EFFECTS OF TEMPERATURE ON COMPETITION BETWEEN *HETERODERA GLYCINES* AND *PRATYLENCHUS SCRIBNERI* ON SOYBEAN†

Dennis A. Lawn[1] and Gregory R. Noel[2]

Centro Internacional de Mejoramiento de Maíz y Trigo (CIMMYT), AP 6-641, Delegación Cuauhtémoc, 06600 México, D.F.,[1] and USDA-Agricultural Research Service, Department of Plant Pathology, University of Illinois at Urbana-Champaign, Urbana, IL 61801-4709, U.S.A.[2]

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ABSTRACT

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Population development of *Heterodera glycines* and *Pratylenchus scribneri*, alone and in combination, at various initial levels on soybean (*Glycine max*) in 70 days at 20, 24, 28, and 32 C was determined in two experiments. Following preliminary 5-day exposure of infested soil at 22 C, population increase of *H. glycines* was not affected by the presence of *P. scribneri* at any subsequent temperature. With an initial 5-day exposure at 28 C, increase of *H. glycines* was suppressed at 20, 24, and 32 C, when 1 000 second-stage juveniles were coinoculated with 5 000 *P. scribneri*. Populations of *P. scribneri* were not affected significantly by concomitant root infections with *H. glycines*, regardless of temperature. Final male:female ratios of *H. glycines* increased with increasing temperature up to 28 C in both experiments. In the first experiment, the male:female ratio was highest for *H. glycines* in combination with an initial population of either 2 000 or 3 000 *P. scribneri*, but the ratio in the second experiment was smallest when *H. glycines* was in combination with 5 000 *P. scribneri*. Decreased shoot weights in the first experiment were associated with high inoculum levels and large population increases of *H. glycines*. No growth reductions occurred with the lower inoculation levels used in the second experiment. *Pratylenchus scribneri* alone did not affect shoot or root weights and did not interact synergistically with *H. glycines*.

Key words: Glycine max, Heterodera glycines, interrelationships, *Pratylenchus scribneri,* sex ratios, soybean, temperature.

RESUMEN

Lawn, D. A., y G. R. Noel. 1990. Efectos de la temperatura sobre la competencia entre *Heterodera glycines* y *Pratylenchus scribneri* en soya. Nematrópica 20:57–69.

En dos ensayos realizados en soya (*Glycine max*), se determinó el desarrollo poblacional de *Heterodera glycines* y *Pratylenchus scribneri*, sólo y en combinación, con varios niveles poblacionales iniciales a los 70 días y a 20, 24, 28 y 32 C. Después de una infestación preliminar del suelo por 5 días a 22 C, el incremento poblacional de *H. glycines* no se vió afectado por la presencia de *P. scribneri* a ninguna temperatura. Con una infestación preliminar del suelo a 28 C, el incremento de *H. glycines* se vió limitado a los 20, 24 y 32 C, cuando 1 000 juveniles del segundo estadío fueron inoculados en forma conjunta con

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5 000 *P. scribneri*. Las densidades poblacionales de *P. scribneri* no se vieron afectadas significativamente por infecciones radiculares concomitantes con *H. glycines*, independientemente de la temperatura. La relación macho:hembra de *H. glycines* aumentó con el incremento de la temperatura hasta los 28 C en ambos experimentos. En el primer experimento, la relación macho:hembra fue más alto para *H. glycines* en combinación con una población inicial de 2 000 o 3 000 de *P. scribneri*. Sin embargo, esta relación en el segundo experimento fue la más baja cuando *H. glycines* estuvo en combinación con 5 000 *P. scribneri*. El bajo peso de la porción foliar en el primer experimento estuvo asociado con altos niveles de inoculación y un alto incremento poblacional de *H. glycines*. En el segundo experimento no se registraron reducciones en crecimiento con niveles bajos de inoculación. En ausencia de *H. glycines*, *P. scribneri* no afectó los pesos radiculares ni la porción aérea y tampoco interactuó en forma sinergística con *H. glycines*.

Palabras claves: Glycine max, Heterodera glycines, interrelaciones, *Pratylenchus scribneri,* proporción sexual, soya, temperatura.

INTRODUCTION

Environmental factors, such as temperature, affect both nematode biology and host plant physiology, and limit interpretations of nematode-nematode interactions under field conditions (19). Soil temperature is influenced by ambient temperatures, insolation, and edaphic factors. Many crop management strategies emphasize reduced tillage practices. Tillage practices which leave the greatest surface residue maintain the coolest soil temperatures (12) and can influence nematode threshold levels and damage to crops.

Host crops and associated nematodes have diverse temperature requirements, and optimum temperatures for some nematode species may be host plant-dependent (7,9,18). Soybean (*Glycine max* (L.) Merr.) is adapted to a wide range of climatic conditions. Hypocotyl elongation occurs in the range of 10–40 C and is correlated with maturity group (8). Rate of both taproot and lateral root extension increase with increasing temperature and are cultivar-dependent (27,28).

Heterodera glycines Ichinohe can complete its life cycle on soybean at 14–35 C (24). Egg production began 18 days after infection at 31 C (14) and 37 days at 17 C (24). Second-stage juvenile (J2) emergence from cysts occurred from 16–36 C with an optimum of 24 C (26). With fluctuating temperatures, extent of emergence was directly proportional to the time of inoculation at 24 C. Higher numbers of *H. glycines* J2 penetrated roots at 28 C than at 22 C (13), and the majority of J2 penetrated within 24 hours (1).

Pratylenchus scribneri Steiner is a thermophylic nematode in which the temperature optimum for reproduction may differ among populations. A Kansas population had maximum reproduction at 35 C on 'Clark 63' soybean but did not reproduce below 27.5 C (6), whereas an Illinois population reproduced at 20 C on the same host and had a temperature optimum of 34 C (2). The optimum temperature for penetration of soybean roots by *P. scribneri* is not known, although penetration of snap and lima beans occurred within 24 hours at 30 C ± 2 C (29).

Interspecific competition among plant-parasitic nematodes occurs frequently in cropping systems. Mutual antagonism between *H. tabacum* Lownsbery & Lownsbery and *P. penetrans* Filipjev & Schuurmans Stekhoven occurred in tobacco fields, although *H. tabacum* eventually predominated (22). Large populations of *Meloidogyne incognita* (Kofoid & White) Chitwood reduced reproduction of *H. glycines* on soybean in microplots (25). Results of greenhouse studies with concomitant populations of *Pratylenchus* spp. and *Meloidogyne* spp. on several hosts suggested that necrosis resulting from infections of the former adversely affected penetration by and reproduction of the latter (3,11,16). However, no competition was found between *H. trifolii* Goffart and *P. penetrans* on red clover (10). Competition between *H. glycines* and *P. scribneri* on soybean under field conditions was indicated when initial levels of *H. glycines* were high (19), but interrelationships of these two species under controlled conditions have not been investigated. The objective of this research was to determine the effects of temperature on population dynamics of *H. glycines* and *P. scribneri* and their effects on soybean growth in controlled soil temperatures.

MATERIALS AND METHODS

Two experiments were conducted in constant temperature tanks in a greenhouse, the first from 1 December 1984 to 8 February 1985 and the second from 1 November 1986 to 9 January 1987. Seeds of 'Williams 82' soybean, susceptible to *P. scribneri* and *H. glycines*, were surface-disinfested in 0.5% sodium hypochlorite and germinated on moist paper towels. Two 3-day-old seedlings were planted into 3-cm-deep holes in 14-cm-diam plastic pots containing 1 500 cm^3 of autoclaved sandy-loam soil that had been infested with *Bradyrhizobium japonicum* (Buchanan) Jordan and different initial population levels (Pi) of the two nematode species, alone or in combination. In experiment 1, Pi were: 4 000 *P. scribneri*, 4 000 *H. glycines*, 1 000 *H. glycines* + 3 000 *P. scribneri*, 3 000 *H. glycines* + 1 000 *P. scribneri*, 2 000 *H. glycines* + 2 000 *P. scribneri*, or no nematodes. Treatments in experiment 2 were: 1 000 *P. scribneri*, 5 000 *P. scribneri*, 1 000 *H. glycines*, 1 000 *H. glycines* + 1 000 *P. scribneri*, 1 000 *H. glycines* + 5 000 *P. scribneri*, or no nematodes.

Inoculum of *P. scribneri* was obtained from carrot disc cultures (20) and contained all life stages. In experiment 1, 38% were adults, 24% were J2, and 38% were J3 and J4. In experiment 2, the percentages were 45%, 30%, and 25%, respectively. *Heterodera glycines* J2 were obtained by mist chamber incubation of cysts extracted from soil. All nematodes were surface disinfested in a solution containing 100 ppm

$HgCl_2$ and 1 000 ppm streptomycin sulfate for 3 minutes followed by two rinses with sterile distilled water. After infestation and planting, pots were maintained for 5 days at 22 C in experiment 1 and at 28 C in experiment 2 to obtain uniform root penetration by all nematodes. Pots then were placed in tightly fitted, waterproof containers, and four replications of each treatment were randomized in temperature tanks at 20, 24, 28, or 32 C ± 1 C. All treatments received 16 hours of light for the first 4 weeks and 13 hours thereafter. Plants were fertilized every 3 weeks with 250 ml of a solution containing 0.48 g potassium nitrate and 0.15 g triple super phosphate per L of water.

Seventy days after inoculation, shoots from each pot were cut at the cotyledonary node and dried for 3 days at 75 C. Root systems were separated from soil in water, rinsed thoroughly and incubated in a mist chamber for 7 days at 20 C. Nematodes in the soil were suspended in 4 L of water and extracted by Cobb's gravity sieving technique (4), using 850-, 180-, and 45-μm-pore sieves. *Heterodera glycines* cysts and white females were collected on a 180-μm-pore sieve. Vermiform nematodes collected on the 45-μm-pore sieve were separated from residue by centrifugal flotation (15). *Pratylenchus scribneri* populations recovered from roots were combined with soil populations to determine total *P. scribneri* population development. *Heterodera glycines* population development was measured by combining gravid brown cysts with yellow and white females. Both data then were transformed to Log_{10} (X + 1) prior to analysis of variance, and means were compared using single degree of freedom comparisons. Male:female ratios (M:F) of *H. glycines* were obtained by combining males recovered from soil with those that emerged from roots.

Data from experiment 1 were analyzed as a 6 × 4 factorial with factor A as inoculum levels and factor B as temperature. Data from experiment 2 were analyzed as four separate 3 × 2 factorials with factor A as the level of *P. scribneri* (0, 1 000, or 5 000/pot) and factor B as the level of *H. glycines* (0 or 1 000/pot), at each temperature. Mean shoot and root weights were separated using single degree of freedom comparisons. Unless stated otherwise, differences are significant at $P < 0.05$.

RESULTS

In experiment 1, single degree of freedom comparisons of *H. glycines* population development from a Pi of 4 000 at the four temperatures showed greater ($P < 0.05$) final population densities (Pf) at 24 and 28 C than at 20 or 32 C (Fig. 1A–D). This reproductive pattern was not affected by simultaneous inoculation of *P. scribneri* at any level except the Pi of 2 000 at 32 C when compared with 28 C (Fig. 1C, D). The Pf of *H. glycines* gravid cysts and white females did not differ at 24 and 28

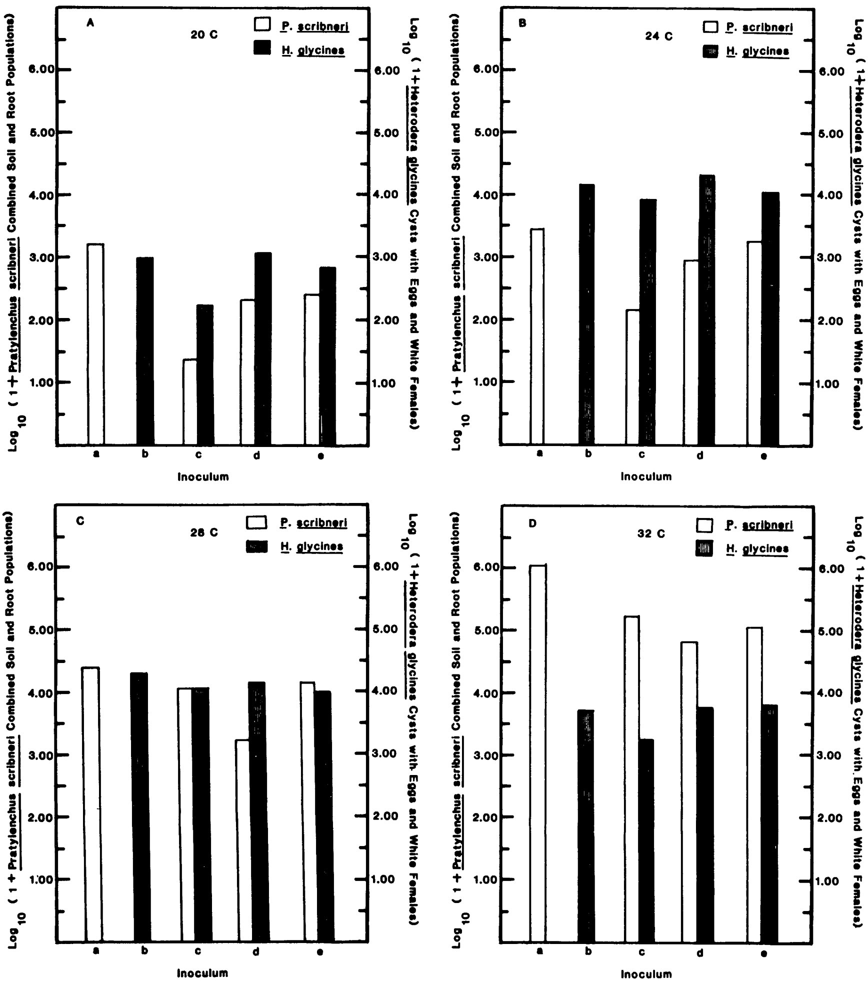

Fig. 1 (A–D). Total *Heterodera glycines* cysts and white females and combined soil and root populations of *Pratylenchus scribneri* recovered from soybeans grown at A) 20 C, B) 24 C, C) 28 C, and D) 32 C, 70 days after inoculation with a) 4 000 *P. scribneri*, b) 4 000 *H. glycines*, c) 1 000 *H. glycines* + 3 000 *P. scribneri*, d) 3 000 *H. glycines* + 1 000 *P. scribneri*, or e) 2 000 *H. glycines* + 2 000 *P. scribneri*. Data were transformed to $Log_{10}(X + 1)$.

C when inoculated with 1 000, 2 000, 3 000, or 4 000 *H. glycines* J2. At 20 and 32 C, however, Pf's were lower at the Pi of 1 000 when compared with a Pi of 2 000, 3 000, or 4 000 (Fig. 1A, D). The Pf of *P. scribneri* increased with increasing temperature when inoculated alone or simultaneously with 1 000, 2 000, or 3 000 *H. glycines* J2. Among the same Pi's, comparisons of *P. scribneri* Pf were greater with increasingly higher temperatures.

With a lower Pi of *H. glycines* in experiment 2 and a higher temperature during the initial 5-day incubation period, population development of *P. scribneri* was greater than that of *H. glycines* at all temperatures. Single degree of freedom comparisons revealed lower population development of *H. glycines* when inoculated simultaneously with 5 000 *P. scribneri* at 20, 24, and 32 C than when inoculated alone or in combination with 1 000 *P. scribneri* (Fig. 2A, B, D). No differences in population increases of *H. glycines* were observed when plants also were inoculated with either 1 000 or 5 000 *P. scribneri* at 28 C (Fig. 2C). At 32 C, a significant linear interaction between reproduction of *H. glycines* and increasing Pi of *P. scribneri* was described by the equation $Y = 2.27 - 0.19X$ where X = level of *P. scribneri* and Y = numbers of *H. glycines*. Both linear and quadratic responses of *P. scribneri* reproduction were detected with increasing Pi at all temperatures. Suppression of reproduction by *H. glycines* was observed at 24 C ($P = 0.07$) when plants were inoculated with 1 000 *H. glycines* and 5 000 *P. scribneri*.

In experiment 1, more males of *H. glycines* were recovered at 24 and 28 C when soybean plants were inoculated with 2 000 *H. glycines* + 2 000 *P. scribneri* than with 4 000 *H. glycines* (Table 1). A significantly larger ratio of males resulted when 1 000 *H. glycines* were inoculated with 3 000 *P. scribneri* than with 4 000 *H. glycines* at 28 and 32 C. In experiment 2, larger M:F ratios occured at 24 and 28 C than at 20 and 32 C at all inoculum levels, except 1 000 *H. glycines* + 5 000 *P. scribneri*. A lower M:F ratio was observed from simultaneous inoculation of 1 000 *H. glycines* with 5 000 *P. scribneri* at 24 C than when inoculated alone or in combination with 1 000 *P. scribneri*.

In experiment 1, inoculation of 4 000 *H. glycines* alone or 3 000 *H. glycines* with 1 000 *P. scribneri* at 24 C resulted in a decrease in shoot weight when compared with the control (Table 2). *Heterodera glycines* at all levels, alone or in combination with *P. scribneri* at 28 C, decreased shoot weight. At 32 C, inoculation with all levels of *H. glycines* also resulted in a decrease in shoot weight, compared with the control; however, greater reductions in shoot weight occurred when 3 000 or 2 000 *H. glycines* were inoculated simultaneously with 1 000 or 2 000 *P. scribneri*, respectively. Root weights were not affected by nematodes or temperature, except at 24 C, where root weights of control plants were greater than those of nematode-infected plants.

Shoot weights in experiment 2 were not affected by either nematode, alone or in combination, at any temperature, when compared with the control (Table 3). Only at 24 C was there an effect of nematodes on dry root weights. Root weights of control plants were greater than plants inoculated with 1 000 *H. glycines* or 1 000 *H. glycines* + 1 000 *P. scribneri*.

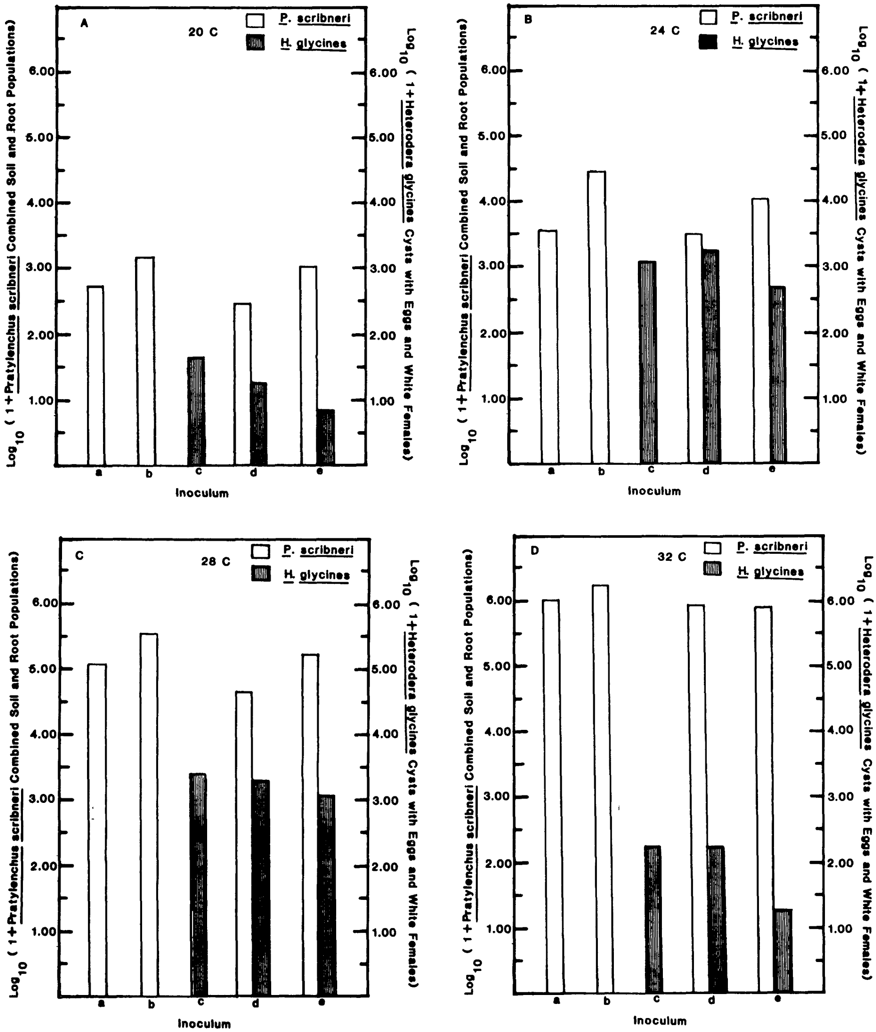

Fig. 2 (A–D). Total *Heterodera glycines* cysts and white females and combined soil and root populations of *Pratylenchus scribneri* recovered from soybeans grown at A) 20 C, B) 24 C, C) 28 C, and D) 32 C, 70 days after inoculation with a) 1 000 *P. scribneri*, b) 5 000 *P. scribneri*, c) 1 000 *H. glycines*, d) 1 000 *H. glycines* + 1 000 *P. scribneri*, or e) 1 000 *H. glycines* + 5 000 *P. scribneri*. Data were transformed to $Log_{10}(X + 1)$.

DISCUSSION

Competitive dominance of *H. glycines* over *P. scribneri* was indicated in the first experiment, where a cooler 5-day preliminary incubation

Table 1. Male:female ratios in final populations of *Heterodera glycines* (HG) recovered from soybean grown at four soil temperatures, 70 days after inoculation with different levels of *Pratylenchus scribneri* (PS).

Temperature (C)	Experiment 1 Inoculum level				Experiment 2 Inoculum level		
	4 000 HG + 0 PS	1 000 HG + 3 000 PS	3 000 HG + 1 000 PS	2 000 HG + 2 000 PS	1 000 HG + 0 PS	1 000 HG + 1 000 PS	1 000 HG + 5 000 PS
20	.04	.18	.09	.10	.64	0	.12
24	.36	.84	.49	1.61[y]	1.33	.71	.12[z]
28	.55	1.92[y]	.48	1.80[y]	1.68	2.54	.79
32	.18	1.21[y]	.23	.68	.58	0	0

[y]Significantly ($P < 0.05$) larger than 4 000 *H. glycines* + 0 *P. scribneri* at the same temperature.
[z]Significantly ($P < 0.05$) smaller than 1 000 *H. glycines* + 0 *P. scribneri* at the same temperature.

Table 2. Mean dry shoot and root weights of soybean (two plants/experimental unit) grown for 70 days at four soil temperatures in 1 500 cm^3 of soil and inoculated with different levels of *Heterodera glycines* (HG) and *Pratylenchus scribneri* (PS). Experiment 1.

Temperature (C)	Inoculum levels											
	0 HG + 4 000 PS	4 000 HG + 0 PS	1 000 HG + 3 000 PS	3 000 HG + 1 000 PS	2 000 HG + 2 000 PS	0 HG + 0 PS	0 HG + 4 000 PS	4 000 HG + 0 PS	1 000 HG + 3 000 PS	3 000 HG + 1 000 PS	2 000 HG + 2 000 PS	0 HG + 0 PS
	Shoot weight (g)						Root weight (g)					
20	11.25	10.12	11.04	9.26	10.12	15.53	7.38	8.44	6.75	6.93	9.69	8.52
24	15.16	7.76[z]	11.78	7.30[z]	10.72	12.72	8.77[z]	7.47[z]	6.61[z]	4.29[z]	7.65[z]	11.49
28	15.42	6.05[z]	9.13[z]	8.34[z]	8.17[z]	13.75	8.60	5.18	7.45	6.08	7.52	7.59
32	13.52	10.86[z]	12.78[z]	9.19[z]	9.75[z]	14.59	6.07	7.47	8.32	7.34	7.12	9.11

Data are means of four replications.

[z]Differs ($P < 0.05$) from treatment with no nematodes using single degree of freedom comparisons.

Table 3. Mean dry shoot and root weights of soybean (two plants/experimental unit) grown for 70 days at four soil temperatures in 1 500 cm^3 of soil and inoculated with different levels of *Heterodera glycines* (HG) and *Pratylenchus scribneri* (PS). Experiment 2.

Temperature (C)	Inoculum levels											
	0 HG + 1 000 PS	0 HG + 5 000 PS	1 000 HG + 0 PS	1 000 HG + 1 000 PS	1 000 HG + 5 000 PS	0 HG + 0 PS	0 HG + 1 000 PS	0 HG + 5 000 PS	1 000 HG + 0 PS	1 000 HG + 1 000 PS	1 000 HG + 5 000 PS	0 HG + 0 PS
	Shoot weight (g)						Root weight (g)					
20	13.55	14.05	13.27	13.25	14.43	13.38	3.75	3.86	3.69	3.48	3.56	3.82
24	15.37	15.58	15.48	13.11	16.30	16.31	3.65	4.03	3.81[z]	3.48[z]	4.40	4.74
28	17.80	17.38	16.75	15.44	16.56	17.15	3.15	3.00	3.02	4.05	4.06	4.06
32	16.53	15.97	16.11	16.68	15.62	16.76	3.39	3.51	3.33	4.08	3.35	3.26

Data are means of four replications.
[z]Differs ($P < 0.05$) from treatment with no nematodes using single degree of freedom comparisons.

temperature apparently was unfavorable for infection by *P. scribneri*. Because of the dominance of *H. glycines* over *P. scribneri* in experiment 1, the preliminary incubation temperature was increased and the Pi of *H. glycines* was decreased in the second experiment. These conditions apparently were more favorable for infection by *P. scribneri* and less favorable for *H. glycines* reproduction. The significant suppression of *H. glycines* population increase at 32 C with concomitant infections of 5 000 *P. scribneri* suggests that soil temperature at the time of primary infection is important in determining the dominant species in interspecific competition between *H. glycines* and *P. scribneri* during the growing season.

Increases in M:F ratios associated with increasing temperature occurred up to 28 C but not at 32 C. The lower ratios at 32 C, also reported previously (21), could be the result of sampling error because of the shorter generation time at the higher temperature and resulting death and degeneration of males. Sex ratios frequently have been a basis for testing the hypothesis that nema.ode behavior patterns are density-dependent (31). High infection densities of certain cyst nematodes increased M:F ratios, resulting from competition for a limited food supply caused by either inadequate formation of syncytia (30) or differential death rates (17). In experiment 1, the highest M:F ratios of *H. glycines* occurred when this species was in combination with 2 000 and 3 000 *P. scribneri* at all temperatures, suggesting that the presence of *P. scribneri* increased the ratios. In contrast, M:F ratios decreased in the presence of 5 000 *P. scribneri* in experiment 2. That decrease may have resulted from the decreased reproduction of *H. glycines* with the lower Pi.

There was little evidence of nematode damage to plants except at relatively high Pi of *H. glycines*. However, detecting growth reduction from nematode parasitism is hampered by the ability of soybean to compensate for damage by stimulating additional root growth (5,23). Inoculating all nematodes in direct proximity to the tap root can result in extensive lateral root development above the site of initial infection. Thus, an extensive root system can become established before uniform nematode distribution occurs. Pathogenicity tests require higher inoculum levels, random distribution of nematodes, and periodic moisture stresses throughout pots to more realistically approach field conditions.

Influence of infection by *P. scribneri* on fecundity of *H. glycines* in the long-term study described herein was not possible because of continual hatch of eggs and incomplete development of second and/or third generations of nematodes. Further studies using gnotobiotic techniques are required to determine whether cyst size and fecundity of *H. glycines* are affected by temperature and the presence of *P. scribneri*.

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