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Heterodera glycines Infectivity and Egg Viability Following Nonhost Crops and During Overwintering[1]

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Abstract: The most effective management program for soybean cyst nematode, *Heterodera glycines,* is a crop rotation that uses nonhost crops and resistant soybean cultivars. However, little is known about the effects of rotation crops and overwintering on *H. glycines* biology. These experiments were initiated to determine the effects of seven alternative crops on *H. glycines'* ability to infect and mature on subsequent soybean crops, and to assess the viability of eggs during the overwintering months. Rotation studies were conducted for 2 years in each of two naturally infested fields, and overwintering tests were conducted in three consecutive growing seasons in one naturally infested field. Rotation crop and fallow treatments did not have a consistent effect on the ability of *H. glycines* to infect soybean or mature. Soybean yields were often higher following fallow or a nonhost crop than following soybean, although not usually significantly so. *Heterodera glycines* egg viability did not differ ($P < 0.05$) between overwintering months at 0-to-10 or 10-to-20-cm soil depths. These results suggest that *H. glycines'* ability to infect a subsequent soybean crop and develop to maturity is not diminished by nonhost crops or during the winter months.

Key words: Avena sativa, Brassica rapa, canola, corn, fallow, *Glycine max, Heterodera glycines,* grain sorghum, infectivity, nematode, nonhost, oat, overwintering, common red clover, rotation, sesame, *Sesamum indicum, Sorghum bicolor,* soybean, soybean cyst nematode, *Trifolium pratense,* viability, *Zea mays.*

Soybean cyst nematode, *Heterodera glycines,* consistently causes greater annual yield losses than any other soybean (*Glycine max*) pathogen in the United States (Pratt and Wrather, 1998; Wrather et al., 1995, 1997, 2001). Estimated losses exceed 5 million metric tons annually (Wrather et al., 2001). A crop rotation program that includes a nonhost and resistant soybean cultivar is the most effective and frequently employed *H. glycines* management strategy (Niblack and Chen, 2004; Riggs and Niblack, 1999).

The results of numerous studies have shown the value of rotating soybean with corn (*Zea mays*) (Koenning et al., 1993, 1995; Noel and Edwards, 1996; Porter et al., 2001; Rodríguez-Kábana et al., 1991, Sasser and Uzzell, 1991; Schmitt, 1991; Weaver et al., 1988; Young, 1998) for the reduction of *H. glycines* population densities and increased yields. Populations may be reduced by as much as 75% or 92% following 1- or 2-year corn rotations, respectively (Wrather et al., 1984). Chen et al. (2001) reported that annual rotation of a resistant soybean with corn resulted in the best combination of nematode population reduction and high yields for both crops and is popular in the midwestern United States. Several other nonhost crops also have been useful for the reduction of *H. glycines* populations. For example, rotations including either cotton (*Gossypium hirsutum*) or grain sorghum (*Sorghum bicolor*) reportedly inhibited *H. glycines* reproduction and produced soybean yields that were as high as those from corn-soybean rotations (Francl and Dropkin, 1986).

Limited information is available on the effects of corn or other crops on *H. glycines* biology and reproduction when used in rotation with soybean. The objectives of these experiments were to: (i) investigate the effects of seven nonhost cropping alternatives on soybean yield and *H. glycines'* ability to infect and develop to maturity on susceptible soybean and (ii) to evaluate the impact of resistant and susceptible soybean cultivars on egg production and their viability in the overwintering months following harvest.

Materials and Methods

Rotation experiment: During 1989 and 1990, soybean (susceptible cultivar Williams 82) and six additional crop species were planted in two fields with natural infestations of *H. glycines* in Missouri. An additional fallow treatment was left unplanted. Plots were 5 m long, four rows wide with 91.4 cm between the rows and arranged in randomized complete blocks with four replications. The crop species included canola (*Brassica rapa*), oat (*Avena sativa*), corn (*Zea mays*), common red clover (*Trifolium pratense*), grain sorghum (*Sorghum bicolor*), and sesame (*Sesamum indicum*). Six 2.5-cm-diam. soil cores were collected to a depth of 20 cm at planting and in the fall from the center two rows of each plot in a zigzag pattern. The cores were combined to represent a composite sample. *Heterodera glycines* cysts were extracted from a 100-cm^3 soil subsample with a semiautomatic elutriator and mechanically macerated to release the eggs (Niblack et al., 1993), which were stained with acid fuchsin (Southey, 1986) and counted at × 64 magnification. Nematode reproduction factors (Rf) were calculated as a ratio of final (Pf) and initial population (Pi) densities, $(Pf + 1)/(Pi + 1)$. Additional eggs were extracted in the same manner and used to evaluate *H. glycines* infectivity and viability as described in the subsequent section.

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During the following year, the same plot areas were divided into two subplots and each subplot was planted randomly with either Williams 82 or 'Linford' (resistant) soybean. Soil was collected from each subplot in the fall and eggs were extracted and used to evaluate *H. glycines* infectivity and viability. Soybean seeds were mechanically harvested from each subplot for yield.

Infectivity and viability of *H. glycines* eggs were assessed for each of the plots (Hill and Schmitt, 1989; Yen et al., 1995). 'Essex' soybean seed was germinated for 48 hour at 28 °C in moist sterilized germination paper, and seedlings with 2.5- to 3.0-cm radicles were selected for infectivity and viability bioassays. Each seedling was planted in a 3-cm-diam. polyvinylchloride tube containing 100 cm^3 sterilized sandy loam soil (74% sand; 16% silt, 10% clay) and infested with 1,000 eggs. Plants were placed in temperature-controlled water baths in the greenhouse that maintained a root-zone temperature of 27 °C. Plants were removed from the sand after 10 days to determine the nematodes' infectivity. Second-stage juveniles (J2) within the root were stained with acid fuchsin (Byrd et al., 1982), and root length was determined with a modified line intersect method (Spaull, 1981). Second-stage juveniles were counted and infectivity was expressed as the number of J2/cm root. Viability of *H. glycines* was assessed 32 days after infestation. Plants were removed from the sand and *H. glycines* females were dislodged from the roots with high-pressure water spray and counted. Viability was expressed as the percentage of females that developed from 1,000 eggs.

Overwintering experiment: In 1988, soybean cultivars Williams 82 (susceptible), Stine 3292 (susceptible), JMS 3609 (susceptible), and Fayette (resistant) were planted in four-row-wide plots that were 91.4 cm wide and 5 m long arranged in a randomized complete block with four replications near Shelbina, Missouri. In 1989 and 1990, only cultivars Williams 82 and Fayette were included in the test. Soil samples were collected at harvest in September of each year and monthly through April of the following year from depths of 0 to 10 cm and 10 to 20 cm. *Heterodera glycines* eggs were extracted from a 100-cm^3 soil subsample from each sample and viability was assessed for 1,000 eggs in a bioassay as described for the rotation experiment.

Statistical analysis: All nematode data were transformed to log 10 (x + 1) values before analysis to reduce the correlation between means and variances. All data analyses were conducted on transformed data, but nontransformed data are presented for clarity. Analyses of variance were performed with the general linear models procedure of SAS (SAS Institute, Cary, NC), and the Waller-Duncan k-ratio *t*-test was used for mean separation in the MEANS option. Means presented of nontransformed data were calculated with least-squares estimates of marginal means (LSMEANS).

Results

Rotation experiment: There were crop species × year ($P < 0.05$) and crop species × location ($P < 0.01$) interaction effects on *H. glycines* reproduction (Table 1). Variability was high (CV = 1,386%) in the nematode reproduction data. Infectivity was affected only by location ($P < 0.05$), such that the population in Baring infected soybean at a higher rate than that in Columbia. There were no crop species main or interaction effects on *H. glycines* infectivity; however, there were crop species × location ($P < 0.05$) and crop species × location × year ($P < 0.01$) interaction effects on *H. glycines* viability.

Initial populations of *H. glycines* were much higher in Baring than in Columbia (Table 2). Mean *H. glycines* Pi in Columbia in 1989 and 1990 were 1,370 and 143 eggs/100 cm^3 soil, respectively, and 23,493 and 11,341 eggs/100 cm^3 soil, respectively, in Baring. In 1989 at

Table 1. Analysis of variance for reproduction (Rf), infectivity, and viability of *Heterodera glycines* in seven crops and fallow in two Missouri locations.[a]

	Rf[b]		Infectivity[c]		Viability[d]	
Source[e]	df	Mean square	df	Mean square	df	Mean square
Year	1	2.63**[f]	1	0.01	1	0.01
Location	1	1.19	1	0.07*	1	0.02
Location × year	1	0.64	1	0.02	1	0.10
Rep (location × year)	12	0.35	12	0.01	12	0.02
Crop[g]	7	2.71****	7	0.01	7	0.05
Crop × year	6	0.87*	6	0.01	6	0.03
Crop × location	6	1.38**	7	0.01	6	0.06*
Crop × location × year	4	0.27	4	0.01	6	0.17**
Coefficient of variation		1386.16		17.23		7.84
r^2		0.66		0.51		0.48

[a] All data were transformed to log 10 (x + 1) values before analyses.
[b] Rf = (Pf + 1)/(Pi + 1) where Pf is the number of eggs per 100 cm^3 of soil at harvest, and Pi is the number of eggs per 100 cm^3 of soil at planting.
[c] Infectivity is the number of second-stage juveniles (J2) per cm of root of the cultivar Essex 10 days following infestation with 1,000 eggs.
[d] Viability is the percentage of cysts produced 32 days following infestation of the cultivar Essex with 1,000 eggs.
[e] Sources of variance.
[f] *$P < 0.05$, **$P < 0.01$, ****$P < 0.0001$.
[g] Crop species or fallow.

TABLE 2. *Heterodera glycines* initial population (Pi), reproduction (Rf), and viability in seven crops and fallow in two Missouri locations.[a]

		Columbia			Baring		
Year	Crop	Pi[b]	Rf[c]	Viability[d]	Pi	Rf	Viability
1989	Soybean	730 a	25.76 a	9.80 bc	22,454 a	1.37 a	27.00 a
	Oat	1,721 a	3.70 ab	15.30 ab	25,860 a	0.64 b	11.18 b
	Canola	1,180 a	1.74 ab	13.22 abc	19,620 a	. . .[e]	. . .
	Sesame	573 a	1.45 b	16.68 a	25,680 a	. . .	. . .
	Corn	880 a	1.39 ab	7.95 ab	21,520 a	1.33 ab	14.70 ab
	Sorghum	620 a	0.76 b	13.80 abc	18,728 a	0.76 ab	10.73 b
	Red clover	1,210 a	0.62 b	10.45 abc	31,044 a	. . .	. . .
	Fallow	4,050 a	0.25 b	15.30 ab	23,040 a	0.89 ab	12.50 b
1990	Soybean	98 ab	136.50 a	27.00 a	8,249 ab	6.55 a	11.28 a
	Oat	493 a	7.71 bc	16.25 ab	16,240 a	0.72 b	12.03 a
	Canola	229 a	6.66 bcd	12.03 b	17,640 ab	0.60 b	13.63 a
	Sesame	. . .	. . .	. . .	. . .	. . .	. . .
	Corn	75 ab	6.02 bc	10.18 b	4,984 b	0.59 b	15.50 a
	Sorghum	10 b	4.28 cd	14.53 b	20,880 a	0.38 b	20.98 a
	Red clover	22 ab	26.45	12.45 b	4,256 b	7.44 a	13.70 a
	Fallow	73 ab	0.28 d	13.65 d	7,140 ab	1.21 ab	10.68 a

[a] All data were transformed to log 10 (x + 1) values before analyses. Means of nontransformed data are presented for clarity. Means separation was performed with the means (MEANS) option of the general linear models procedure of SAS and are across four reps. Means followed by the same letter within year and location are not different ($P = 0.05$) according to the Waller-Duncan k-ratio *t*-test.
[b] Pi = number of eggs per 100 cm^3 soil at planting.
Rf = (Pf + 1)/(Pi + 1), where Pf is the number of eggs per 100 cm^3 at harvest.
[d] Viability is the percentage of cysts produced 32 days following infestation of the cultivar Essex with 1,000 eggs.
[e] No data.

both locations and Columbia in 1990, nematode reproduction was greater in soybean than all other crops or fallow, although not always significantly higher. Reproduction rates on soybean and red clover did not differ in Baring in 1990. Increases in nematode numbers were observed on several nonhost crops in Columbia, particularly oat, canola, corn, and sorghum. Crop species effects on viability were often inconsistent across locations and years. In Columbia, nematode viability was least in samples from corn during both years, but did not differ from viability in samples from soybean, canola, red clover, and sorghum in 1989. In Baring, viability was greatest on soybean in 1989 but did not differ from that on corn, and there were no differences between crops in 1990 in that location.

During the second year of the experiment, soybean cultivar was the only factor that affected *H. glycines* infectivity (Table 3). *Heterodera glycines* mean infectivity on

TABLE 3. Analysis of variance for *Heterodera glycines* infectivity and viability and soybean yield in a resistant and a susceptible soybean cultivar following crops and fallow in two Missouri locations.[a]

	Infectivity[b]		Viability[c]		Yield[d]	
Source[e]	df	Mean square	df	Mean square	df	Mean square
Location	1	<0.01	1	0.02	1	10431.44****[f]
Year	1	<0.01	1	<0.01	1	882.04****
Crop 1[g]	7	<0.01	7	0.04	7	360.04****
Location × crop 1	4	<0.01	5	0.04	4	82.00
Year × crop 1	6	<0.01	6	0.05	6	657.95****
Cultivar[h]	1	0.04*	1	<0.01	1	5428.53****
Location × cultivar	1	<0.01	1	<0.01	1	166.21*
Year × cultivar	1	<0.01	1	<0.01	1	75.64
Crop 1 × cultivar	7	0.02	7	0.04	7	38.61
Location × crop 1 × cultivar	4	<0.01	5	0.07	4	4.06
Year × crop 1 × cultivar	6	<0.01	6	0.04	6	59.86
Rep (location × year)	9	<0.01	9	0.03	9	153.40***
Coefficient of variation	21.27	8.23	12.86			
r^2	0.31	0.30	0.87			

[a] All nematode data were transformed to log 10 (x + 1) values before analyses.
[b] Infectivity is the number of second-stage juveniles (J2) per cm of root of the cultivar Essex 10 days following infestation with 1,000 eggs.
[c] Viability is the percentage of cysts produced 32 days following infestation of the cultivar Essex with 1,000 eggs.
[d] mg/ha.
[e] Sources of variance.
[f] $*P < 0.05$, $***P < 0.001$, $****P < 0.0001$.
[g] Crop species or fallow treatment planted the first year.
[h] Soybean cultivar planted the second year.

the cultivar Linford was 2.4 J2/cm root, and 2.3 J2/cm root on Williams 82 (data not shown). There were no effects on viability due to year, location, rotation crop, or soybean cultivar. However, several factors affected yield, particularly the soybean cultivar × location interaction and the year × crop species interaction. Variability in the infectivity, viability, and yield data was low (CV = 21.3%, 8.2%, and 12.9%, respectively).

Soybean yield in Columbia was higher than in Baring (Table 4), particularly for the resistant soybean cultivar Linford. In Columbia, the yield of both cultivars was less when following soybean. Under very high nematode pressure in Baring, the highest soybean yields were obtained in both cultivars following corn and sorghum but were not different from soybean yields following oat, soybean, and fallow.

TABLE 4. Soybean yield in a *Heterodera glycines*-resistant (Linford) and -susceptible (Williams 82) soybean cultivar following seven crops and fallow in two Missouri locations.[ab]

			Soybean yield	
Years	Cultivar[c]	Crop 1[d]	Columbia	Baring
1989–90	Wms 82	Soybean	1.41 b	0.73 ab
		Oat	1.70 ab	0.77 ab
		Canola	1.76 ab	. . .[e]
		Sesame	1.62 ab	. . .
		Corn	1.63 ab	0.93 a
		Sorghum	1.66 ab	0.86 ab
		Red clover	1.83 a	. . .
		Fallow	1.66 ab	0.69 b
	Linford	Soybean	1.71 b	1.25 bc
		Oat	2.09 a	1.25 bc
		Canola	2.07 a	. . .
		Sesame	1.98 a	. . .
		Corn	1.92 ab	1.38 ab
		Sorghum	1.97 a	1.43 a
		Red clover	2.03 a	. . .
		Fallow	1.89 ab	1.13 c
1990–91	Wms 82	Soybean	1.46 b	. . .
		Oat	0.95 c	. . .
		Canola	1.36 b	. . .
		Sesame	. . .	. . .
		Corn	1.98 a	. . .
		Sorghum	1.36 b	. . .
		Red clover	1.03 c	. . .
		Fallow	1.90 a	. . .
	Linford	Soybean	1.74 a	. . .
		Oat	1.22 b	. . .
		Canola	2.00 a	. . .
		Sesame	. . .	. . .
		Corn	2.12 a	. . .
		Sorghum	1.78 a	. . .
		Red clover	1.76 a	. . .
		Fallow	2.20 a	. . .

[a] All nematode data were transformed to log 10 (x + 1) values before analyses. Means of non-transformed data are presented for clarity. Means separation was performed with the means option of the general linear models procedure of SAS and are across 4 reps. Means followed by the same letter within year, location, and cultivar are not different ($P = 0.05$) according to the Waller-Duncan k-ratio *t*-test.
[b] Soybean yield in mg/ha.
[c] Soybean cultivar planted during the second year of the study.
[d] Crop species planted during the first year of the study.
[e] No data.

Overwintering experiment: The number of *H. glycines* eggs extracted from soil was affected ($P < 0.05$) by year, month, depth, cultivar, and interactions year × depth, month × depth, year × month × depth, and year × cultivar (Table 5). Viability of these eggs was affected by year, month, month × depth, soybean cultivar, and year × cultivar. Variability was very low within *H. glycines* population levels and egg viability data (CV = 5.8% and 9.8%, respectively).

There was no consistent trend in the viability of *H. glycines* eggs at either 0- to 10-cm or 10- to 20-cm soil depths (Table 6). Viability of eggs from the 0- to 10-cm depth was highest in April but did not differ from that of eggs collected in December or March. Viability of eggs collected from 10 to 20 cm was greatest in September, October, and April but did not differ from that of the winter months.

DISCUSSION

In these experiments, the terms infectivity and viability were used to describe the success of *H. glycines* to infect and mature, respectively, on a susceptible soybean cultivar. Infectivity is expressed as the number of J2 per cm root 10 days following infestation with 1,000 eggs. Viability is expressed as the percentage of females that developed to maturity 32 days following infestation with 1,000 eggs. Therefore, both infectivity and viability calculations are dependent upon the number of J2 that immediately hatch and infect. Eggs that do not hatch are not necessarily nonviable because

TABLE 5. Analysis of variance for *Heterodera glycines* eggs per 100 cm^3 of soil and viability at two depths monthly following soybean harvest.[a]

Source[d]	df	Eggs[b] Mean square	Viability[c] Mean square
Year	2	7.04****[f]	2.62****
Month[e]	7	0.16**	0.25****
Year × month	6	0.10	0.05
Depth[e]	1	2.17****	0.15
Year × depth	2	1.25****	0.09
Month × depth	7	0.13*	0.13*
Year × month × depth	6	0.14**	0.03
Cultivar	3	2.22****	0.36****
Year × cultivar	2	1.15****	0.29**
Month × cultivar	15	0.06	0.05
Year × month × cultivar	6	0.10	0.06
Depth × cultivar	3	0.01	0.03
Year × depth × cultivar	2	0.05	0.08
Month × depth × cultivar	15	0.03	0.03
Year × month × depth × cultivar	6	0.06	0.05
Rep (year)	9	0.27****	0.03
Coefficient of variation		5.75	9.75
r^2		0.80	0.57

[a] All data were transformed to log 10 (× + 1) values before analyses.
[b] *Heterodera glycines* eggs per 100 cm^3 of soil.
[c] Viability is the percentage of cysts produced 32 days following infestation of the cultivar Essex with 1,000 eggs.
[d] Sources of variance.
[e] 0 to 10 cm and 10 to 20 cm.
[f] $*P < 0.05$, $**P < 0.01$, $****P < 0.0001$.

TABLE 6. Viability of *Heterodera glycines* eggs at two soil depths in the months following soybean harvest.[ab]

	Depth (cm)	
Month	0 to 10	10 to 20
Sep	22.5 bc	25.1 a
Oct	18.5 bc	24.5 ab
Nov	12.8 c	13.6 c
Dec	25.6 ab	17.0 abc
Jan	14.8 bc	17.2 abc
Feb	19.8 bc	18.5 abc
Mar	24.7 ab	14.8 bc
Apr	35.2 a	22.9 abc

[a] All nematode data were transformed to log 10 (x + 1) values before analyses. Means of non-transformed data are presented for clarity. Means separation was performed with the means (MEANS) option of the general linear models (GLM) procedure of SAS. Means followed by the same letter within depth are not different ($P = 0.05$) according to the Waller-Duncan k-ratio *t*-test.

[b] Viability is the percentage of cysts produced 32 days following infestation of the cultivar Essex with 1,000 eggs averaged across all years and cultivars.

hatching may be delayed due to dormancy (Hill and Schmitt, 1989; Yen et al., 1995). In addition, approximately half of the J2 that hatch and infect are destined to be males (Colgrove and Niblack, 2005) and were not included in the calculation of viability. Infectivity and viability were used here to estimate the immediate potential for damage due to *H. glycines* populations. Similar infectivity and viability assays were performed by Sortland and MacDonald (1987) with corn, oat, soybean, and other plant species. Their results confirmed that oat and corn do not support *H. glycines* maturation but did not investigate these crops' effect on the nematode's ability to infect subsequent soybean crops.

The apparent increase of *H. glycines* on nonhost crops in Columbia probably can be attributed to a combination of several factors. Low initial population densities at that location likely resulted in the inflation of reproduction factors. In addition, tillage between the spring and fall sample dates may have caused the redistribution of nematode populations and contributed to the high experimental error. Tillage has been held responsible for the redistribution of *H. glycines* populations and the production of unexpected results in at least one other report (Koenning et al., 1993). The high experimental error for nematode reproduction is also likely responsible for the lack of significant differences for reproduction on several of the crops, particularly corn and soybean in Columbia in 1989, where nematode reproduction was more than 18 times greater on soybean.

Crop did not consistently affect either *H. glycines* viability or infectivity. Specifically, planting a nonhost crop did not consistently reduce surviving *H. glycines* eggs' ability to infect soybean and develop to maturity. Soybean yields were generally higher in both the resistant and susceptible cultivar following fallow or a nonhost than when following soybean, although not usually significantly greater. These results contrast with those of numerous previously mentioned reports. One reason for this inconsistency could be the lower initial *H. glycines* population levels in Columbia. In addition, the high initial population densities in Baring are probably responsible for the reduction in soybean yields in that location and are probably high enough to require 2 or more years of a nonhost crop to adequately reduce nematode population levels. As nonhost crops do not appear to decrease *H. glycines*' ability to infect and develop on subsequent soybean crops, the benefits of rotating with a nonhost are limited to *H. glycines* population reduction and the frequent increase of yields in subsequent soybean crops.

In the overwintering experiment, there was no consistent trend in the recovery of viable eggs during the overwintering months of September to April. Higher viability observed in April was probably due to the end of dormancy induced, in part, by temperature increase. Egg viability during the previous months may have been reduced by the delay in egg hatch that prevented female maturation by the end of 32 days. There was no effect of month on nematode viability at either depth. In northern Missouri, the upper 10 cm of soil alternately freezes and thaws during the winter months. As there was no change in viability of *H. glycines* at either depth across the overwintering months, the freeze and thaw cycles did not appear to have a detrimental effect on the nematode's survival. These results also indicate that samples can be taken at any time of year to collect viable *H. glycines* eggs for reliable estimates of population density or virulence phenotype.

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