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I am submitting herewith a thesis written by Pennie Lee Jennings entitled "Effect of Wheat on the Soybean Cyst Nematode, Heterodera glycines." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Entomology and Plant Pathology.

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EFFECT OF WHEAT ON THE SOYBEAN CYST NEMATODE, *Heterodera glycines*

A Thesis

Presented for the

Master of Science

Degree

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Pennie Lee Jennings

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DEDICATION

This thesis is dedicated to the family, friends and teachers who have given me much moral support previous to and during my years at this university.

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ABSTRACT

In greenhouse experiments, Heterodera glycines Ichinohe juveniles invaded clover and alfalfa roots to the same degree as 'Essex' soybean, but fescue, rye, barley and wheat were not significantly invaded and thus did not act as trap crops. When wheat and barley were grown simultaneously with soybean, each significantly reduced invasion of H. glycines juveniles into soybean. Sunflower grown simultaneously with soybean significantly reduced the number of females maturing in soybean.

An experiment was conducted to further study the effect of wheat rhizosphere on invasion and maturation of nematodes in soybean. There were three basic treatments: steam-sterilized soil was infested with nematode eggs, then planted with soybean seedlings; steam-sterilized soil was infested with eggs, then greenhouse fallowed (watered at the same times as other treatments) for 15, 30 and 60 days, then planted with soybean seedlings; and steam-sterilized soil was infested with eggs, and planted with wheat allowed to grow for 15, 30 and 60 days before crowns were excised after which soybean seedlings were planted. Soybean roots were harvested at ages 20, 40 and 60 days. In soil with 30 days of pretreatment, soybeans grown for 40 days after killed wheat had greater numbers of female nematodes than

soybeans 40 days old harvested from fresh or fallowed soil. In soil with 60 days of pretreatment, soybeans 40 days old grown after killed wheat had simultaneously fewer juveniles and greater numbers of females than soybeans 40 days old harvested from fresh or fallowed soil. Regardless of length of pretreatment, soybeans 20 or 60 days old in wheat treatments were not significantly different from soybeans in both controls at the same time. These results could be interpreted as evidence that greater initial numbers of H. glycines eggs hatch in response to soybean planted after killed wheat and that a lower rate of hatch over a longer period of time occurs in eggs from fallowed or fresh soil immediately planted with soybean.

In an experiment with nematode eggs placed in soil, nematodes hatched, migrated through root systems of wheat or sunflower or through nylon monofilament in soil, and invaded roots of soybean plants. Significantly fewer female nematodes were found 40 days after infestation of soil in soybean roots surrounded by filament or other plants than in soybean roots surrounded only by soil. The physical presence of nonhost roots, poor-host roots and root-like filaments may interfere with nematode host searching abilities.

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I. INTRODUCTION

The soybean cyst nematode, Heterodera glycines Ichinohe, is a major pathogen of soybeans in the United States (USDA 1985a, 1985b). Where soybeans are grown in easily eroded loessial soils associated with the Mississippi river basin, increasing use is made of conservation tillage and grassy cover crops grown in winter after the soybean season (Phillips 1980; Riggs 1980; Howard 1981). Both tillage practice and choice of cover crop may influence soil populations of the soybean cyst nematode.

Tyler et al. (1983) reported that lower cyst nematode counts were observed in conservation tillage than in conventionally tilled soils even when initial populations of nematodes were similar. In their study of tillage effects on soil properties, diseases, cyst nematodes and soybean yield, fewer cyst nematodes were found in no-till and moldboard-plowed plots at the end of the season than in plots of four other tillage regimes.

Baird and Bernard (1984) reported fewer midseason juvenile cyst nematodes in soybean fields under no-till than in soybean fields conventionally tilled. They noted that the major factor affecting nematodes was apparently the presence of wheat in the regime rather than the type of tillage system. They suggested that use of a winter wheat

cover crop as a possible control for *H. glycines* needed further investigation.

Objectives of This Study

The objectives of this research were to determine if certain cover or rotation plants were trap crops for the nematode; to determine the effect of wheat and other plants on maturation of the nematode; and to measure the duration of a possible suppressive effect of wheat on the nematode.

II. LITERATURE REVIEW

Distribution and Status of the Nematode

In southeastern (USDA 1985a) and delta state (USDA 1985b) surveys, the soybean cyst nematode was ranked second and first, respectively, among all soybean pathogens. Approximately 20% of all soybean acreage in the U.S. was infested with the nematode (Young and Hartwig 1984), which represented a 2.29% loss of potential yield (18.8 million bushels) in 1982 (Wrather et al. 1984). Besides the U.S., the nematode has been reported in China, Colombia, Korea and Japan (Riggs 1977). In Tennessee, the soybean cyst nematode occurs over the western two-thirds of the state, and is particularly damaging in the loessial soils of west Tennessee where it is the most common plant-parasitic nematode in soybean fields (Klobe 1976). Damage is dependent on moisture and nutritional stress on the plant (Tyler and Overton 1982) as well as plant cultivar and race of the pathogen.

Limitations in Management of the Disease

Management of the soybean cyst nematode is largely achieved by crop rotation, use of soybean cultivars resistant to the nematode, and application of nematicides. Each of these approaches can be effective, but each has

disadvantages that prevent universal acceptance and application. Most nematicides are quite toxic to mammals, which has led to cancellation of several of the most effective materials. Newer granular nematicides do not require injection equipment necessary for older liquified gas formulations and are much safer for operators but many are still general biocides that kill other soil organisms in the sphere of treatment including fungal antagonists. Nematicide treatments are sometimes followed by a rebound in population of nematodes from a lower soil depth not reached by the chemical (McKenry 1981). Nematode populations sometimes rebound even in greenhouse steam-treated soil (Sveshnikova 1967). Hussey and Boerma (1983) suggested that chemically protected roots proliferated more rapidly offering more sites of invasion to a resurging nematode population. Recommended rotations include one year of non-host (such as corn or grain sorghum) followed by one or two years of resistant soybean, then one year of susceptible soybean (Price et al. 1976), or the simpler technique of planting blended 1:1 susceptible/ nonsusceptible soybean seeds for two years after a non-host; susceptible cultivars of soybean have been included in rotations to minimize race shifts of the pathogen (Caldwell and Myers 1980). In one study the cyst nematode population declined by 92% in two years but recovered the

third year when susceptible soybeans were grown (Slack et al. 1981). Although a damage threshold of 60-100 eggs and juveniles per 250 cm of soil has been determined (Noel 1980), numbers of cysts in the soil at any one time has a high coefficient of variability. Decreases in yield were not correlated with number of cysts in soil by Hartwig et al. (1982).

Minimum Tillage Effects on Soil and Soybean

In recent years, reduced tillage and no-till cropping regimes have been used on much of the soybean acreage in the southern states to reduce erosion, energy investment, and pollution (Phillips et al. 1980). Winter cover crops further protect the cropland from excessive erosion (Riggs 1980). Minimum-tillage and double cropping alter soil characteristics, which may have an effect on nematode population dynamics. Soil organic matter was increased with no-till (Aina 1979; Bauer and Black 1981; Tyler et al. 1983). Soil bulk density, a measure of soil compaction, was decreased (Aina 1979; Tyler 1983), remained the same (Bauer and Black 1981) or increased (Ketcheson 1980; Threadgill 1982). Soil moisture was increased (Heatherly et al. 1982), which alleviated drought stress in soybeans (Tyler and Overton 1982). Phillips et al. (1980) suggested that conservation of moisture and reduction of soil

compaction are factors that contribute to the production of healthier plants that are able to withstand more disease and insect pressures. Doran (1980) found that anaerobic bacteria may be more prevalent in no-till soils than conventionally tilled soils. Johnston (1957) found that some facultative anaerobic bacteria produce nematicides. Soil microarthropods (Blumberg and Crossley 1983) and general microbial biomass were greater in no-till soil than conventionally tilled soil (Lynch and Panting 1979).

Possible Minimum-Tillage Effects on Nematodes

Stinner and Crossley (1982) found that although the total number of nematodes was not significantly different in no-till vs. conventionally tilled soils, plant parasitic densities were higher in no till soils in the summer and higher in conventionally tilled soils during the winter. In a Nigerian study of plant parasitic nematodes in tillage regimes, numbers of *Meloidogyne incognita* and *Helicotylenchus robustus* were higher in no-till but *Pratylenchus* spp. were higher in conventionally tilled soils (Caveness 1974). In a British study, lower populations of migratory plant parasitic nematodes occurred in untilled than in tilled wheat fields (Corbett and Webb 1970). Thomas (1978) found plant parasitic nematodes most dense under no-till ridged soil than in soil with six other

cropping regimes. Heatherly et al. (1982) found more cysts of H. glycines in the upper soil layer of pots of soybeans grown in wetted soil. Tyler et al. (1983) suggested that less tillage provided less introduction, reproduction and dissemination for the nematodes. Increased organic matter was negatively correlated with plant-parasitic nematodes and positively correlated with fungal-bacterial feeding nematodes (Norton 1971). Microarthropods and other microorganisms are known parasites or predators upon nematodes (Kerr 1982). There are many fungal parasites of H. glycines (Gintis et al. 1983; Carris et al. 1984). Since lack of water can inhibit the rate of parasitism of fungi upon H. glycines females, cysts and eggs (Kerry 1980), no-till conditions can be expected to favor fungal parasites.

Changes in soybean cyst nematode densities in no-till fields may be gradual. Species dominance and diversity for trophic groups and entire communities were not affected by single season changes in cropping and tillage regimes (Baird and Bernard, 1984). Tyler et al. (1983) noted that changes in tillage affected H. glycines populations slowly and suggested that a parasitic or allelopathic mechanism were responsible.

Possible Explanations of Cover Crop Effects on the Soybean Cyst Nematode

For the genus Heterodera, egg hatch is stimulated by root diffusates from host plants (Masume et al. 1982). Soybean cyst nematode was found to mature on many more plants than previously believed but has a limited host range among agricultural crops (Riggs and Hamblen 1966). Diapause occurs in H. glycines eggs but is not fully understood. Many apparently unrelated chemicals may elicit hatch (Clarke and Perry 1977). There are hatching inhibitors and stimulants in cyst walls (Okada 1971, 1974). Plants highly resistant or immune to the nematode (such as wheat) as well as plants that are good hosts for the nematode are used as winter cover crops but even the good hosts may not be fully exploited because they are grown at a time when low temperatures suspend development of the nematode (Riggs and Hamblen 1966; Epps 1969; Miller 1974; Riggs 1980). Whether these plants release hatching factors is unknown.

Plants can cause an abnormal reduction in population of nematodes by killing nematodes, delaying hatch, eliciting hatch but without penetration, or acting as trap crops that induce juveniles to penetrate but not mature. Crotalaria spectabilis was used to trap root-knot nematodes from peach orchards (McBeth and Taylor 1944) and rough

lemon was used as a biological barrier to the burrowing nematode in citrus orchards (Ford 1968). When marigolds (Tagates spp.) were used between rows of high value crops, a nematicidal effect continued even after tops of marigold plants were removed (Winoto Suatmadji 1969). A hatching inhibitor/nematicide identified from the roots of Asparagus officinalis inhibited emergence of H. glycines larvae from cysts even in the presence of their natural hatching stimulants (Takasugi et al. 1975). Wheat was found to be a nonhost in a survey of test plants for matured females but roots were not examined for invasion by juveniles (Riggs and Hamblen 1966).

Residue (mulch) from cover crops shades the soil surface, thus contributing to cooler temperatures in no-till soil (Moldenhauer 1969). Developement of H. glycines is temperature dependent in susceptible soybean cultivars (Melton et al. 1984).

In a study of population dynamics of the soybean cyst nematode in various cropping regimes, the major factor of variation in communities appeared to be presence or absence of wheat rather than the tillage system (Baird and Bernard 1984). Baird and Bernard suggested that exudates or metabolic products of wheat toxic to nematode eggs, juveniles or fecund females, along with climatic or edaphic factors, could be responsible.

Wheat is usually killed with a herbicide prior to planting of soybean seeds. Menon and Williams (1957) found mycofloras of crops were different from mycofloras of soils amended with residues of these crops. Decomposing wheat residue may suppress nematodes by releasing compounds that are directly toxic (as suggested for decomposing rye by Patrick et al. 1965), by favoring nematode parasites and by favoring microbes that produce toxic decomposition products such as hydrogen sulfide (Rodriguez-Kabana et al. 1965), fatty acids (Sayre et al. 1965) and ammonia (Menon and Williams 1957; Hutchinson et al. 1960; Mankau and Minteer 1962; Vassallo 1967; Miller et al. 1968; Walker 1969; Huber and Watson 1970; Johnson and Shamiyeh 1975).

Non-host roots may chemically interfere with nematodes finding host roots. There is morphological evidence that sensory orientation in plant parasitic nematodes is primarily chemical rather than tactile; cephalic sensilla are more reduced in Tylenchida than any other group and have blind endings in the cuticle in the infective juvenile stage (Wright 1980; Zuckerman 1983; Endo 1983, 1984; Noel and Stanger 1983, 1986).

Possibly wheat has no significant effect on H. glycines. Schmitt et al. (1983, 1986) reported that population densities were greater at some time during the growing season in several field treatments with the

herbicides alachlor alone and in combination with nematicides. Bostian et al. (1984a, 1984b, 1986) reported that the herbicide alachlor is nematicidal at recommended rates but elicited greater hatch and survival at lower levels. However, surviving juveniles were not as infective to soybeans as juveniles hatched in water without alachlor. Survival may have been due to suppression of microflora antagonistic to the nematode. Interactions between the nematode, nematicides and even nitrogen fertilizer have been reported (Rodriguez-Kabana 1981). Recently Koenning and Anand (1986) stated that wheat had little influence on the survival of H. glycines. Reduced mid-season populations of nematodes and higher yield in short-season soybeans (that were double-cropped with wheat) compared to full-season soybean fields was attributed to later planting date of the short-season soybeans. Early planting of full-season soybeans resulted in higher populations of soybean cyst nematodes at mid-season but no significant differences in final population densities.

II. MATERIALS AND METHODS

Nematode Inoculum

All experiments were conducted with a Race 3 isolate of soybean cyst nematode (Golden et al. 1970; Burrows and Stone 1985) originally collected in Madison County, Tennessee, and a mixed population of Race 3 derived from North Carolina and Arkansas isolates. Stock cultures were maintained in the greenhouse on soybean (Glycine max L. Merr. 'Essex'). For inoculum, yellow females were harvested from soybeans 33-41 days after soil was infested with eggs, and collected by sieving and flotation-centrifugation (Dunn 1969). A water suspension of eggs was obtained by grinding cysts in 20-30 mesh (500 µm grain) Ottawa sand or by rubbing cysts on an 80 mesh (180 µm pore) standard screen over a 500 mesh (10 µm pore) screen. Eggs were counted and calibrated suspensions were poured in 10-ml aliquots from a hand held automatic pipettor onto autoclaved or steamed soil in pots. Soybean seeds were then planted and covered with a 1-cm layer of soil.

Soybean, Experimental Design and Analysis

For all experiments, soybean seeds were sprouted in vermiculite for three to four days to obtain seedlings with cotyledons just beginning to open. Soil for experiments

was infested with eggs, planted with the appropriate crop plant and maintained in a greenhouse with an ambient temperature of 25-30°C throughout the experiments. Stained roots (Byrd et al. 1983) were examined for nematodes at 12x under a stereomicroscope. All vermiform and sausage-stage juveniles inside roots were counted as juveniles. Nematodes distinctly enlarged to a lemon shape, white and yellow females were counted as females. Fourth stage and adult males were not counted. Each experiment was planned as a randomized complete block design and analyzed with the aid of the Statistical Analysis System, and means were separated by the Waller-Duncan K-ratio t-test (SAS 1985).

Trap Crop Experiment

Seeds of tall fescue (Festuca arundinacea Schreb. 'Kentucky 31'), annual rye grass (Lolium multiflorum Lam.), alfalfa (Medicago sativa L. 'Liberty'), barley (Hordeum vulgare L. 'Volbar'), wheat (Triticum aestivum L. 'Arthur'), white clover (Trifolium repens L.) and soybean were sprouted in vermiculite to obtain seedlings. Eggs collected from 33-day old yellow females were added to steam sterilized soil in 11-centimeter clay pots at a rate of 2,000 eggs/pot. Freshly infested pots were randomly selected for planting with seedlings, then chosen randomly

from each group for each replication. Pots were arranged on a greenhouse bench in a randomized complete block design with five replications of each treatment. Plants were harvested and root systems stained 15 days after soybeans were planted.

Cover Crop Experiment

Thirty boxes of 300 x 303 cm outer dimensions were constructed with 14 x 2 cm lumber grade pine boards (Figure 1). The bottom of each box was covered with two layers of fiberglass window screen to retain soil. Soil volume was 85,050 cm^3 per box.

Eggs were obtained from 41-day old yellow females from the mixed stock culture. Freshly sterilized soil placed in the boxes was infested with 11,000 eggs/box. Two days later, cover crops were planted into boxes so roots could become established (Figure 2). Cover crops included seeds of wheat and barley cultivars found to be non-hosts in the trap crop experiment, and the poor hosts sunflower (Helianthus annuus L. 'Mammoth') added as seed and tomato (Lycopersicon esculentum L. Mill. 'Rutgers') added as two-month old plants (Bernard and Keyserling 1985; Miller 1976). Boxes of soil without cover crops served as controls. Boxes were arranged in randomized complete blocks with six replications. Cover crops were grown for

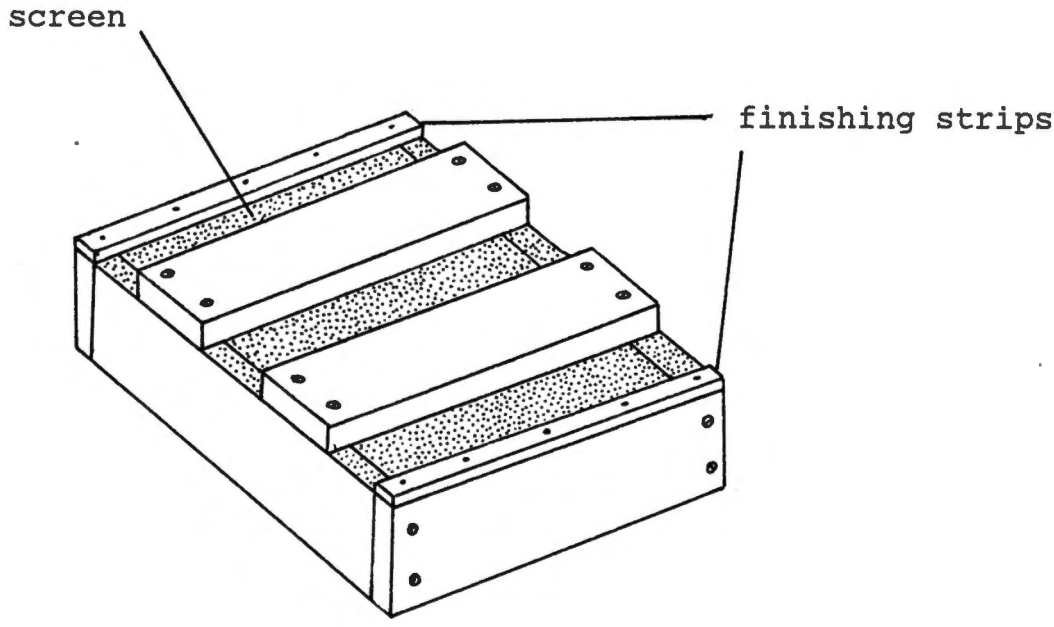

Fig. 1. Boxes used in Cover Crop Experiment, Bottom View.

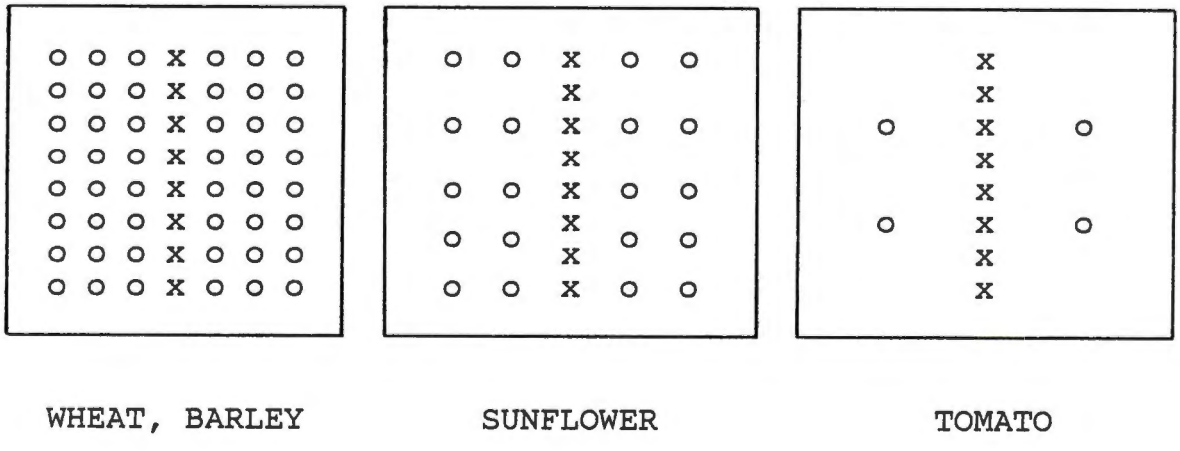

Fig. 2. Arrangements of Plants in Wooden Boxes for the Cover Crop Experiment; (o = cover crop plant, x = soybean plant).

21 days then a row of eight soybean seedlings was transplanted down the center of each box (Figure 2). All plants were harvested 41 days after the soybeans were planted. Entire root masses of all plants except wheat and barley were stained. To check wheat and barley in the event that they were invaded, one-fourth of the barley root mass from one box and one-sixth of the wheat root mass from another box were stained. Soil shaken from roots was mixed by hand for 30 seconds, then a $100cm^3$ sample was taken for extraction of cysts. Cysts/box were calculated from these samples, then pooled with young females observed in soybean roots. Female/cyst data were transformed to natural logarithms for analysis of variance.

Wheat Rhizosphere Experiment

There were three basic treatments modified by time intervals to result in 21 treatments (Table 1). One third of the freshly sterilized soil in 11-cm clay pots was infested with nematode eggs then immediately planted with two soybean seedlings/pot June 19, 1986; another third of the soil was potted, infested, greenhouse fallowed (watered at the same times the first treatments were watered) for 15, 30 or 60 days before soybean seedlings were added; the remaining third was infested, immediately planted with ten wheat seeds (thinned to six upon emergence) and allowed to

Table 1. Treatments in Wheat Rhizosphere Experiment

Treatment / Number of days soybean was grown
1. Soil immediately planted / soybean grown 20 days
2. Soil immediately planted / soybean grown 40 days
3. Soil immediately planted / soybean grown 60 days
4. Soil left fallow 15 days / soybean grown 20 days
5. Soil left fallow 15 days / soybean grown 40 days
6. Soil left fallow 15 days / soybean grown 60 days
7. Soil left fallow 30 days / soybean grown 20 days
8. Soil left fallow 30 days / soybean grown 40 days
9. Soil left fallow 30 days / soybean grown 60 days
10. Soil left fallow 60 days / soybean grown 20 days
11. Soil left fallow 60 days / soybean grown 40 days
12. Soil left fallow 60 days / soybean grown 60 days
13. Wheat grown 15 days / soybean grown 20 days
14. Wheat grown 15 days / soybean grown 40 days
15. Wheat grown 15 days / soybean grown 60 days
16. Wheat grown 30 days / soybean grown 20 days
17. Wheat grown 30 days / soybean grown 40 days
18. Wheat grown 30 days / soybean grown 60 days
19. Wheat grown 60 days / soybean grown 20 days
20. Wheat grown 60 days / soybean grown 40 days
21. Wheat grown 60 days / soybean grown 60 days

grow 15, 30 or 60 days before crowns were excised and soybean seedlings planted into soil. After planting of soybeans, replicates were arranged in a randomized block design with eight replications. Soybeans from each group were harvested at 20, 40 and 60 days. At harvest, entire contents each pot were washed (singly) into a bucket under running water and rubbed to clean the root mass for staining and to collect soil for extraction of yellow females and cysts. Roots of wheat were of smaller diameter and more lightly stained than roots of soybean, so were microscopically distinguished.

Blocked Root Experiment

Cylinders were constructed by sandwiching Nytex® nylon screen (Tetko, Inc., 420 Saw Mill River Road, Elmsford, New York) with 215 µm pores between two pieces of fiberglass window screen to form sheets 23 x 25 cm. Each screen sandwich was then rolled into a cylinder 8 cm in diameter and sewn with polyester thread. Additional nylon screen was unraveled to produce 12-gram masses of monofilament fiber cut into random lengths to simulate roots. Cylinders were placed into 25 cm plastic pots and filled with steamed soil, then the remainder of the pot was filled with soil (Figure 3).

Top view: cylinders around soybeans

Side view of pot:

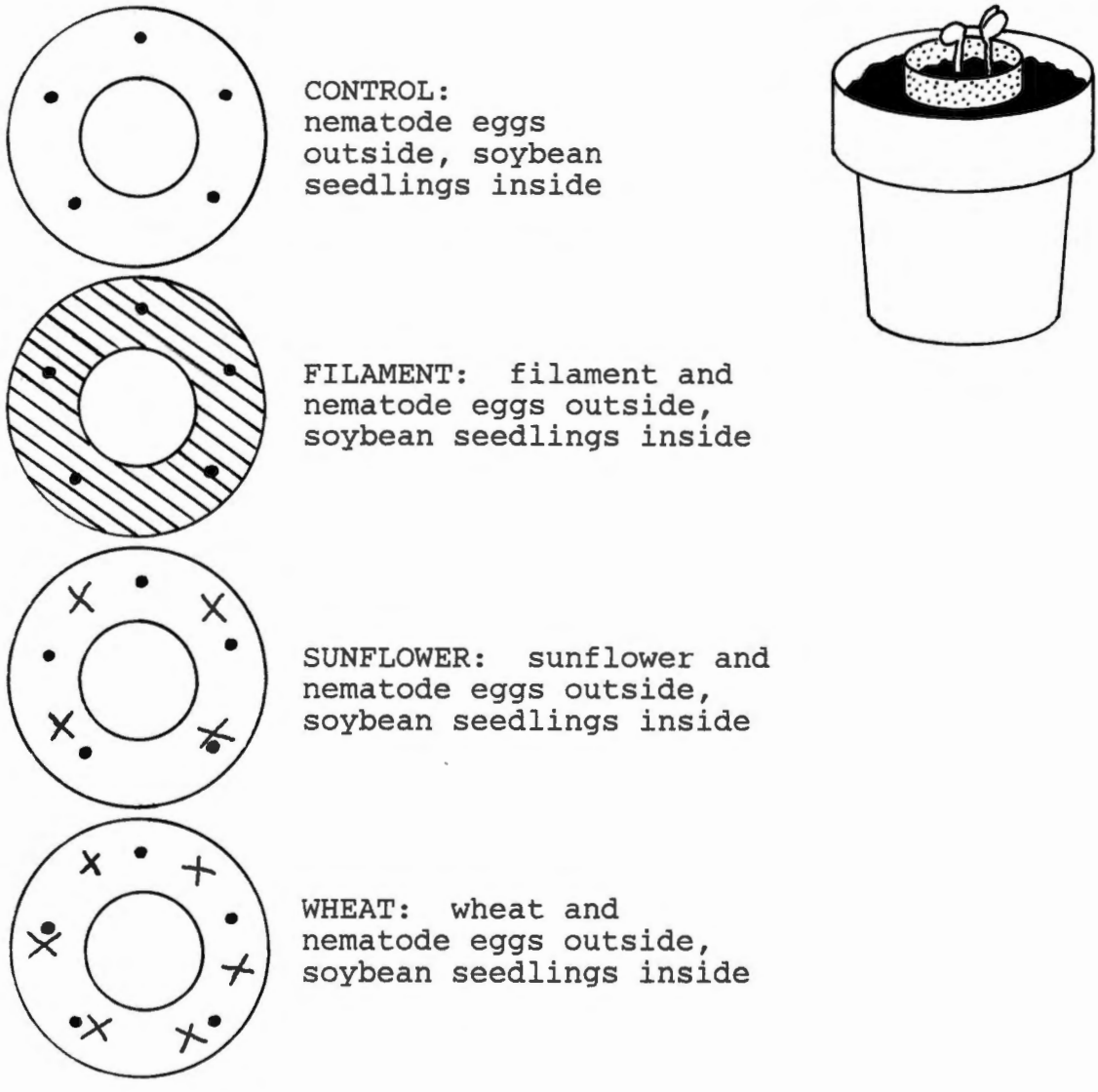

Fig. 3. Arrangement of Plants in Pots for the Root Blocking Experiment (• = infestation point for eggs, ✕ = plant).

Soil outside each cylinder was modified in one of four ways: planted with wheat seedlings; planted with sunflower seedlings sprouted five days previously in vermiculite; amended with a mass of 200 um diameter nylon filaments well mixed with the top two-thirds of soil; or no additional modification. Seven days later the soil outside each cylinder was pierced with a glass rod 9 cm deep in five places. Into each hole was pipetted a 4-ml water suspension of 4,000 freshly harvested eggs from females 41 days old to give a total of 20,000 eggs/pot. Four days after infestation, two soybean seedlings were planted into the center of each cylinder. Soybeans were harvested 41 days after planting at which time soybean roots and soil in cylinders were extracted for females.

III. RESULTS

Trap Crop Experiment

Juveniles of *H. glycines* were found in roots of the legumes clover, alfalfa and soybean, but not in the grasses fescue, rye, barley and wheat (Table 2).

Although the experiment began with autoclaved pots and steam-sterilized soil, the presence of numerous nodules on soybean was evidence that microflora were established in the system prior to harvest. Five bacterivorous nematodes of an unidentified species were observed in the crown of plants in one pot of barley.

Cover Crop Experiment

Wheat and barley significantly reduced the number of juveniles in soybean roots when the crops were grown simultaneously with soybean (Table 3). Invasion by juveniles of roots other than soybean was insignificant, averaging four per box of tomato, .03 per box of sunflower and none per box of wheat and barley. When compared to soybean only, sunflower and barley significantly reduced maturation and development of female *H. glycines* in soybean roots when each was grown simultaneously with soybean (Table 4).

Table 2. Invasion of Roots of Selected Plants by *Heterodera glycines* Juveniles 15 Days After Planting.

Crop	Nematodes/root system[z]
Soybean	126 a
Clover	103 a
Alfalfa	68 ab
Fescue	0 b
Rye	0 b
Barley	0 b
Wheat	0 b

[z] Numbers are means of five replicates. Means with a common letter are not significantly different, according to the Waller-Duncan K-ratio t-test (P = 0.05).

Table 3. Effect of Crops Grown Simultaneously with Soybean on Invasion of Soybean Roots by Heterodera glycines Juveniles

Crop	Juveniles/Box of Soybean Roots[z]
Soybean	684 a
Soybean + Tomato	828 a
Soybean + Sunflower	623 a
Soybean + Wheat	68 b
Soybean + Barley	59 b

[z] Numbers are the means of six replicates. Means with a common letter are not significantly different, according to the Waller-Duncan K-ratio t-test (P = 0.05).

Table 4. Effect of Crops Grown Simultaneously with Soybean on Maturation of Heterodera glycines Females in Soybean Roots

Crop	Females/Box of Soybean Roots[x]
Soybean	719 a
Soybean + Tomato	510 ab
Soybean + Wheat	410 abc
Soybean + Barley	247 bc
Soybean + Sunflower	132 c

[x] Numbers are the means of six replicates. Data were logarithmically transformed for analysis of variance. Means with a common letter are not significantly different, according to Duncan-Waller K-ratio t-test (P = 0.05).

Wheat Rhizosphere Experiment

Means of juvenile nematodes in soybean roots harvested at 20 days from fallowed, wheat-treated and untreated soils were not significantly different (Table 5). Significantly fewer juveniles invaded roots of 40 day old soybeans grown in decomposing wheat rhizosphere for 60 days than invaded soybeans 40 days old grown from seedlings planted into freshly steamed soil or in soil previously fallowed for 60 days. Similarly, 60 day old soybeans grown after 60 days of wheat had fewer juveniles than 60 day old soybeans grown from soil fallowed 60 days.

Soybeans 40 days old grown after 30 days of wheat had significantly more female nematodes than soybean 40 days old grown from seedlings planted into freshly steamed soil or in soil previously fallowed for 30 days (Table 6). Similarly, soybeans 40 days old grown after 60 days of wheat had significantly more females than soybeans 40 days old grown from seedlings planted into freshly steamed soil or in soil fallowed for 60 days. Significantly greater numbers of females were found after 15 days of treatment: 60 day old soybeans grown after 15 days of wheat had a significantly greater number of females than 60 day old soybeans grown from seedlings planted into freshly steamed soil or soil fallowed for 15 days. These significantly different comparisons are summarized in Table 7.

Table 5. Effect of Wheat Rhizosphere on Invasion of Soybean Roots by Heterodera glycines Juveniles

Pretreatment	(Days)	Soybean Age (Days)	Juveniles/Pot[z]	
-	[w]	20	562	cdefg
-		40	1447	a
-		60	558	cdefg
Fallow	15[x]	20	440	defgh
Wheat	15[y]	20	167	fgh
Fallow	15	40	809	bcd
Wheat	15	40	537	cdefgh
Fallow	15	60	253	efgh
Wheat	15	60	677	bcdef
Fallow	30	20	132	gh
Wheat	30	20	16	h
Fallow	30	40	1162	ab
Wheat	30	40	1533	a
Fallow	30	60	684	bcdef
Wheat	30	60	747	bcde
Fallow	60	20	206	fgh
Wheat	60	20	135	gh
Fallow	60	40	1056	abc
Wheat	60	40	230	efgh
Fallow	60	60	857	bcd
Wheat	60	60	47	gh

[w] Steamed soil infested then planted with soybean seedlings.

[x] Steamed soil infested then watered at same times as other treatments

[y] Steamed soil infested then planted with wheat

[z] Numbers are the means of eight replicates. Means with a common letter are not significantly different, according to Waller-Duncan K-ratio t-test (P = 0.05). Replications had significant variation.

Table 6. Effect of Wheat Rhizosphere on Maturation of *Heterodera glycines* Females in Soybean Roots

Pretreatment	(Days)	Soybean Age (Days)	Females/Pot[z]	
-	[w]	20	318	defg
-		40	185	fghi
-		60	882	ab
Fallow	15[x]	20	129	fghi
Wheat	15[y]	20	193	fghi
Fallow	15	40	331	defg
Wheat	15	40	136	fghi
Fallow	15	60	535	cde
Wheat	15	60	987	a
Fallow	30	20	31	ghi
Wheat	30	20	4	i
Fallow	30	40	241	efghi
Wheat	30	40	637	bcd
Fallow	30	60	877	ab
Wheat	30	60	761	abc
Fallow	60	20	29	ghi
Wheat	60	20	11	hi
Fallow	60	40	383	def
Wheat	60	40	832	abc
Fallow	60	60	702	abc
Wheat	60	60	848	ab

[w] Steamed soil infested then planted with soybean seedlings

[x] Steamed soil infested then watered at same times as other treatments

[y] Steamed soil infested then planted with wheat

[z] Numbers are the means of eight replicates. Means with a common letter are not significantly different, according to Waller-Duncan K-ratio t-test (P = 0.05). Replications had significant variation.

Table 7. Significantly Different Groups in Wheat Rhizosphere Experiment, Heterodera glycines Juveniles and Females.

Treatment Days/ Soybean Age (Days)	Significance Grouping[z]: juveniles	females
Fresh 30/40		fghi
Fallow 30/40		efghi
Wheat 30/40		bcd
Fresh 60/40	a	fghi
Fallow 60/40	abc	def
Wheat 60/40	efgh	abc
Fresh 15/60		ab
Fallow 15/60		cde
Wheat 15/60		a
Fresh 60/60	cdefg	
Fallow 60/60	bcd	
Wheat 60/60	gh	

[z] Groups with a common letter are not significantly different, according to Waller-Duncan K-ratio t-test (P = 0.05).

Blocked Root Experiment

The presence of roots or nylon filament in soil reduced the number of female nematodes found in soybean roots inside cylindrical screens 40 days after eggs were added to soil outside the cylinders (Table 8). By harvest, limited growth of soybean roots through the screen into surrounding soil occurred in all pots. Results were similar to those obtained in the cover crop experiment. Wheat and sunflower each reduced the number of female soybean cyst nematodes observed in soybean roots when grown simultaneously with soybean.

Table 8. Effect of Roots or Nylon Monofilament Amendment on Migration and Maturation of *Heterodera glycines* in Soybeans

Treatment Outside of Cylinder	Total Females/Root System of Soybeans Inside Cylinder[z]	
(No Treatment)	135	a
Nylon Filament	67	b
Wheat	39	b
Sunflower	35	b

[z] Means with a common letter are not significantly different, according to Waller-Duncan K-ratio t-test (P = 0.05).

IV. DISCUSSION

There was no evidence for invasion of wheat roots by juveniles in the trap crop experiment. Wheat probably does not function as a trap crop in double-cropped wheat-soybean cropping systems.

The effect of wheat on populations of H. glycines was difficult to interpret from cover crop, wheat rhizosphere, and blocked root experiments. Significantly fewer juvenile nematodes invaded soybean roots when living wheat plants or decomposing wheat roots were present in the same pot with soybeans. Living wheat roots did not significantly reduce numbers of females developing and maturing in soybean roots 40 days after nematode eggs were added to soil in the cover crop experiment, but did significantly reduce numbers of females when soybean roots were segregated from wheat roots with nematode-permeable screens. Decomposing wheat roots increased numbers of females compared to control soybeans. This increase could be a statistical anomaly due to high variation between replications in the rhizosphere experiment resulting from the high number of treatments (twenty-one) compared. Treatments could be reduced in subsequent experiment by elimination of soybeans 60 days old. After 50 days, overlap of generations occurs so that juveniles hatching late from eggs experimentally placed in soil cannot be

distinguished form offspring of females maturing on roots. It is possible that a metabolite exuded from living wheat roots suppressed hatch of H. glycines eggs but was followed by a surge of hatching after wheat plants were killed. Results could be interpreted as evidence that greater initial numbers of H. glycines eggs hatch in response to soybean when exudate from living wheat ceases to be present and that a lower rate of hatch over a longer period of time occurs in eggs from fallowed soil or fresh soil immediately planted with soybean. Additional experiments to measure the effects of wheat rhizosphere using fewer treatments would be useful in determining the nature of wheat rhizosphere effects.

There was evidence that microflora were present in these experiments. Soybean roots were nodulated and small white sclerotia were observed on screens in the root blocking experiment. Invasion and maturation of the nematode was significantly less in soybeans in some fallowed treatments than in soybeans planted into freshly sterilized soil. An experiment with H. glycines, soybean root explants (Lauritis et al. 1982) and wheat in axenic conditions (Ayers and Thornton 1968) could be used to test wheat exudate effects. An experiment is planned to measure survival of intact H. glycines eggs in soil under four treatments; fallow; with living wheat, with wheat killed

in place by excision of crowns; and dead wheat roots mixed into soil as an amendment.

Sunflower roots exerted more suppressive effect on female H. glycines in soybean than wheat in the cover crop and blocked root experiments. The potential of sunflower as a management tool for the soybean cyst nematode could be limited by market economics, parasitism by nematodes other than H. glycines that are parastic upon soybean (Bernard and Keyserling 1985) and growth season (sunflower is not a winter cover crop). However, a strongly suppressive or toxic effect might make sunflower an attractive rotation crop on H. glycines-infested land. Further analysis of sunflower's effect on the nematode is desirable.

The suppression of nematodes in nylon filament-amended soil raises the possibility that H. glycines juveniles orient at least partially to filamentous structures and follow them as if they were roots with suitable invasion sites. Such an orientation would help explain the suppressive effects of several crops used in this research. Nematodes tracking along unsuitable filaments (or roots) would have less chance of eventually locating a root of a susceptible plant species. In the field, H. glycines may be a very poor searcher for host roots in the presence of non-host roots. This nematode was recognized in the United States only after large-scale soybean production had been

underway for several years. Soybean monoculture may have enabled the previously unknown H. glycines to have efficiently located the host without interference from the root of many nonhosts. Experiments with chemical indicators or video recording of nematode movement in simulated soil composed of glass beads (Anderson and Coleman 1977) or Sephadex (Moltmann 1985) with simulated roots composed of inert filaments could test for this behavior.

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