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Population Dynamics of *Heterodera glycines* Life Stages on Soybean[1]

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Abstract: Population fluctuations of *Heterodera glycines* differ in fields with high and low initial population densities. In a field with low initial numbers of nematodes, the numbers of cysts and eggs in soil remained low through 100 days from planting then increased during the remainder of the growing season. In a field with high initial nematode populations, numbers increased at 30 days, decreased to low numbers at 100 days, and then resurged to maximum populations at harvest. Numbers of juveniles were greatest at 100 days in the low initial population density field and at planting in the high initial population density field. The initial numbers of eggs in the soil gave the best correlation to soil and root nematode populations 15 and 30 days later. Juveniles in the soil at planting gave the largest correlation coefficients with nematode populations in the roots at 15 days in the field with the low initial population density. Eggs and juveniles in the soil at harvest were poorly related to numbers that overwintered.

Key words: Glycine max, soybean cyst nematode, ecology, population fluctuations.

The soybean cyst nematode (*Heterodera glycines* Ichinohe) is one of the most important pests on soybean in the United States. The pest is highly virulent and is capable of causing total crop loss in soybean (*Glycine max* [L.] Merr.) fields.

The response of annual crops is generally inversely related to the population density at planting (2,6). Soybean yields were negatively correlated with soil egg numbers in the fall and soil juvenile numbers at planting (3). Diagnostic laboratories use different nematode life stage parameters to predict damage. Some laboratories use numbers of juveniles, and others use numbers of cysts; few use soil egg population densities. Establishment of a data base on the relationship of initial numbers of juveniles, cysts, and eggs of *H. glycines* in soil and roots to soybean growth and yield, as well as population changes over time, is essential for more precise prediction of crop loss.

Plant damage caused by the initial nematode population may influence the population dynamics of *H. glycines.* Factors governing changes in nematode populations, such as environment (8), host suitability (7,9,10), and inoculum density (D. P. Schmitt, unpubl.), are basic to understanding nematode distribution and plant disease (8).

Understanding the factors influencing nematode population changes during the growing season should be useful in predicting the development of damaging populations. Numbers of *H. glycines* juveniles in soil fluctuate erratically during the

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growing season but tend to increase over time with a decrease in the fall (11). The increase in numbers is enhanced by certain pesticides (11). Numbers of eggs generally increase during the growing season, with some fluctuations in mid-season, and increase sharply in the fall, especially in soil treated with certain pesticides (11).

The objective of this research was to characterize the population dynamics of life stages of *H. glycines* on soybean roots and rhizosphere.

Materials and Methods

Experiments were conducted at two North Carolina loamy sand sites naturally infested with *H. glycines*; one near Smithfield (3% clay, 81% sand, 16% silt) and the other at Central Crops Research Station (CCRS) near Clayton (6% clay, 85% sand, 9% silt). Plots were randomly chosen, 21 at Smithfield and 24 at CCRS. Plots at each site were six rows wide (92-cm row spacing) and 7 m long. Soil and plant samples were collected from the center four rows. Soil texture was determined using the Bouyoucos method (4).

Glycine max 'Coker 156' (susceptible to *H. glycines*) was planted at Smithfield on 9 May 1980 and at CCRS on 14 May 1980. Both fields received 350 kg/ha of 4-12-24 fertilizer. Alachlor (2.24 kg a.i./ha) was applied broadcast within 24 hours after planting.

Plots were sampled for nematodes and plant biomass at 15, 30, 50, 100 (R3 stage of soybean growth), 160 (R7 stage), and 215 (harvest) days after planting. Nematode abundance was also determined at planting. At CCRS, the plots were maintained for an additional season and soil sampled 65 and 22 days before planting (22 May) and 24, 52, 85, 118, and 164 days (harvest) after planting.

A composite soil sample consisting of 20 cores, 2.5 cm d and 15–20 cm deep, was collected from the center four rows of each plot in both years. Four additional soil cores, 7.6 cm d × 15–20 cm deep (ca. 650 cm^3), were collected in 1980 from each plot with a bucket auger. Roots from the four bucket auger cores were sieved from the soil for biomass determination. The shoots from these four areas within a plot were used for biomass determination. Roots from the bucket auger samples were chopped into 2-cm lengths, and 0.25 g were randomly selected and stained with lactophenol–acid fuchsin (5). Shoot and root weights were determined at all sampling dates. Fresh plant weights were obtained by weighing plant tissues on the day of sampling. Dry shoot and root weights were determined after exposure to 105 C for 24 hours. Seeds were harvested from the center four rows each year.

Soil samples (500 cm^3) were processed by a combination of elutriation and centrifugation (1). Cysts collected from a 250-μm-pore sieve were counted, then crushed with a 40-ml glass tissue grinder to release the eggs. The eggs were stained with lactophenol–acid fuchsin and counted. Each 0.25 g of stained roots were blended in water for 30 seconds. The suspension was sieved through nested sieves with 355- and 26-μm openings. The nematodes were placed in a mixture of 75% water and 25% glycerin, to prevent leaching of acid fuchsin from the nematodes tissues, and counted. The life stages quantified were eggs, second-stage juveniles (J2), third- and fourth-stage juveniles (J3–4), adult males (M), and adult female cysts (F).

Data were subjected to regression analysis. A standard deviation was determined for each sampling date.

Results

Population dynamics: The initial population densities of cysts, eggs, and J2s of *Heterodera glycines* in the soil were less ($P = 0.01$) at the Smithfield site (12, 402, and 35/500 cm^3 soil, respectively) than at CCRS (87, 6,545, and 546) (Fig. 1). Numbers of the various life stages were similar in the two sites by the end of the season.

There was a trend toward similar population changes for cysts, eggs, and juveniles in the soil at both sites (Fig. 1). Numbers of cysts and eggs peaked at 30 days at CCRS but not at Smithfield. Soil and root juvenile numbers peaked at 100 days. Cysts and eggs increased at each sampling period after 100 days, with maximum densities attained at harvest at both sites.

Numbers of juveniles in the soil at Smithfield remained unchanged for the first 30 days, after which they increased to the maximum number at 100 days. There was a marked decrease after 100 days and a slight increase in numbers between 160

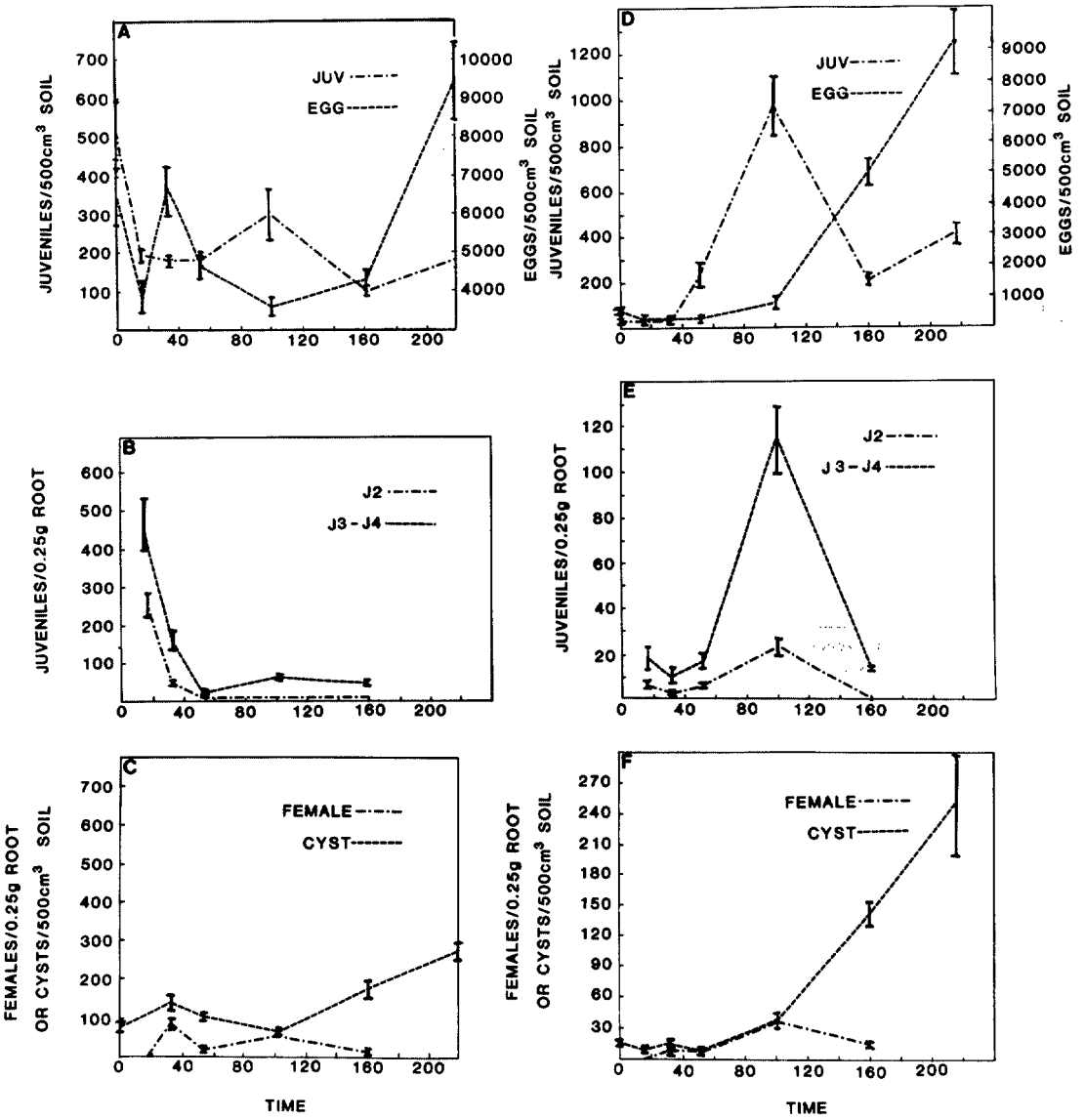

FIG. 1. Population fluctuations of *Heterodera glycines* cysts, eggs, and juveniles in soil or roots in 1980. A–C) At the Central Crops Research Station (CCRS), Clayton, North Carolina. D–F) On a private farm at Smithfield, North Carolina. Bars represent standard deviation. Time refers to days after planting on 9 May 1980 at Smithfield and 14 May 1980 at CCRS.

days and harvest. At CCRS, juvenile populations fluctuated throughout the entire season.

The configurations of early season J2 and J3–4 populations in roots were similar to the juveniles in soil at each site (Fig. 1A, B, D, E). Numbers of J2 and J3–4 at Smithfield increased to a maximum level at 100 days (21 Aug), decreasing sharply at 160 days (20 Oct) (Fig. 1E). The abundance of J2 and J3–4 at CCRS was greatest at 15 days (29 May), with a decrease in numbers by 50 days (5 Jul), after which populations stabilized at low levels through 160 days (25 Oct) (Fig. 1B).

Maximum numbers of adult females in the roots at Smithfield were found at 100 days (21 Aug) (Fig. 1F). At CCRS, two peaks occurred, one at 30 days (15 Jun) and another at 100 days (26 Aug) (Fig. 1C).

At CCRS, the numbers of cysts decreased by 74%, eggs by 73%, and juveniles by 62% between harvest (2 Dec 1980) and planting (22 May 1981). The numbers of

TABLE 1. Correlation coefficients of populations of *Heterodera glycines* at 0, 15, and 30 days after planting at Smithfield, North Carolina, in 1980.

Life stage	P_1P_{15}	P_1P_{30}	$P_{15}P_{15}$	$P_{30}P_{30}$
Cysts-soil vs. cysts-soil	0.63	0.54		
Cysts-soil vs. eggs	0.58	0.43	0.81	0.76
Cysts-soil vs. J2-soil	0.48	0.62	0.64	0.90
Cysts-soil vs. J2-roots	n.s.	n.s.	n.s.	n.s.
Cysts-soil vs. J3–4-roots	0.43	n.s.	n.s.	n.s.
Cysts-soil vs. cysts-roots	0.58	n.s.	n.s.	0.58
Eggs vs. cysts-soil	n.s.	0.68		
Eggs vs. eggs	0.55	0.51		
Eggs vs. J2-soil	0.58	0.73	0.65	0.63
Eggs vs. J2-roots	n.s.	0.45	n.s.	n.s.
Eggs vs. J3–4-roots	0.50	0.45	n.s.	n.s.
Eggs vs. cysts-roots	0.47	0.55	n.s.	n.s.
J2-soil vs. cysts-soil	n.s.	0.76		
J2-soil vs. eggs	n.s.	0.84		
J2-soil vs. J2-soil	0.53	0.65		
J2-soil vs. J2-roots	0.76	n.s.	0.54	n.s.
J2-soil vs. J3–4-roots	0.84	n.s.	0.63	n.s.
J2-soil vs. cysts-roots	0.41	0.47	n.s.	0.42
J2-roots vs. J3–4-roots			0.85	0.93
J2-roots vs. cysts-roots			n.s.	0.77
J3–4-roots vs. cysts-roots			n.s.	0.81

P_1P_{15} = nematodes at planting correlated with nematodes at 15 days; P_1P_{30} = nematodes at planting correlated with nematodes at 30 days; $P_{15}P_{15}$ = numbers of one life stage correlated with another life stage at 15 days; $P_{30}P_{30}$ = numbers of one life stage correlated with another life stage at 30 days. Correlation coefficients of 0.42–0.48 are significant at $P = 0.05$, and those greater than 0.48 are significant at $P = 0.01$.

cysts and eggs increased from 70 and 3,542 to 179 and 4,526 during the 24 days after planting in 1981, then decreased to their lowest density of 33 and 1,850 by 85 days (15 Aug 1981). The highest levels of 329 cysts and 27,784 eggs were attained at harvest (2 Nov 1981). Juveniles were fewest (n = 27) in the soil in 1981 on 15 June (24 days), peaked (n = 704) on 15 August (85 days), and decreased to 262–384/500 cm^3 soil from 17 September (118 days) until harvest (2 Nov; 164 days).

The correlation coefficients of initial population densities in soil at Smithfield were cysts versus eggs—$r = 0.66^{**}$, cysts versus juveniles—$r = 0.54^{**}$, and eggs versus juveniles—$r = 0.75^{**}$. In addition, at 15 and 30 days, numbers of cysts, eggs, and juveniles recovered from soil were also positively correlated with each other (Table 1). Most of the significant regressions occurred with initial numbers versus those at 15 and 30 days, eggs being the most significant ($P = 0.05$).

At Smithfield, numbers of cysts in soil were not correlated with numbers of nematodes in roots at any time. Egg population densities in the soil at 15 and 30 days were not correlated with root nematode population densities of the same date, but initial numbers of eggs were correlated with root population densities at 15 and 30 days. Initial numbers of juveniles in the soil correlated best with various life stages in roots at 15 and 30 days.

The initial soil population densities of cysts and eggs were positively correlated ($r = 0.89^{**}$) at CCRS. Cyst populations at 15 and 30 days were also correlated with numbers of eggs at the same date (Table 2). Initial cyst population in the soil was positively correlated ($r = 0.50^{*}$) with J2 population in roots at 15 days. The greatest number of correlations occurred at 15 and 30 days (Table 2).

Juvenile soil populations at harvest in 1980 were not correlated ($r = -0.02$) with numbers of juveniles in soil at planting in 1981. The relationship of cyst and egg numbers at harvest in 1980 to numbers of juveniles and eggs at planting in 1981 were poor (1980 cysts vs. 1981 juveniles: $r = 0.38$, $P = 0.11$; 1980 cysts vs. 1981 eggs: $r = 0.36$, $P = 0.12$; 1980 eggs vs. 1981 juveniles: $r = 0.36$, $P = 0.13$).

Relationship of numbers of nematodes to plant biomass: Numbers of nematodes early in the season versus plant biomass were neg-

TABLE 2. Correlation coefficients of populations of *Heterodera glycines* at Central Crops Research Station, Clayton, North Carolina, in 1980.

Life stage	$P_{15}P_{15}$	$P_{30}P_{30}$
Cysts-soil vs. eggs	0.52	0.54
Cysts-soil vs. J2-soil	0.56	n.s.
Eggs vs. males-roots	0.46	n.s.
J2-roots vs. J3–4-roots	−0.46	n.s.
J3–4-roots vs. cysts-roots	n.s.	0.83
J3–4-roots vs. males-roots	0.88	0.73
Cysts-roots vs. males-roots	n.s.	0.81

$P_{15}P_{15}$ = numbers of one life stage correlated with another life stage at 15 days; $P_{30}P_{30}$ = numbers of one life stage correlated with another life stage at 30 days. Correlation coefficients of 0.42–0.48 are significant at $P = 0.05$, and those greater than 0.48 are significant at $P = 0.01$.

atively correlated (mostly nonsignificant), but this trend was reversed late in the season. Nematode data did not correlate significantly with yield in 1980 because of drought during the summer. In 1981, yield (1,900–5,300 g/28 m of row) was correlated with initial numbers of juveniles (0–250/500 cm^3 soil) ($r = -0.42$, $P = 0.07$), numbers of cysts at 52 days (13 Jul 1981) ($r = 0.45$, $P = 0.05$) and numbers of juveniles at 85 days (15 Aug 1981) ($r = 0.80$, $P = 0.01$).

Discussion

Populations of *Heterodera glycines* fluctuate in response to several factors, including initial soil population density and environmental conditions (11). Initial soil population density is important because it largely determines the amount of damage to annual crops inflicted by the nematode (2,12). The larger initial population density at CCRS, compared with Smithfield, may account for the difference in population fluctuations at the two sites. A larger initial soil J2 population would induce much root damage early in the season, limiting subsequent invasion and reproduction. Conversely, the low initial J2 population at Smithfield caused little early root damage, resulting in large root systems that could sustain high soil and root nematode populations at 100 days. The maximum level of soil and root juveniles at 100 days may have been possible because of new soybean root growth providing more feeding niches perhaps combined with a high percentage of successful matings.

Numbers of eggs were highest at the end of the season. Thus, the most sensitive assay for *H. glycines* may be eggs. Overwintered eggs would provide juveniles for the next growing season. Apparently, overwintered eggs continue to hatch and make a major contribution to numbers of soil J2s through 30 days or more after planting because there was a positive correlation ($r = 0.73$) between numbers of eggs at planting and juveniles in the soil at 30 days.

Soil assays of *H. glycines* for predictive purposes would be more reliable if numbers of eggs rather than J2s or cysts were used. Regardless of the initial soil population density, reproduction of *H. glycines* on a susceptible soybean results in a sufficient number of progeny that would damage a susceptible soybean crop grown in the following one or two seasons even with significant mortality of eggs during the winter. As more is learned about the population dynamics of this important soybean pest, more effective management systems will be developed. Ultimately, mathematical models will be developed to predict from fall assays population densities of *H. glycines* and yield losses that would be sustained by a susceptible soybean cultivar.

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