

Heterodera glycines Population Dynamics and Relation of Initial Population to Soybean Yield

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ABSTRACT

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Soybean (*Glycine max* 'Forrest') was grown in monoculture and in a 2-, 3-, and 4-yr rotation with corn (*Zea mays*), cotton (*Gossypium hirsutum*), and grain sorghum (*Sorghum bicolor*). The effects of these crops and rotation lengths on soybean cyst nematode (SCN) (*Heterodera glycines*) population dynamics and soybean yield responses were measured. Annual and overwinter decline of cysts and eggs in the absence of soybeans, overwinter decline of eggs, and population increase when soybeans were grown were dependent on the initial population density. Overwinter survival of cysts was density-independent. There were no significant differences among rotational crops in their effects on SCN population dynamics and soybean yield. Two and 3 but not 1 yr in a nonhost crop resulted in significant soybean yield increases over yields obtained from monoculture. SCN population levels were at or near the limits of sampling detection after 3 yr of a nonhost. The Seinhorst equation estimated a tolerance threshold at 3 cysts or 470 eggs per kilogram of soil.

Management of soybean cyst nematode (SCN) (*Heterodera glycines* Ichinohe) populations to minimize damage to soybean (*Glycine max* (L.) Merr.) has returned millions of dollars to growers (2). Resistant cultivars, crop rotations, and nematicides are management options, and biological control offers promise for the future. Of these options, nematicides are used on the fewest hectares because of the expense, erratic results, and unavailability of some effective products after cancellation of registration. Resistant cultivars are grown widely, but they put selection pressure on genetically diverse wild-type SCN populations that can result in SCN phenotypes that complete their life cycle and eventually cause lower yields (10,18). Crop rotation remains a viable management choice on land infested with SCN, but acceptance of

alternative crops usually requires that their profit potential be above the probable return from a soybean crop (4,12).

Information about SCN decline during nonhost periods, the multiplication rate during a host season, and the relationship between the SCN population level and soybean yield are needed to advise growers about suitable rotations. Overwinter survival rate of SCN is important to help adjust advisory recommendations for fall vs. spring sampling times. Several crop rotation studies have been reported, and SCN population dynamics varied among years and geographical regions (3,13,14,16). SCN populations persisted in soil for 4 yr

or longer without a host (3,14). The rate of SCN decline in the midsouthern United States and the effect of nonhost crops and their associated cropping systems on SCN populations have not been reported.

Our objectives were to quantify the effects of rotation length and nonhost field crops on SCN population decline and on soybean yields and to assess soybean damage in relation to an initial population of SCN. The results are specific for prevailing climate and edaphic factors; however, they also increase our knowledge about SCN field population behavior and provide a basis for developing predictive models.

MATERIALS AND METHODS

Soybean cultivar Forrest was grown in monoculture and in a 2-, 3-, or 4-yr rotation with corn (*Zea mays* L.), cotton (*Gossypium hirsutum* L.), and grain sorghum (*Sorghum bicolor* (L.) Moench) (Table 1). Forrest is grown widely in areas suitable to maturity group V and is resistant to wild-type SCN populations also known as race 3 (8). This experiment was begun in 1980 after a soybean crop in 1979, but only data from March 1982 to March 1985 are presented. Temperature and precipitation were measured at a weather station 4 km from the experiment. The soil was a Tiptonville silt loam (Typic Arguidolls) with an alluvial sandy loam

Table 1. Temporal arrangement of rotations in experiment^a

Rotation	1980	1981	1982	1983	1984
Monoculture	SOY	SOY	SOY	SOY	SOY
2-yr Rotation	NH SOY	SOY NH	NH SOY	SOY NH	NH SOY
3-yr Rotation	NH NH SOY	NH SOY NH	SOY NH NH	NH NH SOY	NH SOY NH
4-yr Rotation	NH NH NH SOY	NH NH SOY NH	NH SOY NH NH	SOY NH NH NH	NH NH NH SOY

^aSOY = Forrest soybeans; NH = nonhost (corn, cotton, or grain sorghum).

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overwash; in 1984, the pH was 5.7, organic matter was 1.5%, K averaged 603 kg/ha, and P₂O₅ averaged 133 kg/ha according to Bray's P1 test.

Field plots were four rows wide on 96-cm centers and were bordered by grass strips to isolate treatment effects. Soybeans and rotational crops were planted annually in mid- to late May. Soybean yield data were collected by harvesting a 12.2-m length of the two middle rows. Yields were corrected to 13% moisture content.

A bulk soil sample for SCN assay was composed of 20 soil cores 19 mm in diameter × 15 cm deep taken in the middle two rows. Soil samples were collected in late March or early April before cultivation, in May at planting, and in October or November at harvest (overwinter, planting, and harvest samples, respectively). Bulk samples were thoroughly mixed and 100-g wet weight subsamples were drawn. Three subsamples were taken in 1982 and 1983; four subsamples were taken in 1984 and 1985. Another subsample was air-dried to obtain soil dry weight, and SCN data were adjusted to a soil dry weight basis. Cysts were extracted from subsamples by a semiautomatic elutriator with an extraction efficiency of about 75%. Cysts were counted directly and eggs and juveniles were counted directly from crushed cysts or counted from an aliquant. To minimize error, aliquants were observed until egg and juvenile counts exceeded 50 (9). Eggs and juveniles hereafter are referred to as eggs for simplicity.

A bioassay was performed when mechanical extraction resulted in zero cyst and egg counts. Essex soybeans were grown for 30 days in 300 g of soil in a greenhouse, and roots were assayed for females. Counts were adjusted to an arbitrary one cyst and 50 eggs per 500 g dry weight of soil if the bioassay results were positive.

Agronomic practices common to the area agriculture were followed in growing

these crops and may have had some bearing on the results of this experiment. Corn and grain sorghum were side-dressed annually with 112 kg/ha N and had a preemergence application of atrazine at 2.5 kg a.i./ha. Cotton was side-dressed with 55 kg/ha N and had a preemergence application of fluometuron at 1.1 kg a.i./ha. Soybeans received a preemergence application of alachlor at 3.4 kg a.i./ha and linuron at 0.4 kg a.i./ha in 1982. Only alachlor at 2.2 kg a.i./ha was applied in 1983 and 1984. All crops were fertilized in 1983 with 135 kg/ha K. Five centimeters of water was applied by an overhead system annually in mid- to late July.

Analyses. The experimental design was a randomized complete block with four replicates. Rotations were arranged sequentially so that soybeans could be grown in each year regardless of rotation length (Table 1). Some rotations were identical to one another for varying lengths of time during the experiment. These identities were considered as multiple observations nested within a single rotation sequence.

Differences in SCN populations among nonhosts and lengths of rotation were analyzed after homogenizing the variance with a base 10 logarithmic transformation, log₁₀ (x_i + 1). This transformation decreased the importance of differences among high cyst and egg counts while improving the resolution of differences among low counts.

Changes in SCN population were determined for overwinter, oversummer, and annual periods. The appropriate sampling time was used to calculate initial (P_i) and final populations (P_f). Annual decline of SCN was measured from March, year_i to March, year_{i+1}, and plots with soybeans in year_{i-1} were excluded to avoid sample bias caused by population stratification (7). Natural logs (ln) of nonzero P_f/P_i values were regressed on nonzero ln(P_i) values to determine if population change was density-dependent (5). A sloping line indicates density dependence, and

presence of slope is testable statistically. P_f/P_i values for nonhost periods were constrained to an upper limit of 1.0 to minimize the influence of sampling errors.

Soybean yield data were subjected to an analysis of variance after a square-root transformation. Data from 3 yr were analyzed together, and yields from different nonhost crops and rotation lengths were contrasted.

The relationship between the initial SCN population and soybean yield was determined using the equation: $y = m + (1 - m)z^{P_i - T}$ for P_i > T, and y = 1.0 for P_i < T (15). Relative yield (y) is measured on a 0.0–1.0 scale, m indicates the minimum yield, z is indicative of SCN damage and is less than 1.0, P_i is the base 2 log of the initial population, and T is the tolerance threshold. The overwintered population was chosen as P_i to conform to a scenario where a grower must sample early to have information for making a management decision. A FORTRAN program for finding the least-squares fit to the Seinhorst equation (6) was kindly provided by H. Ferris, University of California-Davis. Curves were fit on the weighted density class averages of cysts per kilogram and eggs per 100 g (6).

RESULTS

Population dynamics. SCN population levels after harvesting a soybean crop show that the population reproduced on Forrest (Table 2). There were few significant differences in SCN population levels on soybeans among rotations within a given year. The population at harvest under monoculture in 1983 was higher than the 4-yr rotations with corn and sorghum and the 3-yr corn rotation. The 4-yr corn and sorghum rotations also had significantly lower harvest cyst numbers in 1984 than did monoculture, but only the corn rotation had significantly fewer eggs.

SCN populations at planting were significantly affected by the rotation length (Table 3). High populations developed in the soybean-cotton rotation during 1982, and there was a significant difference among the nonhost crops in a 2-yr rotation at planting in 1983. Otherwise, the three nonhost crops had identical effects on SCN population survival.

Analyses of density-dependent survival are presented as regression equations in an untransformed format (Table 4). The intercept term indicates survival at P_i = 1, whereas the exponent estimates the rate of survival over time. The overwinter rate of decline for cysts was independent of the original population density, but the overwinter rate of decline of eggs was dependent on their density at harvest in 1982–1983 and 1983–1984 (Table 4). The survival rate of cysts was 59–69% over three winters. The oversummer period

Table 2. *Heterodera glycines* population at soybean harvest as affected by rotation length, crop, and seasonal variability

Rotation	Cysts/100 g soil			Eggs/g soil		
	1982	1983	1984	1982	1983	1984
Continuous soybeans	38 ab ²	14 a	115 a	74 a	12 abc	24 bc
Soybeans after						
1 yr of						
Corn	39 ab	12 ab	241 a	71 a	14 ab	61 a
Cotton	32 ab	19 a	110 ab	53 a	24 a	31 abc
Sorghum	32 ab	9 abc	98 ab	41 a	10 abc	23 bcd
2 yr of						
Corn	29 b	5 bc	94 ab	65 a	6 bc	36 abc
Cotton	51 a	10 ab	145 a	94 a	9 abc	38 abc
Sorghum	31 ab	8 abc	108 ab	69 a	8 bc	34 abc
3 yr of						
Corn	...	3 c	20 c	...	5 c	10 d
Cotton	...	8 abc	117 a	...	9 abc	46 ab
Sorghum	...	5 bc	41 bc	...	5 c	20 cd

² Values in a column followed by the same letter are not significantly different at P < 0.05 according to an LSD mean separation test.

showed a density-dependent decline in the absence of a host for both cysts and eggs in 1982 and 1984. The rate of decline was greater in the summer than in the winter. The annual rates of decline under a nonhost showed dependence on the initial density in 1982–1983 and 1983–1984 but not in 1984–1985.

Population increase from planting to harvesting a soybean crop was dependent on density over all 3 yr (Table 5). Population equilibria occurred outside the range of the data and were calculated as the point on the regression line where $P_t/P_i = 1$. The maximum seasonal multiplication rate was difficult to derive because it occurred at a P_i below the threshold of sampling detection. A reasonable value for maximal multiplication is the intercept term where $P_i = 1$.

Fifty-seven soil samples were bioassayed over the 3-yr period. Twelve of the 57 samples were positive for SCN females. SCN always was detected in the soil sample after harvesting a soybean crop, even if the population was below the level of detection at planting.

Changes in SCN population levels were affected by environmental conditions prevailing during this field experiment. Midseason to late-season rainfall typically is sporadic in southeastern Missouri, and 1983 was the driest of the 3 yr included in this experiment. Total precipitation during July and August was about 116, 30, and 96 mm in 1982, 1983, and 1984, respectively. Apparently, late-season soil moisture is crucial to significant SCN population increase, because populations at harvest in 1983 were lower than harvest population in 1982 or 1984. A cursory examination of winter temperatures over 3 yr revealed no apparent relationship between severity of weather and population decline.

Soybean yield. A nonhost for 1 yr resulted in a nonsignificant yield improvement for the soybean crop that followed (Table 6). Yields after 2 yr of a nonhost were significantly better than monoculture and soybeans after 1 yr of a nonhost. Yields continued to improve significantly when soybeans were preceded by 3 yr of a nonhost. Yields after a 3-yr nonhost period were not represented in 1982 because the experiment was begun in 1980. There were no significant differences in the effects of any of the three nonhost crops on soybean yields.

A relationship between SCN P_i and yield was established using the Seinhorst model in 1982 and 1984 but not in 1983. A 10% yield reduction from a maximum yield of 255 g/m² occurred at 33 cysts per kilogram or 305 eggs per 100 g for 1982 and 1984 combined (Fig. 1). Separate tolerance estimates for 1982 and 1984 were zero and three cysts per kilogram and 46 and 47 eggs per 100 g.

DISCUSSION

Yearly fluctuations were apparent in SCN population dynamics, presumably

caused largely by variable weather conditions during the growing seasons. The effect of SCN on 1983 yields probably was overshadowed by the late-season soil moisture deficit. Seasonal variability hinders the predictive power of a model of SCN population behavior and associated yield for the midsouthern region. A program that models population

dynamics and yields in a coarse manner will be supplied on request for validation studies.

SCN populations decline rapidly in the absence of a host, but prolonged survival of the remnant prevents easy eradication. Two years of a nonhost is sufficient to control damage to soybeans in the mid-South, a finding that agrees with current

Table 3. Population levels of *Heterodera glycines* at soybean planting as influenced by rotation length, nonhost crops, and seasonal effects

Rotation	Cysts/100 g soil			Eggs/g soil		
	1982	1983	1984	1982	1983	1984
Continuous soybeans	10 a ²	20 a	10 a	8 a	14 a	4 a
Soybeans, then						
1 yr of						
Corn	2 bc	5 c	10 a	2 bc	4 c	5 a
Cotton	3 b	8 b	10 a	2 b	7 b	7 a
Sorghum	2 bcd	4 c	8 a	2 b	3 c	4 ab
2 yr of						
Corn	1 d	2 d	3 bc	1 c	2 d	2 bc
Cotton	1 cd	2 de	6 ab	1 bc	2 d	4 ab
Sorghum	2 bcd	2 de	3 bc	2 bc	2 d	2 c
3 yr of						
Corn	...	1 e	2 c	...	1 d	1 c
Cotton	...	1 e	1 c	...	1 d	1 c
Sorghum	...	1 e	2 c	...	1 d	1 c

² Values in a column followed by the same letter are not significantly different at $P < 0.05$ according to an LSD mean separation test.

Table 4. Decline of *Heterodera glycines* cysts and eggs in soil over winter, over summer, and annually in the regression model $P_t/P_i = b_0 P_i^{b_1}$

	Year	b_0	b_1	P^a	r^2
		Over winter			
Cysts/100 g	1982–1983	0.69	0.024	0.44	0.01
	1983–1984	0.69	-0.046	0.23	0.02
	1984–1985	0.59	-0.035	0.25	0.01
Eggs/g	1982–1983	0.57	-0.107	0.005	0.08
	1983–1984	0.68	-0.086	0.03	0.04
	1984–1985	0.63	-0.015	0.65	0.01
		Over summer			
Cysts/100 g	1982	0.68	-0.218	<0.001	0.37
	1983	0.47	-0.115	0.06	0.05
	1984	0.48	-0.242	<0.001	0.20
Eggs/g	1982	0.67	-0.115	0.05	0.07
	1983	0.53	-0.092	0.32	0.02
	1984	0.29	-0.292	<0.001	0.19
		Annual			
Cysts/100 g	1982–1983	0.74	-0.475	0.001	0.44
	1983–1984	0.38	-0.285	0.004	0.27
	1984–1985	0.31	-0.206	0.24	0.05
Eggs/g	1982–1983	0.56	-0.624	<0.001	0.52
	1983–1984	0.34	-0.345	0.003	0.29
	1984–1985	0.21	-0.273	0.097	0.09

^a A low probability (P) that $b_1 = 0$ indicates density-dependent survivorship.

Table 5. Increase of *Heterodera glycines* cysts and eggs in soil from planting to harvest of Forrest soybeans in the regression model $P_t/P_i = b_0 P_i^{b_1}$

	Year	b_0^x	b_1	P^y	r^2	E^z
Cysts/100 g	1982	33.8	-0.932	<0.001	0.90	44
	1983	6.2	-0.530	<0.001	0.32	31
	1984	55.2	-0.807	<0.001	0.64	144
Eggs/g	1982	62.8	-0.919	<0.001	0.92	90
	1983	8.4	-0.564	<0.001	0.38	43
	1984	35.5	-0.924	<0.001	0.77	48

^x Seasonal multiplication rate when $P_i = 1$.

^y A low probability (P) that $b_1 = 0$ indicates a density-dependent rate of increase.

^z Equilibrium point where $P_t = P_i$.

Table 6. Soybean yields from land infested with *Heterodera glycines* as affected by rotation length and nonhost crops

Rotation	Soybean yield (g/m ²)		
	1982	1983	1984
Monoculture	265.5 bc ^z	194.3 efg	159.0 h
1 yr Corn	265.0 bc	210.4 de	171.0 gh
1 yr Cotton	259.9 bc	198.1 defg	169.7 gh
1 yr Sorghum	289.3 ab	192.8 efg	170.8 gh
2 yr Corn	307.0 a	170.6 gh	186.6 efgh
2 yr Cotton	306.2 a	177.2 efgh	168.3 gh
2 yr Sorghum	315.3 a	174.1 fgh	201.2 defg
3 yr Corn	...	207.7 def	195.2 efg
3 yr Cotton	...	232.7 cd	191.1 efgh
3 yr Sorghum	...	211.0 de	213.3 de
Contrasts		P < 0.01	
Monoculture vs. 1 yr nonhost		ns	
Monoculture vs. 2 yr nonhost		**	
Monoculture vs. 3 yr nonhost		**	
Corn vs. cotton		ns	
Corn vs. sorghum		ns	
Cotton vs. sorghum		ns	

^zValues followed by the same letter are not significantly different at $P < 0.05$ according to LSD mean separation test on square-root transformation.

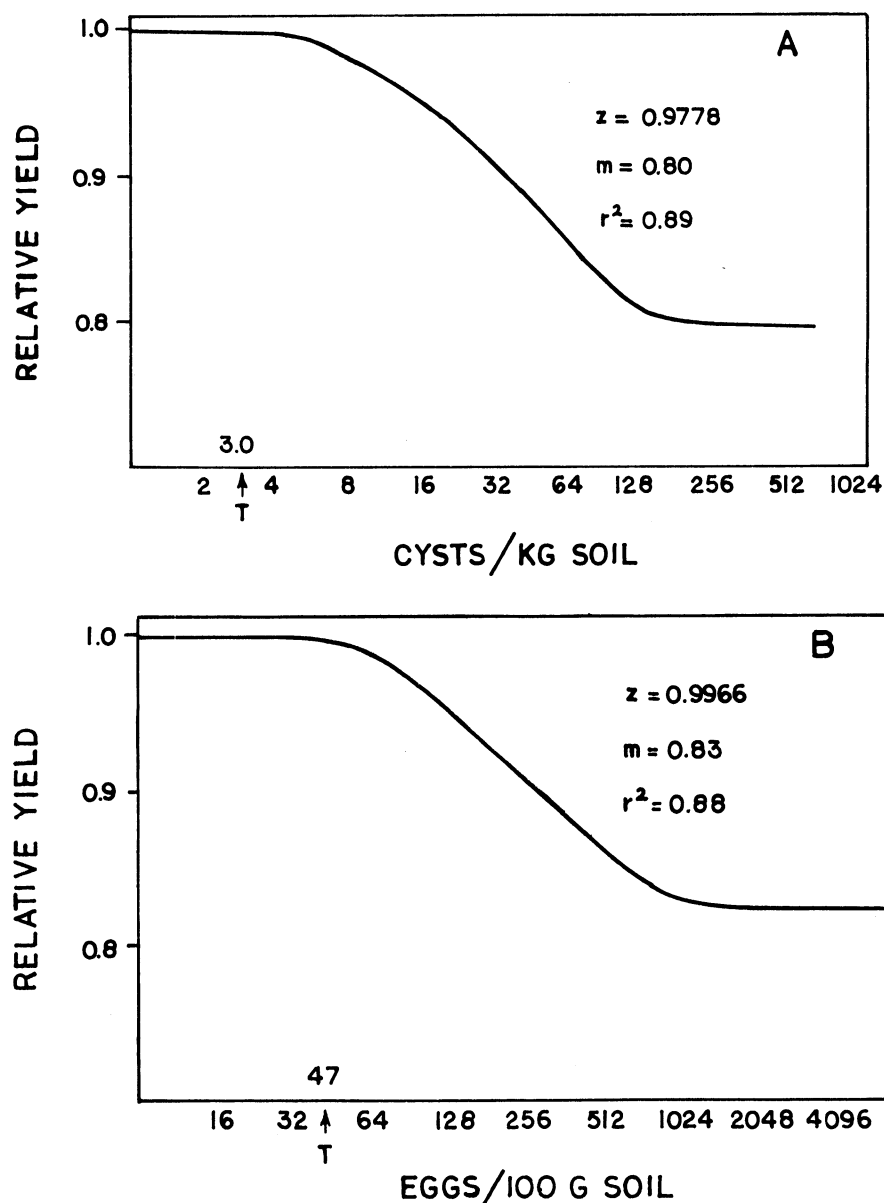


Fig. 1. Fit of the Seinhorst model to the relationship between soybean yield in 1982 and 1984 and *Heterodera glycines* (A) cysts or (B) eggs collected from soil in the spring before cultivation.

recommendations (17). Although a rotation where 2 yr of soybeans follow a nonhost was not included as a treatment, SCN populations at soybean harvest after a nonhost were usually as high as or higher than those from monoculture. Therefore, 4-yr or shorter rotations cannot be expected to reliably control the SCN population beyond the first crop of soybeans. Survival of the nematode population largely was unaffected by nonhost crop and associated differences in cultural practices.

Density-dependent population changes over most time periods imply that percent decrease/increase concepts are inadequate descriptors and that this SCN population conformed to a negative exponential model of population dynamics (5). The one consistent exception to the density-dependence model was overwinter decline of cysts. Cyst survival in undisturbed soil ranged from 59 to 69%, precise enough for advisory purposes. This compares to a 74% overwinter decline in cysts in a cultivated soil in North Carolina (1). Density-dependent survivorship in other time periods may have been influenced by the age structure of the population.

High rates of decline of the SCN population during the summer indicate temperature-dependent mortality. Activities of nematodes and many of their enemies are slowed in the winter in the mid-South. Numerous species of parasitic fungi were found within cysts collected from an adjoining field (11). Overwinter decline of eggs probably overestimates mortality, because only eggs within cysts were counted. Before the overwintering sampling date, some of the eggs probably had hatched and juveniles had left cysts as the soil warmed. Juveniles of an Arkansas population were recovered from a Baermann funnel in large numbers when soil samples were brought indoors in January (16).

Some results from the analysis of SCN population increase should be interpreted cautiously. Population equilibria were estimated by extrapolating regression lines and occurred outside the range of the data. Maximum seasonal multiplication rates occur at low population levels where there is much uncertainty because of sampling error and were estimated from the intercept of the regression equations. P_f samples were from the plant row and were probably higher than the whole-plot P_f mean because of population stratification (7). Differences in SCN reproduction among soybean cultivars are likely.

There was little difference between using overwintered cysts or eggs as P_f for the Seinhorst models. The coefficients of determination were 0.89 and 0.88 for cysts and eggs, respectively (Fig. 1). There seemed to be no advantage of one expression over the other in several other results as well (Tables 2, 3, and 5). The

minimum yield of about 0.80 may have been due to good soil fertility, genes for resistance in the cultivar, and/or a relatively low SCN P.

The choice of a nonhost was inconsequential in terms of soybean yields, but other managerial decisions certainly will decide the best alternative for a particular farm management situation. An economic analysis is dependent on the prevailing economic climate and will not be discussed here. Rather, specific recommendations based on a linear programming model will be provided to growers in Missouri (C. Headley, *personal communication*).

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