The treatment design was a factorial, with eight (or seven) cultivars × two nematicide treatment levels × seven replications at Boone or five replications at Hancock, arranged in randomized complete blocks. The nematicide treatment levels were "+" or "−" aldicarb at 2.24 kg a.i./ha applied in a 15-cm band at planting. Each site was treated with trifluralin 2 wk before planting and hand-weeded thereafter. Plots were four rows spaced 91 cm apart, 5 m long, with 2-m alleys, planted at 169 seeds per meter. Rows were end-trimmed before harvest, so that 3 m of each of the two center rows were harvested for seed yield. Seed were harvested when mature with a seed moisture of 11-13%. Seed yields were standardized to 13% moisture before analysis. Seed weight was determined for 100 arbitrarily chosen seeds per plot. Plant height at harvest was determined by averaging measurements taken from three arbitrarily chosen plants from the center rows of each plot. Lodging scores were based on the average erectness of the main stems at maturity, where 1 = all plants erect, 2 = slight lodging, 3 = plants lodged at a 45° angle, and 5 = all plants flat (21).

The center two rows of each plot were sampled for nematodes at planting for initial populations and harvest for final populations; however, the respective abbreviations Pi and Pf in this paper refer to egg densities. Ten soil cores measuring 2.5 cm in diameter × 15-20 cm were combined, mixed, subsampled, and processed within 2 wk of sampling. Vermiform nematodes were extracted from 100 cm^3 subsamples by sieving (19) and sucrose centrifugal flotation (10). Cysts were extracted from 250 cm^3 subsamples by sieving (19), enumerated, and processed for egg extraction by a mechanical method (2). Vermiform nematodes were identified to genus and enumerated at 60× magnification. Extraction efficiency averaged 44% for *H. glycines* second-stage juveniles (J2). Egg suspensions were diluted to 100 ml total volume, and a 5-ml subsample was removed and counted at 40×.

Plots were assessed at several growth stages (7) for disease development. Stands were observed at V1-V2 for Phytophthora rot symptoms and disease incidence was recorded. In 1986, plots were rated at V2-V3 on a 1-5 scale for iron deficiency chlorosis symptoms, where 1 = little or no yellowing, 2 = slight yellowing, 3 = moderate yellowing, 4 = intense yellowing, and 5 = very severe yellowing (3,6). Three plants within each plot were rated at R7-R8 for brown stem rot symptoms: stems were sliced longitudinally, and the percentage of browning relative to plant height was recorded (20). Chlorosis and brown stem rot were observed at both locations in 1987 but not rated.

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Data were subjected to analysis of variance with appropriate single degree of freedom comparisons. Soybean yield was regressed on nematode densities after $\log_{10}$ transformation to reduce correlations between means and variances. For all analyses, unless otherwise noted, $P = 0.05$.

Table 1. Maturity and disease reactions[y] of eight soybean cultivars studied in Hancock and Boone counties, Iowa, in 1986 and 1987

Cultivar	Maturity group	*Heterodera glycines* (race 3)	*Phytophthora megasperma*	*Phialophora gregata*	Iron deficiency chlorosis
Asgrow 3307	III	R	T (3,4)[z]	T	MR
BSR 101	I	S	R (1)	HR	MR
BSR 201	II	S	R (1)	R	S
CN 210	II	R	S	HS	S
Corsoy 79	II	S	R (1,3)	S	S
Elgin	II	S	S	S	S
Pride B216	II	S	S	MR	HS
Weber	I	S	S	S	MR

[y] R = resistant, S = susceptible, T = tolerant, HR = highly resistant, HS = highly susceptible, MR = moderately resistant.

[z] Numbers in parentheses indicate races.

Table 2. Effects of aldicarb treatment, location, and cultivar disease reaction on soybean seed yield and growth indicators, and *Heterodera glycines* reproduction at two locations (Boone and Hancock counties) in Iowa in 1986

Comparison[w]	Seed yield (g/plot)	Seed weight (g/100 seeds)	Plant height (cm)	Lodging (visual rating)	Pf/Pi[x]
Treated vs. untreated[y]	NS[z]	NS	**	**	NS
Boone vs. Hancock	**	NS	**	**	**
Cultivars, resistant vs. susceptible to:					
H. glycines	*	**	**	**	*
Iron deficiency chlorosis	**	NS	NS	NS	NS
Brown stem rot	NS	NS	NS	NS	NS
Phytophthora rot	NS	NS	NS	NS	NS

[w] All comparisons have one degree of freedom. The "treated vs. untreated" and "Boone vs. Hancock" comparisons are applicable to all four cultivar comparisons. Cultivar comparisons were constructed from the same cultivar set according to published disease reactions, and thus are nonorthogonal.

[x] Change in densities of *H. glycines* eggs ([final population/initial population]/100 cm^3 soil).

[y] Treated plots had aldicarb applied in a 25-cm band at planting at 2.24 kg a.i./ha. Untreated plots received no nematicide.

[z] For each response variable, the comparison is either NS = not significant, * = significant at $P < 0.05$, or ** = significant at $P < 0.01$.

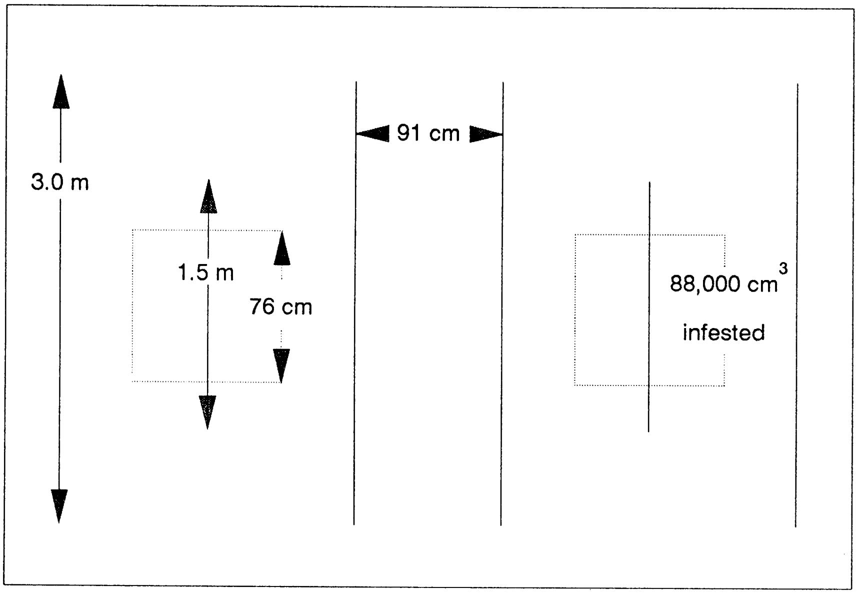

Fig. 1. Microplot design for study of the relationship between infestation level of *Heterodera glycines* on soybean in Story County, Iowa, in 1986 and 1987. Solid lines, with and without arrowheads, represent planted rows. Dotted lines represent the surface outlines of plots infested with *H. glycines* to a depth of 15 cm.

Artificial infestations. A modified field microplot technique was used in a 2-yr study on an Iowa State University–owned farm in Story County that had a low natural infestation of *H. glycines* (average 15 eggs per 100 cm^3 soil). The soil type was a clay loam (35% sand, 30% silt, and 35% clay), with a 7.4 pH and 4.1% organic matter. Each plot comprised three rows (Fig. 1), with the outer two rows mechanically planted. The center row included the microplot, a 76 × 76 cm square area infested to a depth of 15 cm with *H. glycines* race 3 eggs or eggfree filtrate. Plot rows were planted by hand at the same seed density as the mechanically planted border rows, 169 seeds per meter. The treatment combinations used were 5 Pi of *H. glycines* race 3; one nematicide treatment; and two soybean cultivars, Corsoy 79 (susceptible to *H. glycines*) and CN 290 (resistant). The 5 Pi were 0, 10, 50, 250, and 1,250 added *H. glycines* eggs per 100 cm^3 of soil. Aldicarb was applied as described above to an additional 0 Pi microplot. The experimental design was a randomized complete block with five replications. Microplots were sampled at planting and harvest for vermiform nematodes and *H. glycines* eggs, and seed yields were collected at harvest maturity as described above. Data were subjected to analysis of variance and regression analysis, and $P < 0.05$ unless otherwise noted.

RESULTS

Natural infestations. Because variances associated with years were heterogeneous for seed yields and *H. glycines* reproduction (Pf/Pi) according to Bartlett's test (18), the two years were analyzed separately. Location effects were highly significant ($P < 0.0001$) but not significantly heterogeneous. In 1986, Phytophthora rot symptoms occurred at both locations but were limited to areas within the plot alleys, confirming the pathogen's presence in the plot areas. Iron deficiency chlorosis and brown stem rot developed in the plots at both locations. The effects of aldicarb, location, and cultivar disease reaction on seed yield, seed weight, plant height, lodging, and *H. glycines* Pf/Pi were investigated through single degree of freedom comparisons (Table 2). In each comparison, cultivars were grouped as either resistant or susceptible to each disease; cultivars rated tolerant were classified with those rated resistant for this analysis. Because the same cultivar sets were used in each comparison, they are nonorthogonal. The comparisons for aldicarb and location effects were computed over all cultivars and are thus applicable to all four cultivar comparisons. Plant height and lodging were highly correlated ($r = 0.86$) and were the only responses affected by aldicarb treatment. Seed yield and *H. glycines* Pf/Pi both differed according to location.

Cultivar reaction to *H. glycines* affected all response variables, and cultivar reaction to iron deficiency chlorosis affected seed yields. Cultivar reaction to brown stem rot and Phytophthora rot had no impact on any measured response.

Soybean cultivars differed for all of the responses measured in both years at both locations. For example, in 1986, seed yields differed ($P < 0.01$) because of soybean cultivar, location, and a cultivar × location interaction (Table 3). *H. glycines*-resistant cultivars averaged 8.7 and 12.9% higher than susceptibles at Boone and Hancock, respectively. Brown stem rot disease severity was dependent on cultivar ($P < 0.001$) and was directly related to cultivar reaction (Table 1), except for the reportedly tolerant cultivar Asgrow 3307 and the resistant BSR 101, which had low and high disease severity ratings, respectively. Chlorosis ratings were similarly dependent on soybean cultivar ($P < 0.001$) and agreed with reported chlorosis ratings, except for the two *H. glycines*-resistant cultivars. Although there was a significant regression of yield on chlorosis rating ($P < 0.02$), the fit was very poor ($R^2 = 0.08$). Over both locations, seed yields of chlorosis-susceptible cultivars were 5.8 and 15.8% lower than those of resistant cultivars in 1986 and 1987, respectively.

A pattern of responses at both locations in 1987 was identical to the pattern obtained for 1986 (Tables 2 and 3), except for a seed yield response to aldicarb at Boone (Table 4). As in 1986, plants were taller in aldicarb-treated plots than in untreated plots, and lodging scores were correspondingly higher (*data not shown*). Seed weight was higher for *H. glycines*-susceptible than resistant cultivars, but seed yield was higher for the resistant cultivars, 12.3% in aldicarb-treated plots and 35.8% in untreated plots over both locations.

Plant-parasitic genera other than *Heterodera* were identified from each site. They included species in the genera *Helicotylenchus, Paratylenchus, Pratylenchus, Tylenchorhynchus*, and *Xiphinema*. Densities were lower than 10/100 cm^3 of soil for each genus, so data were not analyzed. *H. glycines* J2 at planting averaged 86 and 30/100 cm^3 at Boone and Hancock, respectively, but were not used in analyses, because of high variability in the counts (CV = 250%).

For *H. glycines*-susceptible cultivars at Boone in 1986, the $\log_{10}$ (Pi + 1) transformation was a reasonable predictor of seed yield, where predicted yield = 2,132.3 g − 334.5 ($\log_{10}$ [eggs/100 cm^3] + 1) ($R^2 = 0.55$, $P < 0.0001$). In 1987, $\log_{10}$ (Pi + 1) predicted yields ($P < 0.02$), but the fit was poor ($R^2 = 0.14$). At Hancock, there was no significant correlation between cyst or egg densities at planting and seed yield of susceptible

Table 3. Effect of soybean reaction to *Heterodera glycines* on seed yields at two locations, and to iron deficiency chlorosis and brown stem rot disease ratings at one location, in *H. glycines*-infested sites in Iowa in 1986

Cultivar	Reaction to *H. glycines*[v]	Seed yield (g/plot) Hancock Co.	Seed yield (g/plot) Boone Co.	Chlorosis rating[w]	Brown stem rot index[x]
Asgrow 3307	R	1,085.9 b[y]	1,195.8 a	2.5 c	3.2 d
CN 210	R	1,112.5 a	1,162.6 a	2.3 c	35.8 b
BSR 101	S	1,123.2 a	1,146.3 a	1.8 d	24.0 c
BSR 201	S	775.3 d	1,102.0 ab	3.3 a	7.6 d
Corsoy 79	S	913.1 cd	1,085.5 ab	2.8 b	47.4 a
Elgin	S	995.3 abc	1,167.6 a	2.9 b	24.5 c
Pride B216	S	953.7 bc	987.7 b	3.4 a	9.0 d
Weber	S	981.4 abc	969.2 b	1.8 d	38.9 ab
Site mean[z]		992.5	1,100.3**		

[v] R = resistant, S = susceptible.

[w] Plots were rated visually at V2–V3 on a 1–5 scale for iron deficiency chlorosis symptoms, where 1 = little or no yellowing, 2 = slight yellowing, 3 = moderate yellowing, 4 = intense yellowing, and 5 = very severe yellowing.

[x] Three plants within each plot were rated at R7–R8 for brown stem rot symptoms; stems were sliced longitudinally, and the percentage of browning relative to plant height was recorded.

[y] Means sharing letters within columns are not significantly different according to the Waller-Duncan *k*-ratio *t* test (*k*-ratio = 100, $P = 0.05$).

[z] Site main effect highly significant (**), $P < 0.001$.

Table 4. Effect of aldicarb treatment of soybean cultivars resistant and susceptible to *Heterodera glycines* on plant height, seed yields, and seed weight at an *H. glycines*-infested site in Boone County, Iowa, in 1987

Cultivar	Plant height (cm) T[x]	Plant height (cm) NT	Seed yield (g/plot) T	Seed yield (g/plot) NT	Seed weight (g/100 seeds)
Resistant to *H. glycines*					
Asgrow 3307	113.5	101.2	1,114.6	933.5	12.8 c[y]
CN 210	98.9	94.1	890.9	998.4	14.9 b
Mean	106.2	97.6	1,002.3	965.9	13.8
Susceptible to *H. glycines*					
BSR 101	103.2	80.7	1,125.3	924.2	15.9 a
BSR 201	77.8	68.3	699.8	578.4	15.9 a
Corsoy 79	100.1	83.6	1,039.8	607.7	14.8 b
Elgin	89.0	77.5	896.7	673.6	15.6 a
Weber	96.3	88.3	980.8	771.5	11.6 d
Mean	93.3**[z]	79.7**	948.5**	711.1**	14.9*

[x] T = treated with aldicarb at 2.24 kg a.i./ha; NT = not treated.

[y] Means sharing letters are not significantly different according to the Waller-Duncan *k*-ratio *t* test (*k*-ratio = 100, $P = 0.05$).

[z] Means of susceptible cultivars were significantly different from those of resistant cultivars based on single degree of freedom comparisons, where * = $P < 0.05$ and ** = $P < 0.01$.

Table 5. Effect of soybean cultivar on reproduction of *Heterodera glycines* in two Iowa locations

Cultivar	Pf/Pi[y] Hancock Co. 1986	Pf/Pi[y] Hancock Co. 1987	Pf/Pi[y] Boone Co. 1986	Pf/Pi[y] Boone Co. 1987
Resistant to *H. glycines*				
Asgrow 3307	0.96	0.85	0.97	0.86
CN 210	0.43	0.64	1.03	0.98
Mean	0.69	0.75	1.00	0.92
Susceptible to *H. glycines*				
BSR 101	0.48	0.64	1.12	3.62
BSR 201	0.51	1.86	1.01	1.49
Corsoy 79	0.70	1.12	1.39	1.83
Elgin	0.54	0.93	1.26	1.81
Pride B216	0.54	. . .	1.26	. . .
Weber	0.48	0.84	0.97	2.82
Mean	0.54 NS[z]	1.07**	1.16**	2.31**

[y] Pf = egg density of final populations, Pi = egg density of initial populations. The center two rows of each plot were sampled at planting for initial nematode populations and at harvest for final populations.

[z] In single degree of freedom comparisons, susceptible cultivars were compared with resistant cultivars; NS = not significantly different and ** = highly significantly different ($P < 0.01$).

cultivars in either year. We noted, however, that 41.0–63.2% of the J2 present in each Hancock sample were parasitized by fungi; parasitized eggs were present but not enumerated. The two locations also differed in numbers of eggs per cyst at planting and harvest regardless of *H. glycines* reaction; for example, Boone cysts averaged 181 eggs compared with 38 for Hancock at planting in 1986. Pf/Pi differed according to location and cultivar reaction to *H. glycines* except at Hancock in 1986 (Table 5). Overwinter retention of eggs in cysts, derived by dividing overall Pf in 1986 by Pi in 1987, was 76% at Hancock and 48% at Boone.

Artificial infestations. Seed yields at the Story location did not differ by years, but they were less variable in 1986 (CV = 14%) than in 1987 (CV = 33%). In both years for Corsoy 79 (susceptible), the $\log_{10}$ (Pi + 1) transformation was a good predictor of seed yields (Fig. 2), although the regression slopes differed according to year. In 1986, the Pi treatment of 10 eggs per 100 cm^3 ($\log_{10}$ [Pi + 1] = 1.0) resulted in a significantly lower yield for Corsoy 79 than that for the 0 Pi treatment. In 1987, seed yield for the 10 Pi treatment was higher than at the 0 Pi, but lower for the 50 Pi ($\log_{10}$ [Pi + 1] = 1.7) than at the 0 Pi. Regression of seed yield on $\log_{10}$ (Pi + 1) for CN 290, the resistant cultivar, resulted in a negative slope in 1986 and a positive slope in 1987, both with poor fit.

For both Corsoy 79 and CN 290, in plots not artificially infested with *H. glycines*, populations of *Paratylenchus projectus* Jenkins were significantly higher (672/100 cm^3) than in *H. glycines*-infested plots (215/100 cm^3), and there was a low negative correlation between *P. projectus* and *H. glycines* infestation levels ($r = -0.28$).

Aldicarb treatment had the effect of increasing seed yields of Corsoy 79 and CN 290 to 341.8 and 282.7 g per plot in 1986, and 351.7 and 341.4 g per plot in 1987, respectively, compared with seed yields in untreated 0 Pi plots (Fig. 2). Densities of *H. glycines* in the treated and untreated 0 Pi plots did not differ in either year, nor did they differ from the preinfestation level of the microplot field.

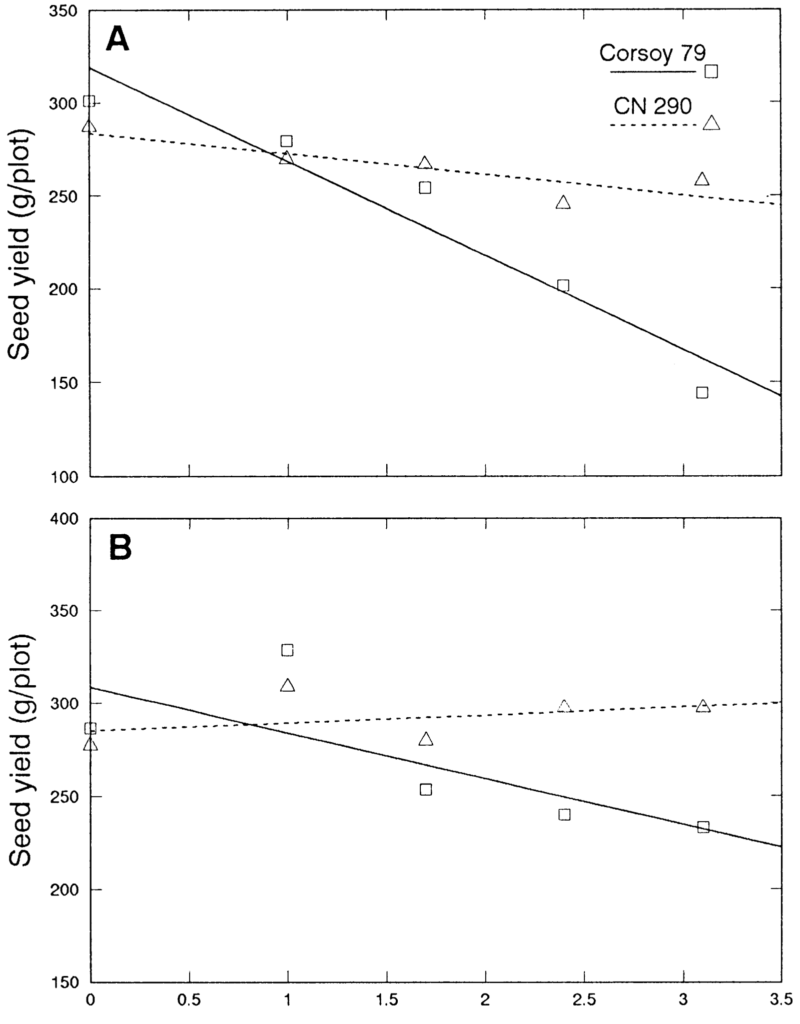

Fig. 2. The relationship between initial populations (Pi) of *Heterodera glycines* and seed yields of resistant (CN 290) and susceptible (Corsoy 79) soybean cultivars in Story County, Iowa. **(A)** 1986: For Corsoy 79, seed yield (y) (g/plot) = 319.8 − 50.6 ($\log_{10}$ [Pi + 1]), $R^2 = 0.92$; for CN 290, $y = 284.0 - 11.2$ ($\log_{10}$ [Pi + 1]), $R^2 = 0.26$. **(B)** 1987: For Corsoy 79, $y = 308.4 - 24.2$ ($\log_{10}$ [Pi + 1]), $R^2 = 0.54$; for CN 290, $y = 285.0 + 4.3$ ($\log_{10}$ [Pi + 1]), $R^2 = 0.15$.

DISCUSSION

The first question that must be answered in preparing local management recommendations for a potentially yield-reducing crop pest is whether the pest causes yield reductions at naturally occurring infestation levels. The answer, for *H. glycines* on soybean in central and northern Iowa, is yes. But that conclusion is not straightforward, according to the data reported herein. In each of the four naturally infested environments, the average seed yields of *H. glycines*-resistant cultivars were 8.7–35.8% higher than those of susceptible cultivars, although there was considerable variation among cultivars, environments, effects of aldicarb, and host reaction to iron deficiency chlorosis. We did not simultaneously check cultivar performance in a noninfested environment, nor did nematicide treatment provide consistent control of *H. glycines*; either data would help provide a truer estimate of the yield reductions caused by *H. glycines* in Iowa. However, yields for four susceptible cultivars (BSR 101, Corsoy 79, Elgin, and Weber) from comparably designed and managed tests in three noninfested locations in northern Iowa in 1986 averaged 45.1 bu/acre (21). Expressed in the same units, the average yield for the same cultivars in our northern Iowa test (Hancock) in 1986 was 27.5. Similar comparisons for year and location combinations (21,22) show that *H. glycines*-susceptible cultivars yielded about 40% less in infested than in noninfested fields. If, as in our tests, resistant cultivars yield up to 35.8% higher than susceptibles in infested sites, then the use of resistant cultivars would provide significant economic returns to soybean farmers with infested fields.

Phytophthora rot, brown stem rot, and iron deficiency chlorosis also cause soybean yield reductions in Iowa (4,6,16), so the next question is whether other diseases were responsible in part for the yield reductions noted in our tests. Although Phytophthora rot was observed at each location, its development was not severe enough to rate, and host reaction to the disease had no effect on yields. Brown stem rot was widespread in all four environments, and disease severity was determined in 1986. Brown stem rot can reduce soybean seed yields (4), but we observed no relationship between disease severity and yields. Iron deficiency chlorosis was also widespread in all four environments, and chlorosis-resistant cultivars yielded an average of 12% higher than susceptibles. We expected a greater increase; in studies by Fehr (6), each unit increase in chlorosis rating resulted in a 20% yield reduction. We detected no interaction between cultivar reaction to *H. glycines* and cultivar reaction to chlorosis. However, our experimental design and paucity of disease severity ratings prevent us from concluding that no interaction exists. As cultivars are available with combinations of reactions to each of the diseases, the most prudent recommendation at this point would be to choose cultivars according to diseases that are likely to occur.

In the microplot study, no other diseases were noted. Seed yield of the susceptible cultivar, Corsoy 79, was significantly reduced at the 10 Pi in 1986 and the 50 Pi in 1987. A damage threshold between 10 and 50 eggs per 100 cm^3 of soil compares favorably with the damage threshold estimated for Illinois of 20 eggs and juveniles per 100 cm^3 of soil (5); however, the actual damage threshold in our study would be somewhat higher than 10 eggs, because the field had a low natural infestation. Ten eggs per 100 cm^3 of soil is just above the detection level. Seed yield decreased with increasing Pi in both years, in contrast to our results in naturally infested fields. The contrast may be a reflection of the difficulty in estimating naturally occurring nematode populations compared with applying carefully quantified inoculum, or it may be that the inoculum preparation or application process somehow resulted in a higher infection rate. Yield reductions in the microplots and naturally infested field plots cannot be compared directly, but it is clear from both data sets that once *H. glycines* populations exceed the detection level, there is a potential for yield reduction.

In this discussion, we have concentrated on seed yields rather than other plant responses because yield is the response of immediate concern to soybean producers with infested fields. Other responses to *H. glycines* were not simply incidental, however. The plant height and lodging responses showed that infestations of *H. glycines* were not completely symptomless, as they can be in high-yield environments (Niblack, *unpublished*), but they may not be noticeable. The seed weight response (lower seed weight for resistant cultivars) was cultivar-dependent and unrelated to *H. glycines* infection. The plant growth and yield responses to aldicarb treatment were inconsistent. Aldicarb is known to stimulate plant growth in the absence of nematode pressure (1), and its stimulation of resistant cultivars in 1987 and in both years of the microplot study confirms that its stimulation of susceptible cultivars in the same environments was not entirely due to nematode control. Zirakparvar et al (24) found aldicarb to be more effective than other nematicides in increasing yields of a *H. glycines*-susceptible cultivar in Iowa, and Noel (12) found aldicarb to be a reasonable management alternative for *H. glycines*-infested fields in Illinois. Conversely, Smith et al (17) concluded than aldicarb was not an economical choice for *H. glycines* control in Missouri. The effect of soil type on such results (15) signal caution in generalizing recommendations for Iowa, but the use of aldicarb should probably be restricted to situations in which other management options are not available.

Further information is needed on *H. glycines* ecology and population dynamics in Iowa. We observed a potential biocontrol agent, lower reproduction than expected on susceptible cultivars, lower numbers of eggs per cyst than expected, and low diversity of other plant-parasitic nematodes in *H. glycines*-infested fields. High organic matter soils may provide suitable environments for biocontrol agents (9). At Hancock in 1986, Pf/Pi was less than 1.0 for all cultivars, and a large percentage of the J2 were parasitized. The low Pf/Pi cannot be unequivocally linked to the parasitic fungus or fungi, partly because Pf/Pi at both locations was lower than during the following year and could have differed between locations because of other factors. Along with the lower Pf/Pi, the number of eggs per cyst was low. Young and Heatherly (23) showed that this quotient is related to soil type, with high clay soils having lower quotients; however, in our study, the higher clay soil (Boone) also had higher numbers of eggs per cyst. This contradiction could be accounted for by the effect of a parasitic fungus. Overwinter retention of eggs in cysts also differed between locations. The survival rate of these eggs should be determined for predictive purposes; however, because we were not able to consistently relate *H. glycines* Pi to seed yields in naturally infested environments, the predictive value of *H. glycines* population estimates in Iowa also needs supplemental study.

The densities of other plant-parasitic nematodes in the *H. glycines*-infested fields were too low for analysis, except for *Paratylenchus* at Story, where densities were found to be highest where those of *H. glycines* were lowest. The range of genera in Iowa soybean fields (Niblack, *unpublished*) is highly similar to that we observed at our research locations and to that reported for soybean fields in Illinois, Indiana, and Missouri (8; Niblack, *unpublished*). It appeared, however, that although the range of genera may not be narrower in *H. glycines*-infested fields than in noninfested fields, the densities of other plant parasites are reduced. In high densities, *H. glycines* restricts root growth (11), so the introduction and buildup of the nematode in a soybean field may simply reduce the substrate available for other plant parasites. The negative correlation between *Paratylenchus* densities and soybean yield also deserves investigation to determine whether it exists in the absence of *H. glycines*.

Management recommendations should continue to be developed and refined for *H. glycines* in Iowa. The studies reported herein provide evidence that the nematode can be a pathogen even in the absence of severe symptoms. The absence of symptoms renders it difficult to educate farmers about the potential for yield losses caused by the nematode. Interactions between *H. glycines* and other disease causes deserve more study, especially when they commonly coexist in soybean fields.

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