

Soybean Photosynthesis and Yield as Influenced by *Heterodera glycines*, Soil Type and Irrigation¹

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Abstract: The effects of soil types and soil water matric pressure on the *Heterodera glycines*-*Glycine max* interaction were examined in microplots in 1988 and 1989. Reproduction of *H. glycines* was restricted in fine-textured soils as compared with coarse-textured ones. Final population densities of this pathogen in both years of the study were greater in nonirrigated soils than in irrigated soils. The net photosynthetic rate of soybean (per unit area of leaf) was suppressed only slightly or not at all in response to infection by *H. glycines* and other stresses. Relative soybean-yield suppression in response to *H. glycines* was not affected by water content in fine-textured soils, but slopes of the damage functions were steepest in sand, sandy loam, and muck soils at high water content (irrigated plots). Yield restriction of soybean in response to this pathogen under irrigation was equal to or greater than the yield suppression under dry conditions. Although yield potential may be elevated by irrigation when soil-water content is inadequate, supplemental irrigation cannot be used to circumvent nematode damage to soybean.

Key words: Damage function, ecology, edaphic factors, *Glycine max*, *Heterodera glycines*, irrigation, photosynthesis, soil moisture, soil texture, soil water matric pressure, soybean, soybean cyst nematode.

The soybean cyst nematode (SCN), *Heterodera glycines* Ichinohe, is a destructive parasite of soybean, *Glycine max* (L.) Merr. (19). This economically important parasite is found in most areas where soybean is grown in the United States (19). Much effort has been expended by nematologists over the last 2 decades in characterizing the damage caused to soybean by this pathogen and in developing related damage thresholds.

Soil type and texture, as well as cultivar resistance and initial population density (Pi), are important factors that influence both nematode population density and crop-yield suppression caused by plant-parasitic nematodes (2,6,13,19,20,23,27). Research in microplots demonstrated the effects of soil type and texture on *H. glycines* and *Meloidogyne incognita* (Kofoid &

White) Chitwood and their damage functions on soybean (20,25). Reproduction by these nematodes and their effects on soybean yield were greatest in the soil types with highest sand contents. Thus, variation in soil texture may significantly alter damage functions and affect *H. glycines* population densities even within a given area of a field (13).

Rainfall and associated soil moisture effects are primary determinants of soybean growth and yield potential. Similarly, soil water matric pressure impacts the nematode's ability to hatch, move through soil, locate and penetrate a host, and mate. Soil water content may well influence the damage potential of plant-parasitic nematodes on various crops, but this important parameter has received limited study. Incorporating the impact of soil moisture into damage functions should ultimately lead to more accurate damage thresholds and functions for this nematode. Unfortunately, only limited information is available about the effects of soil water matric pressure on *H. glycines*, especially in regard to soybean-yield suppression. The influence of soil water content on the nematode and host is mediated by soil type and texture because these and other physical factors affect soil-water matric pressure and gas exchange characteristics of the soil (22).

Received for publication 3 March 1994.

¹ The research reported in this paper was supported, in part, by USDA Southern Regional IPM Grant No. 87-CRSR-2-3063 and the North Carolina Agriculture and Life Sciences Experiment Station. Use of brand names in this publication does not imply endorsement of the products named or criticism of similar ones not mentioned.

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The authors thank C. E. Echerd, D. W. Corbett, and the staff at the Central Crops Research Station for technical assistance and Katherine Kershaw for help in editing and manuscript preparation. Dr. M. L. Gumpertz provided valuable advice on statistical treatment of the data.

The results from limited studies conducted on the effects of irrigation and matric pressure on *H. glycines* and SCN-affected soybean, as well as other nematode-host systems, have been somewhat variable and unclear. Reproduction of *H. glycines* in a Dubbs silt loam soil was greater at -20 to -40 kPa than at -60 to -80 kPa in a greenhouse study (26). The optimum soil-water matric pressure for *H. glycines* reproduction in a Vicksburg sandy loam soil was -30 to -40 kPa in another greenhouse study (9). Soil-water had no influence on numbers of *H. glycines* cysts in the 0–15 cm depth in microplots, but treatments at high pressures (> -40 kPa) resulted in larger cyst numbers from 15–30 cm compared with low pressures (< -40 kPa) (26). In the greenhouse, population densities of this pathogen declined over time in a Sharky clay but increased in a Dubbs slit loam soil when both were maintained at -30 kPa (9). This last finding suggests that interactions may occur between soil texture and soil-water matric pressure. Still, the impact of *H. glycines* on soybean yield often appears to be independent of soil-water matric pressure in microplot and field experiments (7,8,26). Irrigation tended to increase soybean yield in the presence of this pest, but susceptible cultivars did not yield as well as resistant cultivars when irrigated (7). Also, the effects of *M. incognita* on growth of flue-cured tobacco were greater at high soil-water matric pressure than at moderate pressure (24). Water stress was a greater limiting factor for tobacco growth than was nematode inoculum density under dry conditions (24).

A number of factors, including soil texture and soil-water matric pressure, may affect the same plant physiological processes that are often impacted by nematodes. Greenhouse research has shown that the net photosynthetic rate of soybean was suppressed by *H. glycines* at high population densities, and this process was affected by moisture and host nutrition (1, 10,17). Potuska et al. also found that *H. glycines* suppressed photosynthesis of soy-

bean under controlled conditions (16). Potato cyst nematode (*Globodera pallida* Stone) suppressed photosynthetic and transpiration rates of potato *Solanum tuberosum* L. at high inoculum densities (18).

The purpose of the current research was to evaluate the effects of soil texture and moisture on *Glycine max-Heterodera glycines* interactions. Objectives focused on: 1) the influence of irrigation on yield and photosynthetic rate of soybean in the presence of *H. glycines*; 2) the effects of soil-water matric pressure on the damage functions of the nematode in different soil types; and 3) the impact of irrigation on population changes of *H. glycines*.

MATERIALS AND METHODS

This study was conducted at the Central Crops Research Station near Clayton, North Carolina, in 1988 and 1989. The experimental design was a $2 \times 4 \times 6$ factorial with two levels of soil-water matric pressure—high (irrigated) and low (nonirrigated); four levels of *H. glycines*, and six soil types. The six soil types (five of which were collected from the plow layer [Ap horizon material] from other sites) were located at a common site in microplots (0.76-cm-d) arranged in five randomized complete blocks.

Microplots were covered with a plastic tarp and fumigated in the fall of 1987 with 100 g methyl bromide + 2 g chloropicrin/ m^2 . The polyethylene cover was removed after 3 weeks and the soil tilled in the spring of 1988. The scientific classification of the soils in their native sites, percentages of sand, silt, clay, and organic matter for these soils were: Fuquay sand (loamy, siliceous, thermic, arenic plinthic Kandiodults—the indigenous soil), 91, 6, 3, 0.6; Norfolk sandy loam (fine-loamy, siliceous, thermic Kandiodults), 84, 12, 4, 1.4; Portsmouth loamy sand (fine-loamy over sandy or sandy-skeletal, mixed, thermic, Typic Umbraqueults), 72, 18, 10, 3.8; muck (Medisaprists), 58, 33, 9, >30 ; Cecil sandy clay loam (clayey, kaolinitic, thermic, Typic Kanhapludults), 53, 18, 29, 2.2; and Cecil

sandy clay (clayey, kaolinitic, thermic, Typic Kanhapludults), 48, 13, 39, 0.9.

Inoculum of *H. glycines* race 1 (originally collected from New Hanover County, North Carolina, in 1954) was reared in the greenhouse on 'Ransom' soybean and extracted from roots and soil the day prior to soil infestation in 1988. Cysts were crushed with a Ten-Broeck tissue homogenizer to free the eggs from the cysts. The top 15 cm of soil in microplots was infested with 0, 100, 800, or 6,400 eggs/500 cm³ soil. Initial inoculum levels (Pi) in 1989 were the residual populations from 1988 and were determined by sampling on 31 May 1994 before planting. Initial levels of SCN eggs + juveniles were partitioned within soil type, ranked from low to high (0–350,000/500 cm³), and irrigation levels were assigned at random to each soil type such that a range of inoculum levels occurred at each combination of soil type and soil-water matric pressure. Population densities of *H. glycines* eggs + juveniles/500 cm³ soil for the different soil types in the spring of 1989 were: Norfolk sandy loam—0–350,000; Fuquay sand—0–320,000; Cecil sandy clay loam—0–80,000; Cecil sandy clay—0–100,000; Muck—0–200,000; Portsmouth loamy sand—0–160,000. A suspension containing ca. 1,000 chlamydozoospores of *Glomus macrocarpus* Tul. and Tul., obtained from a soybean (greenhouse) culture was added to the soil and incorporated with the nematode inoculum in 1988. Soybean seeds were inoculated with a commercial preparation of *Bradyrhizobium japonicum* (Kirchener) Jordan. Ransom soybean was planted in a row (one row/microplot) at the rate of one seed per three cm of row. Soybean was planted on 25 May 1988 and 13 June 1989.

Opaque, white plastic covers were placed over the top of the microplots to minimize rainfall into plots. Trickle irrigation treatments were started 3–4 weeks after soybean planting each year. The drier treatments (i.e., those with low soil-water pressure) received irrigation only when soils approached the permanent wilting point (–1,500 kPa). Differential irrigation treat-

ments for the high soil-water matric pressure treatments were used because of the different drainage characteristics of the different soils. The order of drainage from well to poorly drained was as follows: Muck > Fuquay sand > Norfolk sandy loam > Portsmouth loamy sand > Cecil sandy clay loam > Cecil sandy clay. The high irrigation treatment received trickle irrigation twice weekly at the rate of 8 liters/hour for the muck soil; 4 liters/hour for the Fuquay sand and Norfolk sandy loam; and 2 liters/hour for the Cecil sandy clay, Cecil sandy clay loam, and the Portsmouth loamy sand. The irrigation periods were 2 hours/session from planting to approximately the V6 growth stage (5), 4 hours from V7 to R1, and 6–8 hours for R1–R7. Irrigation was terminated at physiological maturity (R7).

Soil-water content was monitored with a Troxler Series 2000 (Troxler Inc., Research Triangle Park, NC) neutron probe 30 cm deep in three replications of all soil types at three inoculum levels (0, 800, and 6,400) and both irrigation regimes. Control (uninfested), moderate, and high nematode population density plots were monitored in 1989. Three measurements (2 per week, 1 following irrigation, and 1 before irrigation) were taken in 1988 and 4 weekly measurements in 1989. Count ratios from the neutron probe were calibrated to gravimetric water content. A soil-water characteristic curve was used to convert percentage soil-water content by weight to soil-water matric pressure for each soil type.

Numbers of *H. glycines* cysts, eggs, and juveniles were determined at midseason (August) and before soybean harvest in 1988 and 1989, and before planting in 1989. Soil samples consisted of 8–10 cores (2.5-cm-d) taken 15–20 cm deep. A 500-cm³ soil sample was processed by elutriation (3) and centrifugation (12) to extract cysts and juveniles from soil. Cysts were crushed with a Ten-Broeck tissue homogenizer to release eggs.

A Licor 6200 Portable Photosynthesis System (Li-Cor Inc., Lincoln, NE) was used

to determine the photosynthetic rate of the uppermost fully expanded middle trifoliate soybean leaf from a representative plant in selected treatments. An entire leaf was used for measurements, and the leaf area and net photosynthetic rates (mg CO_2 consumed) $\text{dm}^{-2} \text{hr}^{-1}$ were calculated. Five readings per leaf were averaged on four replicates of all treatments in the Fuquay sand and the Cecil sandy clay on 9 August 1988. Photosynthetic data in 1989 consisted of an average of six readings per leaf on all treatments with five replications. In 1989 since only one replication could be completed per day, measurements, therefore, were made from 3–23 August. Determinations of photosynthetic rates were made between 10:00 a.m. and 3:00 p.m.

Statistical analyses consisted of analysis of variance (ANOVA) for a factorial design with five replicates. Regression was used to evaluate quantitative effects of inoculum level on plant yield, photosynthetic rate, and nematode reproduction. PROC GLM of the SAS system was used to develop a model by year to relate Pi to soybean yield or photosynthesis within soil types and irrigation levels (15). The program statements were: PROC GLM; CLASS IRRIGATION SOILTYPE; MODEL Y = IRRIGATION(SOILTYPE) PI(SOILTYPE) IRRIGATION*PI(SOILTYPE)/NOINT SOLUTION. Heterogeneity of slopes tests was used to evaluate differences in response to a quantitative variable (inoculum level) for the two irrigation treatments within a given soil type. Nematode data were transformed to $\text{Log}_{10}(X + 1)$ to standardize the variance where X = number of eggs + second-stage juveniles (J2). Repeated measures analysis of variance was used to analyze differences in soil-water matric pressure.

RESULTS

Soil-water matric pressure differentials: Soil-water matric pressures among the six soil types were different ($P < 0.01$) in 1988 but not in 1989. The most evident irrigation treatment effects were in Norfolk, Fuquay,

and Cecil sandy clay soils. The largest difference in soil-water matric pressure within a given soil either year was in the Cecil sandy clay, which is the most poorly drained of these soils. The interaction between soil type and soil-water matric pressure, however, was not statistically significant either year. The difference in soil-water matric pressure between the irrigation treatments increased as the season progressed both years ($P < 0.01$; repeated-measures ANOVA) (Table 1). Similarly, nematode-inoculated plots had greater ($P < 0.01$) soil-water matric pressure (wetter) than uninoculated plots, indicating that less soil water was being extracted from infested plots (data not included).

Heterodera glycines populations levels: Soil type was associated with major differences in *H. glycines* population densities at every sampling date (Tables 2,3) with the exception of the 1989 final population density (Table 3). Highest egg + J2 numbers were in soil types with high sand content (the Norfolk sandy loam and Fuquay sand), intermediate population densities occurred in the soils with high organic-material content (muck and Portsmouth loamy sand), and lowest nematode numbers occurred in the soils with clay contents $> 25\%$ (the Cecil sandy clay and Cecil sandy clay loam) (Table 2). A similar trend was evident in the spring of 1989; greater *H. glycines* eggs + J2 numbers were found in the coarse textured Norfolk sandy loam and Fuquay sand soil types. Midseason population densities of *H. glycines* in 1989 were somewhat lower than the previous year, and differences between soil types were less clear (Table 3). Still, the muck, Fuquay sand, and Portsmouth loamy sand had greater ($P < 0.10$) nematode numbers than the other soil types. Final population densities of *H. glycines* did not differ among soil types at the end of the 1989 season.

Irrigation treatments affected the population densities of *H. glycines* at every sampling date except midseason 1988 (Table 2). Nonirrigated plots had greater ($P = 0.01$) numbers of this parasite than irrigated treatments (Tables 2,3). The num-

TABLE 1. Mean soil-water matric pressure (kPa) 30-cm deep and standard deviation (SD) for irrigated (+) and nonirrigated (-) microplots determined on three dates in 1988 and four dates in 1989 for six soil types.†

	1988‡												1989§			
	July 5/8				July 19/23				Sept. 27							
	+	SD	-	SD	+	SD	-	SD	+	SD	-	SD	+	SD	-	SD
Cecil sandy clay	-25.2	18.6	-51.3	39.7	-77.2	186.3	-77.7	73.7	-26.2	14.0	-112.2	185.9				
Cecil sandy clay loam	-25.2	12.8	-44.7	18.4	-30.8	11.2	-64.4	26.4	-22.5	9.4	-64.2	26.6				
Fuquay sand	-40.9	25.0	-82.6	12.9	-38.1	20.8	-89.2	24.9	-25.4	13.9	-55.7	17.9				
Norfolk sandy loam	-42.0	30.1	-115.3	25.7	-48.4	27.2	-123.2	45.8	-25.9	17.8	-62.5	31.9				
Muck	-22.7	14.8	-31.9	14.2	-29.0	13.1	-79.5	71.3	-27.5	21.7	-60.7	52.9				
Portsmouth loamy sand	-30.3	14.3	-47.5	12.0	-37.1	15.4	-78.2	22.2	-19.4	8.5	-52.7	19.5				
	July 18/21				Aug 22/25				Sept 5/8				Oct 3/6			
Cecil sandy clay	-33.7	31.6	-40.1	30.5	-44.2	66.6	-50.4	32.1	-30.3	26.6	-59.9	46.4	-23.4	18.7	-119.9	294.3
Cecil sandy clay loam	-34.5	24.1	-21.8	9.9	-34.3	23.4	-100.9	186.6	-46.3	34.1	-42.3	11.9	-23.7	17.7	-22.9	12.8
Fuquay sand	-43.3	22.0	-52.5	17.7	-40.4	21.6	-85.4	33.3	-41.1	21.2	-111.5	100.2	-23.8	16.2	-51.6	18.9
Norfolk sandy loam	-46.1	26.9	-39.4	23.2	-60.8	36.1	-114.2	159.8	-61.5	37.1	-139.7	157.1	-23.6	15.6	-29.5	22.8
Muck	-17.6	6.3	-29.0	14.3	-40.0	51.7	-111.8	103.7	-23.0	16.5	-83.9	79.3	-23.8	26.5	-40.0	19.2
Portsmouth loamy sand	-34.3	11.5	-36.1	12.5	-47.2	32.5	-63.0	32.8	-54.7	38.9	-101.0	115.3	-23.8	13.8	-36.9	23.9

† Data for each year were analyzed by repeated-measures ANOVA. Irrigation treatments were significant ($P = 0.0001$), and the difference between irrigated and nonirrigated became greater ($P = 0.0001$) as the season progressed.

‡ Data are means of weekly measurements (two/week) determined for 3 weeks during the growing season for the three inoculum levels with three replications.

§ Data are means of weekly measurements (two/week) determined for 4 weeks during the growing season for various levels of *H. glycines* with three replications.

TABLE 2. Influence of irrigation level (+, -) and six soil types on numbers of eggs + second-stage juveniles (in 1,000s) of *Heterodera glycines*/500 cm³ at three sampling dates—midseason (Pm), harvest (Pf), and spring (Pi), (1988–89), Clayton, North Carolina.†

Soil type	14 August 1988 (Pm)			23 October 1988 (Pf)			31 May 1989 (Pi)		
	Irrigation			Irrigation			Irrigation		
	+	-	Mean‡	+	-	Mean	+	-	Mean
Cecil sandy clay	20.4	12.8	16.6 C	13.7	39.7	26.7 C	18.0	40.5	29.3 B
Cecil sandy clay loam	16.2	23.6	19.9 B	13.7	56.3	35.0 C	10.9	25.5	19.0 C
Fuquay sand	29.4	36.4	32.9 AB	148.1	173.6	160.9 A	97.4	115.9	106.6 A
Muck	37.2	23.9	30.6 AB	58.1	68.4	63.3 B	31.6	40.3	35.7 B
Norfolk sandy loam	41.9	43.4	42.7 A	127.6	191.4	159.5 A	98.7	113.2	105.9 A
Portsmouth loamy sand	33.9	29.4	31.7 AB	65.8	95.4	80.6 B	26.2	57.1	41.6 B
Mean§	29.8	28.3		71.2	104.1**		48.4	65.9**	

† The population densities of *Heterodera glycines* fit a quadratic equation with respect to Pi at midseason ($P = 0.0001$, $R^2 = 0.26$) but were inversely proportional to Pi at other sampling dates ($P < 0.01$, $R^2 = 0.30$ and 0.27 for August and October samples, respectively).

‡ Means in columns followed by the same letter are not significantly different according to Waller-Duncan k-ratio *t*-test (k -ratio = 50).

§ Means between irrigation levels followed by an ** are different ($P < 0.01$).

bers of nematodes were influenced by soil type and irrigation giving a significant first-order interaction ($P = 0.05$ for the 1988 and 1989 harvest samples; $P = 0.11$ for the spring 1989 preplant sampling). Nematode numbers were two- to four-fold greater in the nonirrigated treatments in the Cecil sandy clay and Cecil sandy clay loam compared with treatments with high soil water matric pressure in 1988 (Table 2). A similar trend was evident in 1989 with much greater *H. glycines* population densities in the Cecil sandy clay loam and the Portsmouth loamy sand in treatments

with low soil water matric pressure compared with other soil types.

Midseason population densities (Pm) of *H. glycines* fit a quadratic ($P = 0.05$) equation relating initial inoculum level to Pm in 1988, with highest Pm for the Pi of 800 eggs/500 cm³ soil (Table 2). Final population densities of *H. glycines* eggs and juveniles were inversely proportional to Pi in 1988 (Table 2) but not in 1989 (Table 3). Numbers of this nematode at midseason were positively related to Pi ($P = 0.05$) in 1989. The interactions between irrigation level or soil type with initial inoculum level

TABLE 3. Effects of six soil types and two irrigation levels (+, -) on egg + second-stage juvenile population densities (in 1,000s) of *Heterodera glycines*/500 cm³ soil at midseason (Pm) and soybean harvest (Pf) in 1989.†

Soil type	29 August 1989 (Pm)			5 November 1989 (Pf)		
	Irrigation			Irrigation		
	+	-	Mean‡	+	-	Mean
Cecil sandy clay	5.6	6.5	6.1 B	8.7	12.9	10.7 A
Cecil sandy clay loam	6.0	8.3	7.2 B	4.1	17.4	11.0 A
Fuquay sand	10.6	11.4	11.0 A	21.0	16.2	18.6 A
Muck	11.1	16.1	13.6 A	12.7	23.6	18.1 A
Norfolk sandy loam	3.7	9.0	6.3 B	15.3	16.4	15.9 A
Portsmouth loamy sand	6.9	14.0	10.4 A	8.7	25.0	16.9 A
Mean§	7.3	10.8**		11.9	18.5**	

† Preplant population density was positively correlated ($P < 0.01$, $R^2 = 0.04$) with midseason population densities, but had no consistent effect on harvest population densities.

‡ Means in columns followed by the same letter are not different—Waller-Duncan k-ratio *t* test (k -ratio = 50).

§ Means in rows followed by ** are different ($P < 0.01$).

were significant ($P = 0.05$) for both samplings in 1988 and for the spring 1989 sample. Final population density was depressed in the coarse textured soils as compared with the fine textured Cecil soils as a result of high Pi. High initial nematode inoculum level resulted in a low final density, regardless of moisture level. Second-order interactions were not significant either year.

Soybean yield: Soil type, irrigation, and nematode inoculum level affected soybean seed yield both years ($P = 0.01$). All first-order interactions were significant ($P = 0.0001$), but not second-order interactions. Soybean-yield suppression caused by *H. glycines* was greater in the Fuquay sand, Norfolk sandy loam, and muck soil types than in the clay soils or the Portsmouth loamy sand (Fig. 1A–F). The slopes of the regressions comparing high irrigation versus no irrigation treatments were steeper ($P = 0.10$) for the Norfolk sandy loam and the muck soils than for the other soils in 1988 (Fig. 1C,E). Only the irrigated plots in the Fuquay sand had a steeper slope ($P = 0.05$) than the corresponding nonirrigated plots in 1989 (Fig. 1F). Yields varied across soil types in uninoculated plots and across years (Fig. 1A–F). The y intercept for nonirrigated yields ranged from 529 to 180 for the same soils in 1988. The range in yields followed a similar pattern in 1989, although yields were about 20% lower than in 1988.

Photosynthetic rate of soybean: Photosynthesis of soybean was suppressed slightly ($P = 0.01$) in low soil-water pressure treatments compared with high soil-water matric pressure treatments both years. The soybean photosynthetic rate was related negatively to SCN Pi in the Fuquay sand under low soil-water matric pressure in 1988 (Fig. 2F). A quadratic model adequately described the relationship between inoculum density and photosynthesis in the irrigation treatment for this soil in 1988, with a marked increase in photosynthetic rate at intermediate Pi (Fig. 2F). The inoculum density of *H. glycines* had no definitive effect on the photosynthetic rate

of soybean in the Cecil sandy clay soil at either level of soil-water matric pressure in 1988 (Fig. 2A).

The effects of initial *H. glycines* population density on photosynthesis in 1989, when all soil types were evaluated, were affected by irrigation and were highly variable. Soybean photosynthetic rate in the low-moisture regime was related negatively ($P < 0.05$) to Pi for the muck and Fuquay sand soils only (Fig. 2C,F). Soybean grown under high soil-water matric pressures showed a decrease ($P < 0.10$) in photosynthetic rate in response to increasing *H. glycines* Pi in the Cecil sandy clay, Fuquay sand, and Norfolk sandy loam (Fig. 2A,E,F). In fact, most regressions were NS; therefore, the relationship was not evident in all but six treatments.

DISCUSSION

The soil-water matric pressure differences established with the experimental methods herein were adequate for the described research, although some variation in soil-water matric pressure between soil types and years was evident. Higher rates of irrigation were used on the Muck, Norfolk sandy loam, and Fuquay sand than on other soil types based on previous experience with these soils and their drainage characteristics. The greatest variation in soil-water content among these soil types occurred in the Cecil sandy clay, which is also the most poorly drained. The influence of nematode Pi on soil water content was the result of the severe stunting of soybean plants caused by nematode damage. Suppression of soybean root and shoot growth by *H. glycines* limits the plant's total water requirements. Similar effects of nematode damage on soil-water content have been reported for the potato cyst nematodes, *Globodera rostochiensis* (Wollenweber) Stone and *G. pallida* (4).

The impact of soil type on *H. glycines* population increase was similar to results obtained with *M. incognita* on soybean (25). *Heterodera glycines* population densities were much greater in the sandier soils

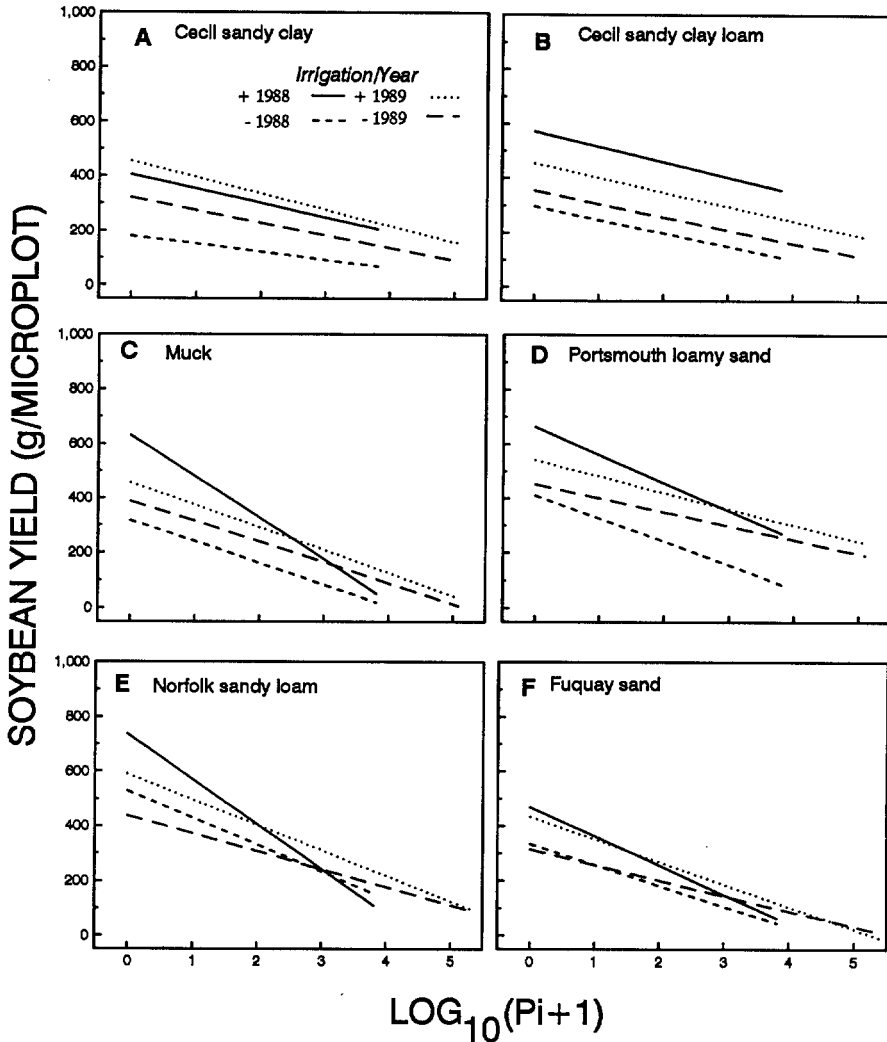


FIG. 1. Regression analyses of inoculum density of *Heterodera glycines* versus soybean yield as affected by irrigation (+, -), and six soil types (A-F) in 1988 and 1989. Abbreviations: + = irrigated, - = nonirrigated; followed by year 88 or 89. A) Cecil sandy clay regressions: +88 yield = $404 - 52.5X$, -88 yield = $180 - 29.6X$, ($R^2 = 0.64$, $P = 0.01$ for both equations) slopes do not differ ($P = 0.24$); +89 yield = $453 - 59.4X$, -89 yield = $319 - 46.1X$ ($R^2 = 0.70$, $P = 0.01$) slopes do not differ between irrigation treatments ($P = 0.21$). B) Cecil sandy clay loam regressions: +88 yield = $570 - 56.1X$, -88 yield = $296 - 48.9X$ ($R^2 = 0.52$, $P = 0.01$ for both equations) slopes do not differ ($P = 0.83$); +89 yield = $450 - 50.5X$, -89 yield = $350 - 46.0X$ ($R^2 = 0.49$, $P = 0.01$ for both equations) slopes do not differ ($P = 0.82$). C) Muck soil regressions: +88 yield = $631 - 152X$ ($R^2 = 0.67$, $P = 0.01$), -88 yield = $317 - 77.9X$ ($R^2 = 0.65$, $P = 0.01$) slopes differ ($P = 0.01$); +89 yield = $456 - 82.6X$, -89 yield = $388 - 74.8X$ ($R^2 = 0.65$, $P = 0.01$ for both equations) slopes do not differ ($P = 0.70$). D) Portsmouth loamy sand regression: +88 yield = $663 - 103X$, -88 yield = $410 - 84.8X$ ($R^2 = 0.66$, $P = 0.01$ for both equations) slopes do not differ ($P = 0.53$); +89 yield = $540 - 59.9X$, -89 yield = $451 - 51.0X$ ($R^2 = 0.42$, $P = 0.01$ for both equations) slopes do not differ ($P = 0.70$). E) Norfolk sandy loam regressions: +88 yield = $736 - 164X$ ($R^2 = 0.77$, $P < 0.01$), -88 yield = $529 - 99X$ ($R^2 = 0.64$, $P = 0.01$) slopes are different ($P = 0.06$); +89 yield = $589 - 93.0X$, -89 yield = $438 - 65.5X$ ($R^2 = 0.61$, $P = 0.01$ for both equations) slopes do not differ ($P < 0.21$). F) Fuquay sand regressions: +88 yield = $469 - 107X$, -88 yield = $334 - 76.1X$ ($R^2 = 0.59$, $P = 0.01$ for both equations) slopes do not differ ($P = 0.26$); +89 yield = $432 - 82.1X$ ($R^2 = 0.91$, $P = 0.01$), -89 yield = $314 - 56.4X$ ($R^2 = 0.77$, $P = 0.01$) slopes are different ($P = 0.01$). The regression coefficients for the combined model of soil type, moisture, and Pi effects are: 1988 - $R^2 = 0.66$, $P = 0.01$; 1989 - $R^2 = 0.66$, $P = 0.01$.

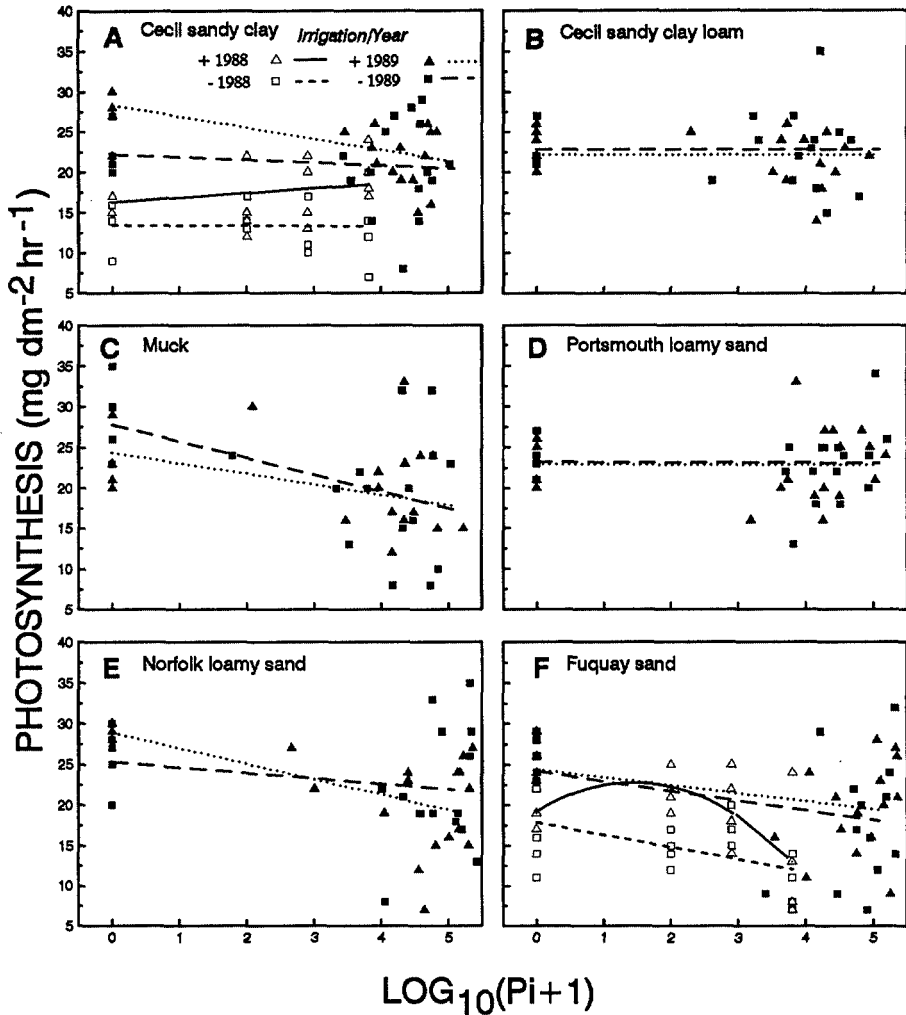


FIG. 2. Effects of irrigation (+, -), inoculum density (Pi), and six soil types (A-F) on soybean photosynthetic rate $\text{mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$ consumed. Abbreviations: + = irrigated, - = nonirrigated; followed by year 88 or 89 for 1988 and 1989. A) Cecil sandy clay regressions: +88, photosynthetic rate = $16.6 + 0.466X$ ($R^2 = 0.03$, $P = 0.50$), -88 photosynthetic rate = $13.4 - 0.109X$ ($R^2 = 0.002$, $P = 0.88$) lines do not differ ($P = 0.78$), +89 photosynthetic rate = $27.9 - 1.28X$ ($R^2 = 0.3157$, $P = 0.01$), -89 photosynthetic rate = $22.1 - 0.303X$ ($R^2 = 0.01$, $P = 0.01$) slopes do not differ ($P = 0.31$). B) Cecil sandy clay loam regressions: +89 photosynthetic rate = $23.6 - 0.478X$, -89 photosynthetic rate = $22.7 - 0.017X$ ($R^2 = 0.00004$, $P = 0.98$) slopes are not different ($P = 0.51$). C) Muck soil regression: +89 photosynthetic rate = $24.5 - 1.32X$ ($R^2 = 0.13$, $P = 0.12$), -89 photosynthetic rate = $27.88 - 2.09X$ ($R^2 = 0.24$, $P = 0.03$) interaction is not significant ($P = 0.53$). D) Portsmouth loamy sand regressions: +89 photosynthetic rate = $22.9 + 0.025X$ ($R^2 = 0.000137$, $P = 0.96$), -89 photosynthetic rate = $23.2 + 0.0112X$ ($R^2 = 0.00028$, $P = 0.98$) slopes do not differ ($P = 0.98$). E) Norfolk sandy loam regressions: +89 photosynthetic rate = $28.7 - 1.79X$ ($R^2 = 0.33$, $P = 0.01$), -89 photosynthetic rate = $25.3 - 0.617X$ ($R^2 = 0.000028$, $P = 0.98$) slopes are not different ($P = 0.21$). F) Fuquay sand regressions: +88 photosynthetic rate = $19.0 + 5.35X - 1.82X^2$ ($R^2 = 0.38$, $P = 0.04$), -88 photosynthetic rate = $17.8 - 1.51X$ ($R^2 = 0.26$, $P = 0.04$), +89 photosynthetic rate = $24.5 - 0.98X$ ($R^2 = 0.15$, $P = 0.10$), -89 photosynthetic rate = $24.3 - 1.21X$ ($R^2 = 0.10$, $P = 0.18$) slopes are not different ($P = 0.83$). Regression coefficients and $P > F$ values for combined models of soil type, irrigation and Pi for 1988 $R^2 = 0.27$ $P = 0.01$. Combined 1989 model for soil type, moisture level, and Pi: $R^2 = 0.17$, $P = 0.01$.

compared with the Cecil sandy clay loam and Cecil sandy clay. This result indicates that *H. glycines* can maintain a higher equilibrium population density in soils with higher sand content. The low nematode numbers in the Fuquay sand and Norfolk sandy loam at the end of the 1989 season were a result of severe damage to soybean in these soils because of high preplant inoculum levels. Relatively high SCN population densities were achieved in the clay soils at the end of the 1988 season, but these numbers declined to relatively low levels in 1989 because of early severe root damage. Although *H. glycines* may increase to damaging levels in fine textured soils, the low rate of increase in these soils limits the damage potential of this nematode to soybean, as does the fact that damage is less severe per unit increase in population density. The low reproductive rate in soils with high clay content results in a longer time period being necessary for the nematodes to attain damaging levels. Therefore, several crops may be required for the population density to reach damaging levels in fine-textured soils. When the crop is damaged, nematode numbers will decline to levels at which soybean yield suppression in subsequent years is not perceptible to the casual observer. Such fluctuations of SCN numbers in fine-textured soils could be associated with damage to soybean being cyclical on a yearly or longer basis and thus more difficult to predict.

The greater numbers of *H. glycines* in nonirrigated plots than irrigated plots may be due to a more favorable soil-water content/oxygen content ratio. Also, soybean responds to moisture stress by increasing root biomass (11), which would favor reproduction of SCN. Research in another region showed little or no effect of irrigation on *H. glycines* cyst population densities in rain-sheltered microplots 0–15 cm deep, although greater population densities of *H. glycines* were found in irrigated versus nonirrigated microplots 15–30 cm deep (26). The low soil-water pressures achieved in the current work were generally not as low as those reported by Young and

Heatherly (26). Other research showed that numbers of *H. glycines* cysts increased above initial levels in a Dubbs silt loam, but actually declined in a Sharkey clay when both were maintained at -30 kPa (8). Soil-water pressure and soil-type effects may be confounded by soil aeration, because saturated soils are often deficient in oxygen. Soil-oxygen levels may become the limiting factor for the aspects of the nematode's life cycle that require aerobic respiration, such as movement, hatch, and development. Slow drainage (low hydraulic conductivity), associated with fine-textured soils, often results in anaerobic conditions persisting for relatively long periods of time (21), and may impede nematode activity.

An important aspect of this research, however, is the interaction between the damage function and soil water-matric content. The negative slopes of the damage functions for irrigated treatments were equal to or steeper than the slopes for nonirrigated treatments. Thus, soybean yield suppression caused by *H. glycines* is not alleviated to a large degree with supplemental irrigation. Low soil-water matric pressure generally resulted in a greater restriction of soybean yield than did nematode inoculum level. This was especially apparent in the Cecil sandy clay loam, Cecil sandy clay, and Portsmouth loamy sand in 1988. The effects of low soil-moisture level and soybean cyst nematode are, therefore, additive. If soil moisture is the limiting factor for soybean yield, nematode management then becomes a secondary concern. Soil-water content levels that support optimal growth and yield of healthy soybean also enhance yields of SCN-infected plants, but do not generally circumvent the extensive damage caused by the pathogen. Researchers in Tennessee (7) found that irrigation during the reproductive phase did not alter the seed-yield suppression caused by soybean cyst nematode on susceptible cultivars. Our current research supports these findings.

The suppression of soybean photosynthetic rate as a result of moisture stress concurs with previous work (10). Soybean

photosynthesis was generally lower in nonirrigated than in irrigated treatments. Of the two soils tested in 1988, the photosynthetic rate of soybean was significantly affected by SCN level only in the Fuquay sand. This result is reasonable, because damage caused by *H. glycines* was most severe in this soil type, as compared with the clay soil.

Inconsistencies in photosynthetic response are difficult to interpret. In general, the response of net photosynthetic rate to nematode inoculum level was relatively small; therefore any limiting factor, such as low soil-water matric potential could restrict the rate of photosynthesis such that a response to the nematode could not be measured. Inoculum densities were clustered at relatively high nematode levels in 1989, and this factor contributed to the poor fit of linear equations. If data points for uninoculated plots were deleted, a significant relationship between Pi and photosynthetic rate would not exist, as indicated by the large scatter of individual data points. Third, there was a trend toward increased damage to soybean grown under the wet regime as opposed to the nonirrigated treatments that would explain this response. A fourth factor is the interaction of moisture stress and high nematode Pi. Heavily infected plants are stunted, thus require less water, and may actually be under less moisture stress than healthy ones.

The maximum decrease in net (per leaf-area basis) photosynthetic rate measured in these experiments was $7.4\%/\log_{10}(\text{Pi} + 1)$ for the muck at high moisture in 1989. The corresponding yield loss in this soil was $18.1\%/\log_{10}(\text{Pi} + 1)$. Clearly, only a portion of soybean yield suppression can be attributed to restricted net photosynthesis caused by *H. glycines* infection. An even greater primary effect of *H. glycines* on photosynthesis was through the restriction of total photosynthetic area. The leaf area of individual leaves was greatly limited in response to nematode infection (data not included), as was total plant biomass.

A portion of the restriction in soybean

photosynthetic rate may have been in response to nitrogen deficiency induced by *H. glycines*. The race 1 population of *H. glycines* used in this research inhibits soybean nodulation at moderate to high inoculum levels, which results in nitrogen-deficient plants (1,14). Soybean photosynthetic rate is coupled to nitrogen levels in the plant. Nitrogen-stressed soybean plants have altered leaf carbohydrate metabolism and reduced carbon exchange ratios (17). Soybean plants may be able to compensate partially for nematode damage, provided other factors such as nodule function or soil-water matric pressure potential are not limiting.

We have focused on continuous moisture stress versus periodic moisture stress in the current work. The effects of periodic stress on soybean yield and photosynthesis may be different from the effects of continuous stress observed under our conditions. Water-stressed soybean plants achieved photosynthetic rates equivalent to unstressed plants when water stress was relieved (10). In other research with *Meloidogyne incognita* on 'Lee 68' soybean, moisture stress imposed at different growth stages tended to have a cumulative effect on soybean yield (Koening & Barker, unpubl.).

The effects of soil-water matric pressure and texture on the interaction of *H. glycines* with soybean has important economic and theoretical implications. Soybean-yield suppression caused by *H. glycines* cannot be generally circumvented by irrigation. Yield restriction in response to this pathogen under high moisture conditions was equal to or greater than the yield reduction under dry conditions. Alleviating moisture stress, however, is most important to overall soybean growth and yield. Dry conditions favored reproduction of *H. glycines* in our research, although there was a moisture by soil type interaction.

More intensive research is needed to evaluate the influence of soil-water matric potential on specific stages in the life and infection cycle of *H. glycines* on soybean. Information about soil-water matric pres-

sure effects on the hatch, movement, and host penetration by second-stage juveniles of *H. glycines* would be useful in modeling this host-pathogen system.

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