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Population Development of *Heterodera glycines* and Soybean Yield in Soybean-maize Rotations Following Introduction into a Noninfested Field

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Abstract: An 11-year field study was initiated in 1979 to monitor population development of *Heterodera glycines*. Fifty cysts of a race 5 population were introduced into plots in a field with no history of soybean production and that had been in sod for 20 years. Soybean cultivars either susceptible or resistant to *H. glycines* were grown either in monoculture or rotated with maize in a 2-year rotation. During the first 5 years, resistant cultivars with the Peking source of resistance were planted. After year 5, monoculture of Peking resistance resulted in 18 cysts/250 cm^3 of soil, whereas populations resulting from the continuous cropping of susceptible soybean resulted in 45 cysts/250 cm^3. Some plots in all treatments, including control plots, were contaminated at the end of year 5. Crop rotation delayed population development of *H. glycines*. During years 6 through 11 cv. Fayette (PI88.788 source of resistance) was planted. In year 6 numbers of cysts declined to 1/250 cm^3 of soil in the treatment consisting of monocultured Fayette. At the end of year 10, cysts were below the detection level in all treatments in which Fayette was planted. Yield of susceptible soybean in monoculture with or without *H. glycines* infestation was lower beginning in year 6 when compared to yield of soybean grown in rotation and remained lower throughout the duration of the experiment except for 1987 (year 9). Yields of susceptible and resistant soybean were different each year except for drought years in 1980 and 1988. From 1979 to 1982 differences in yield were due to lower yield potential of resistant cultivars. Except for the drought year, yield of cv. Fayette was greater than susceptible Williams 82 during years 6 through 11.

Key words: crop loss, crop rotation, cropping system, resistance, *Glycine max*, *Heterodera glycines*, integrated pest management, maize, race, population dynamics, soybean, soybean cyst nematode, *Zea mays*.

Following the discovery of soybean cyst nematode, *Heterodera glycines* Ichinohe, in the United States in 1954 (18), the distribution became widespread with infestations reported in eight states by 1965, 15 states infested by 1976, and 24 states infested by 1986 (12). In 1987, *H. glycines* was reported in Ontario, Canada (1). A federal quarantine was established in the United States in 1957 to prevent spread of the nematode into "noninfested" soybean, *Glycine max* (L.) Merr., production areas (14). In 1972, the quarantine was judged ineffective and was rescinded. However, some production areas apparently were not infested, whereas in other geographically isolated areas, introduction of the nematode was believed due to instances of long-range movement of infested soil on transplants, used farm machinery, and equipment used to install power poles and natural gas lines. The number of years required for the nematode to increase to population levels either capable of being moved in soil adhering to equipment or to those levels that cause crop loss was not known. The objectives of the research reported herein were to (i) determine the number of years necessary for the nematode to increase to damaging levels following introduction into different soybean-maize rotations in a field having no known history of soybean production, and (ii) determine the effect of rotating sources of resistance on population development of *H. glycines* and soybean yield.

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Materials and Methods

The experiment was established during 1979 in a field that had no history of soybean production and had been in sod for 20 years. The field was sampled before initiation of the experiment to ensure that *H. glycines* was not present. The soil was a series Drummer (fine-silty, mixed, mesic Typic Haplaqualls; surface layer texture = silty clay loam, organic matter = 6%, CEC = 14.4). The experimental design was a split-split-plot arranged in a randomized complete block design with *H. glycines* infestation as the main plot, crop rotation as sub-plots, and year as sub-sub-plots. Treatments were: (i) continuous susceptible soybean, (ii) continuous resistant soybean, (iii) maize (MO17 × A634) followed by susceptible soybean, (iv) maize followed by resistant soybean, (v) susceptible soybean followed by maize, and (vi) resistant soybean followed by maize. Table 1 lists the cultivars, source of resistance, maturity group, and years planted. In 1979, cv. Amsoy 71 was a popular *H. glycines* susceptible cultivar and cv. Franklin (Peking source of resistance, [5]) was the only agronomically acceptable resistant cultivar available in the north-central United States. During subsequent years of the experiment, promising resistant genotypes and closely related susceptible cultivars were planted. From 1980 to 1983, resistant cvs. CN290 (Beeson × Peking source [4]) and Beeson 80 were planted. From 1983 to 1989, cvs. Fayette

TABLE 1. Cultivars, source of resistance to *Heterodera glycines*, maturity group, and years in which cultivars were planted.

Cultivar	Source of resistance	Maturity group	Years planted
	Susceptible		
Amsoy 71		II	1979, 1980
Beeson 80		II	1981–1983
Williams 82		III	1984–1989
	Resistant		
Franklin	Peking	IV	1979
CN290	Peking	II	1980–1983
Fayette	PI88.788	III	1984–1989

(Williams × PI88.788 source [3]) and Williams 82 were planted.

Individual plots (experimental units) were four rows wide with 76-cm row spacing and measured 3.0 × 6.0 m. A 4.5-m length of row was harvested from the two middle rows. Soybean was harvested mechanically, and maize was harvested manually and shelled. Seeds and kernels were dried and harvest weight was based on 14% moisture. In an attempt to prevent spread from infested to noninfested plots, 3-m-wide grass borders were established between main plots, and borders consisting of a 5-m length of fallow soil were maintained between experimental units within main plots. Farming operations were conducted on noninfested main plots first, and equipment was cleaned with high-pressure water after use.

Based on the numbers of cysts recovered from soil on a commercial field cultivator (Noel, unpubl.) and to mimic introduction during preparation for planting and at cultivation, 25 cysts were added twice the first year to a 10-cm-deep hole in the center of each infested sub-plot. Numbers of *H. glycines* cysts were determined at the end of each growing season by bulking 12 2-cm-diam. × 12-cm-deep soil cores collected in a zig-zag pattern from the harvest rows. Cysts were extracted from 250 cm^3 of soil by wet sieving using 850-μm-pore and 250-μm-pore sieves and counted (6).

Race determinations were made on the introduced population and after termination of the experiment on populations from plots planted to resistant and susceptible soybean (16). Since cysts were not detected at the end of the experiment in plots planted to Fayette, Williams 82 was planted for two seasons and the nematode was then increased on Williams 82 in a greenhouse.

Fertilizer was applied at rates recommended by the University of Illinois for both maize and soybean (17). Soil pH was maintained between 5.5 and 6.5. Weed control consisted of preplant incorporation of metolachlor at the recommended rate, mechanical cultivation, and manual cultivation.

Maize yields were determined, but the data are not shown. The general linear models procedure was conducted on soybean yield and nematode population densities (SAS Institute, Cary, NC). Tests of hypotheses for mixed model analysis of variance for yield and transformed $\log_{10}(x + 1)$ cyst numbers were conducted using replication and infestation as the random factors and year and rotation as the fixed factors. The normality test for residuals for transformed cyst data demonstrated that cyst numbers were normally distributed. Where appropriate, error terms were combined. Significance of main effects and interactions were determined, and single degree of freedom contrasts were made for pertinent comparisons.

Results

At the end of the second year (1980), cysts were detected in all treatments that were infested in 1979, and noninfested plots remained cyst free (Table 2). Despite efforts to prevent spread of *H. glycines* within the experimental area, cysts were found the fifth year (1983) in all treatments, but not in all plots. In 1983, the number of cysts had increased to 45/250 cm^3 of soil in the infested continuous susceptible treatment and to 18/250 cm^3 of soil in the continuous resistant treatment. From 1984 to 1989, numbers of cysts

TABLE 2. Numbers of *Heterodera glycines* (HG) cysts and soybean yields at harvest during an 11-year period following infestation in different soybean-maize rotations.

		Cysts/250 cm^3 of soil and yield (kg/ha) at harvest										
Rotation[a]	HG	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989
							Cysts					
CS	+	—	<1	1	5	45	14	40	48	19	36	36
CS	−	—	0	0	3	3	<1	1	21	19	48	4
M–S	+	—	<1	<1	6	5	<1	2	2	0	15	18
M–S	−	—	0	0	1	2	1	<1	<1	<1	0	0
S–M	+	—	<1	<1	2	3	1	2	<1	<1	9	7
S–M	−	—	0	1	2	2	1	2	<1	<1	<1	0
CR	+	—	<1	0	<1	18	1	<1	0	1	0	0
CR	−	—	0	0	2	1	0	<1	2	0	0	0
M–R	+	—	1	0	<1	2	1	2	3	0	0	0
M–R	−	—	0	0	4	5	1	<1	<1	0	0	0
R–M	+	—	1	<1	2	2	<1	2	0	0	0	0
R–M	−	—	0	<1	<1	2	<1	0	<1	0	0	0
							Yield					
CS	+	3,458	2,544	3,208	3,203	1,949	2,342	2,300	2,448	2,346	1,191	1,497
CS	−	3,967	2,556	3,570	2,750	2,253	2,470	2,357	2,436	2,285	1,388	1,317
M–S	+	Maize	2,661	Maize	3,212	Maize	2,764	Maize	2,783	Maize	1,538	Maize
M–S	−	Maize	2,706	Maize	3,198	Maize	2,990	Maize	2,762	Maize	1,876	Maize
S–M	+	3,698	Maize	3,346	Maize	2,320	Maize	3,387	Maize	2,078	Maize	1,705
S–M	−	3,645	Maize	3,510	Maize	2,176	Maize	2,891	Maize	1,988	Maize	1,781
CR	+	3,048	2,738	2,915	1,770	756	2,889	2,913	2,547	2,309	1,656	1,815
CR	−	3,060	2,526	2,810	2,056	666	3,043	3,226	2,895	2,701	1,435	1,891
M–R	+	Maize	2,547	Maize	2,111	Maize	3,029	Maize	3,320	Maize	1,410	Maize
M–R	−	Maize	2,372	Maize	2,156	Maize	2,918	Maize	3,282	Maize	1,485	Maize
R–M	+	2,939	Maize	3,128	Maize	920	Maize	3,696	Maize	2,459	Maize	1,996
R–M	−	3,092	Maize	3,132	Maize	704	Maize	3,568	Maize	2,614	Maize	2,003

Data are the means of four replications.

[a] CS = continuous susceptible soybean, M–S = maize-susceptible soybean rotation, S–M = susceptible soybean-maize rotation, CR = continuous resistant soybean, M–R = maize-resistant soybean rotation, and R–M = resistant soybean-maize rotation.

ranged from 14 to 48/250 cm^3 of soil in the infested continuous susceptible treatment. In the infested maize-susceptible soybean rotation, numbers of cysts were low but increased to 15 and 18/250 cm^3 of soil in 1988 and 1989, respectively. Low numbers of cysts were found in the noninfested maize-susceptible soybean treatment from 1982 to 1987, but no cysts were found in 1988 and 1989. From 1982 to 1987, numbers of cysts in the infested susceptible soybean-maize rotation ranged from <1 to 3 cysts/250 cm^3 of soil, but in 1988 and 1989 numbers of cysts were 9 and 7, respectively. In 1987, only one cyst was recovered from the plot planted to continuous Fayette treatment, and no cysts were recovered either from the continuous noninfested treatment or from any of the rotation treatments. In 1988 and 1989, cysts were not recovered from either monoculture plots of Fayette or rotation plots planted to either Fayette or maize.

There was a significant effect of infestation, rotation, and years but not block on numbers of cysts (Table 3). All interactions were significant. Significant differences in numbers of cysts recovered from susceptible and resistant soybean were found in 1982 and 1983 and from 1985 to 1989 (Table 4). Differences in numbers of cysts recovered from susceptible soybean grown in monoculture and susceptible soybean grown in rotation were significantly different from 1983 to 1989. From 1979 to 1989, there were no significant differences in numbers of cysts recovered from continuous resistant soybean and resistant soybean grown in rotation.

Yield of Franklin in 1979 and yield of CN290 from 1980 to 1983 were lower than Amsoy 71 and Beeson 80 (Tables 2–4). In 1983, severe phytophthora root rot was diagnosed in plots planted with CN290.

From 1984 to 1987 and in 1989, infestation of *H. glycines* was associated with lower yield of Williams 82 when compared to resistant Fayette (Tables 2–4). In 1980 and 1988, yields were affected by drought and there were no cultivar differences. From 1984 to 1986 and in 1988 and 1989, yield of Williams 82 grown in monoculture was lower than Williams 82 grown in rotation. However, chlorosis was not observed and stunting of plants was indiscernible. In 1985 and 1986, yield of rotated Fayette was greater than Fayette grown in monoculture.

The experimental design was able to account for effects on yield within the exper-

TABLE 3. Analysis of variance for numbers of cysts/250 cm^3 of soil and soybean yield (kg/ha) in six soybean-maize rotations, 1979–1989.

	Cysts[a]		Yield	
Source of variation	df	Mean squares	df	Mean squares
Block (B)	3	0.71876	3	1,448,704***
Infestation (I)	1	21.14507***	1	119,180
I × B	3	1.55952*	3	252,807
Rotation (R)	5	25.11842***	3	1,728,259**
R × I	5	3.46805***	3	63,474
R × I × B + R × B	30	0.80852**	18	232,123**
Year (Y)	9	4.50140***	10	14,036,177***
Y × I	9	1.30866**	10	54,278
R × Y	45	2.06790***	30	1,370,019***
R × Y × I	45	1.02450***	30	106,155
Y × I × B	54	0.63350*	60	196,910**
Y × I × B × R + Y × B × R	270	0.44758	180	20,281,698
CV (%)		97.9		13.5

*, **, *** denote significance at $P \leq 0.05$, ≤ 0.01, or ≤ 0.001, respectively.
[a] Numbers of cysts were transformed to $\log_{10}(x + 1)$ for statistical analysis.

TABLE 4. Significance of single degree of freedom contrasts for numbers of cysts and yield in a soybean-maize rotation study, 1979–1989.

	Year										
Comparison[a]	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989
						Cysts					
S vs. R				**	**		***	***	***	***	***
CS vs. RS					*	*	*	***	***	***	**
CR vs. RR											
						Yield					
S vs. R	***		***	***	***	**	***	***	**		**
CS vs. RS						**	***	*		**	*
CR vs. RR							***	***			

*, **, and *** denote significance at $P \leq 0.05$, $P \leq 0.01$, or $P \leq 0.001$, respectively.
[a]S vs. R = continuous and rotated susceptible soybean vs. continuous and rotated resistant soybean, CS vs. RS = continuous susceptible soybean vs. rotated susceptible soybean, CR vs. RR = continuous resistant soybean vs. rotated resistsant soybean.

imental area as shown by the significant block effect. The main effect of infestation was not significant for yield. The effects of rotation and years were both significant for yield. The rotation × year and year × infestation × block interactions were significant (Table 3).

The original population used to infest the field was identified as race 5. The female indices (FI) based on reproduction on Lee 68 were 71% for Pickett 71, 4% for Peking, 27% for PI88.788, and 3% for PI90.763. The population from plots planted with resistant soybean was identified as race 4. The FI were 93% for Pickett 71, 24% for Peking, 16% for PI88.788, and 12% for PI90.763. In plots planted with susceptible soybean the activity was identified as race 6 based on FI of 63% for Pickett 71, 9% for Peking, 7% for PI88.788, and 5% for PI90.763.

DISCUSSION

Once *H. glycines* was introduced into the field plot, the nematode population increased to yield-reducing levels within 5 to 6 years of monoculture of susceptible soybean even though stunting and chlorosis were not evident and were not observed after 6 additional years of planting monocultured-susceptible soybean upon termination of the experiment. The significant effect of infestation and the year × infestation interaction on numbers of cysts was due to relatively low numbers of cysts during the first 3 years of the experiment, and higher numbers of cysts found in continuous susceptible and continuous resistant soybean in 1983. High numbers of cysts were found in susceptible continuous soybean plots from 1984 to 1989, and recovery of either low numbers of cysts or none recovered from resistant treatments from 1984 to 1989 also contributed to the significant year × infestation interaction. The rotation × year interaction more clearly demonstrates the differences found between planting susceptible and resistant soybean, especially during the last 3 years of the experiment when only one cyst was found in any resistant soybean treatment.

Rotation of a susceptible soybean with maize was effective in slowing population increases of *H. glycines*. Similarly, rotating corn with a cultivar having a moderate level of resistance can slow long-term population increases of *H. glycines*. A field study in New York demonstrated that *Heterodera schachtii* spread from infested to adjacent noninfested fields when rotations consisted of either 1:2 or 1:1 ratios of nonhosts to hosts (9). When nonhost-to-host ratios were either 5:1 or 2:1, spread was not detected. Our data indicate that under commercial production practices, in which farmers use a 2-year rotation, soybean yield loss will occur before nematode population densities are great enough to cause the diagnostic symptoms of stunting and chlorosis. Under the soybean-maize production systems common to the midwestern United States, detectable symptoms would require 15 to 20 years to occur in a field once the nematode is introduced. The population density of cysts would provide ample opportunity to contaminate field equipment and more cysts in infested soil to other fields. *Globodera rostochiensis* population densities not detectable by soil sampling resulted in an average of 10 cysts recovered from a field cultivator (2). Spread of a cyst nematode from field to field or over longer distances can occur with only one cyst, but is more likely if the numbers of cysts are high. Thus, by the time a quarantine is instituted the nematode likely has been spread to other fields or longer distances on equipment. Following the discovery of *H. glycines* in Brazil (11), establishment of a quarantine was considered. However, the results of a survey for *H. glycines* (15), the data presented herein, and the long-range movement of equipment by growers from their farms in known areas of infestation in the central production region to farms in the southern production region of Brazil were reasons cited why the quarantine was not implemented (C. C. Machado, pers. comm.). The nematode subsequently has been found in the southern production region (C. C. Machado, pers. comm.).

In spite of precautions taken to prevent plot-to-plot spread during this experiment, cysts were found in all treatments, but not all experimental units, and had increased to moderate levels in the noninfested continuous susceptible treatment. Occasional flooding and dissemination by animals may have caused some spread within the experimental area. The experiment was terminated when the continuous noninfested susceptible treatment became highly infested and populations in the resistant treatments were not detectable.

The highly significant effect of year on yield was not unexpected given that there were two drought years (1980 and 1988) when overall yields were reduced, phytophthora root rot appeared in 1983, and a general decline in yield occurred from 1979 to 1989. Lack of a significant effect of infestation on yield was due in part to low nematode population densities in continuous susceptible plots during the first 4 years of the experiment and lack of yield reduction in plots planted with resistant cultivars.

Contamination of noninfested plots occurred but remained lower than in noninfested treatments. The effect of infestation on yield is better understood in the context of rotation. The significant effect of rotation and the year × rotation interaction were due to inferior yield potential of *H. glycines*-resistant cultivars (Franklin and CN290) grown from 1979 to 1983 and low yield associated with *H. glycines* in plots planted with susceptible cv. Williams 82 for the duration of the experiment except for the drought year 1988. Cyst numbers exceeded damage thresholds (13) in infested continuous susceptible plots from 1984 to 1989 and in the noninfested continuous susceptible treatment from 1987 to 1989. However, when compared to yield of resistant Fayette, yield loss apparently occurred in the noninfested continuous susceptible treatment at nematode numbers below the previously reported damage threshold (13), indicating that crop loss may occur in research plots at the nematode detection level.

Lower yield of CN290 in 1982 probably resulted from a low incidence of phytophthora root rot. In 1983 phytophthora root rot was diagnosed, thus prompting an earlier-than-desired rotation of *H. glycines*-resistant cultivars. Although Fayette has no known resistance genes to *Phytophthora sojae,* we planted it instead of CN290 because in other experiments it had exhibited "field tolerance" to phytophthora rot.

The concept of rotating resistance genes to control *H. glycines* resulted from the greenhouse studies of McCann et al. (10) and Luedders and Dropkin (8). Although rotation of resistance sources is recommended in several states in the United

States where adapted resistant cultivars are available, field research has not supported this recommendation (7,19). A previous attempt to control *H. glycines* by rotating cv. Forrest (Peking source of resistance) and cv. Bedford (Peking and PI88.788 sources of resistance) was unsuccessful (7). In that study, the initial population densities of *H. glycines* were large and rotation with a nonhost was not done. Thus, selection pressure was great, and the two cultivars apparently did not have mutually incompatible reactions to the populations of *H. glycines* selected on them. In a subsequent long-term study involving rotation with maize, cvs. Bedford, Essex (susceptible to *H. glycines*), and Forrest, yield of monoculture Bedford was not different than Bedford rotated with Forrest and Essex and was less than Bedford rotated with maize in only 1 of 11 years (19). However, in the last 3 years of that experiment, the index of parasitism for monocultured Bedford was significantly greater than Bedford grown in rotation, and numbers of cysts were numerically greater in the monocultured plots. In the research reported herein, cysts were not detected the last 2 years in treatments involving Fayette, but selection pressure apparently caused the population to change from one identified as race 5 at the beginning of the experiment to one described as race 4 at the end of the experiment. The race 6 designation of the population that developed in plots planted to susceptible soybean was unexpected. Williams 82 may have a resistance gene that might have exerted selection pressure (8), resulting in a population with a low reproductive capability on PI88.788.

The reduction of *H. glycines* populations to below detectable levels demonstrates that rotating resistance genes to control the nematode is a viable management option. However, individuals in other populations of *H. glycines* undoubtedly express different allelic frequencies for parasitism of soybean having the Peking and(or) PI88.788 source(s) of resistance. Consequently, rotation of resistant cultivars may not be as effective as reported herein if populations of *H. glycines* have higher allelic frequencies for parasitism. Our data support advising growers to rotate resistance sources in absence of specific knowledge of allelic frequencies for parasitism of soybean by *H. glycines* encountered in growers' fields, provided that populations of *H. glycines* have been reduced to low levels with nonhost crops.

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